EVOLUTIONARY DYNAMICS

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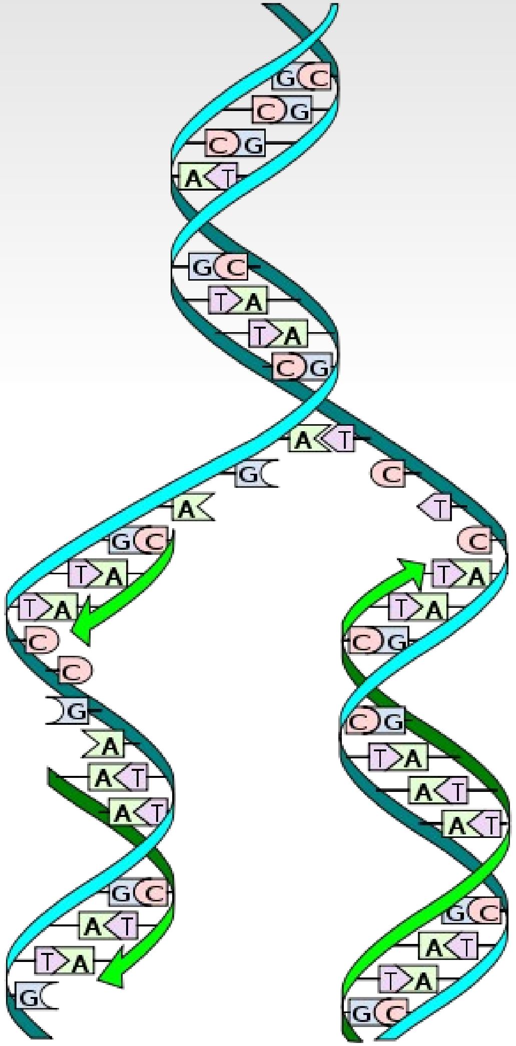
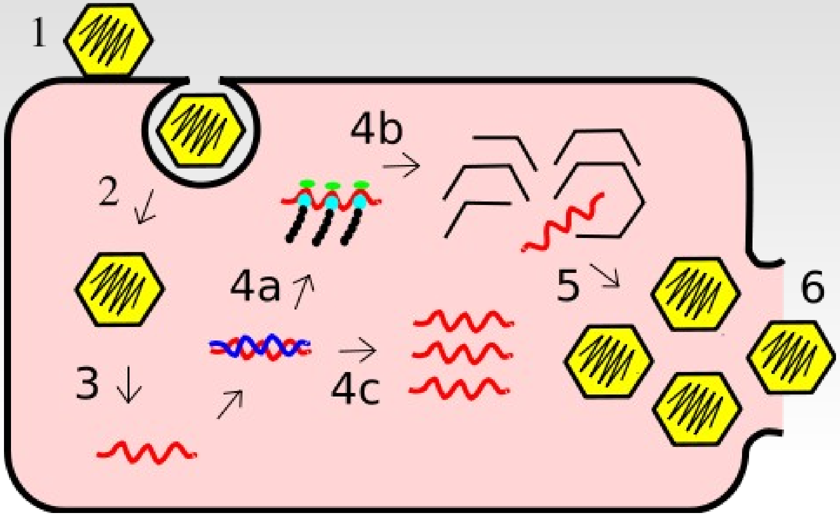
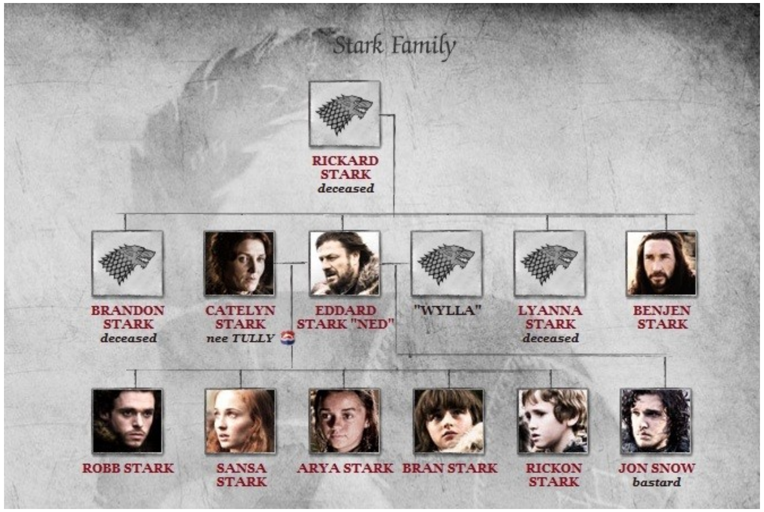
Replication

Replication

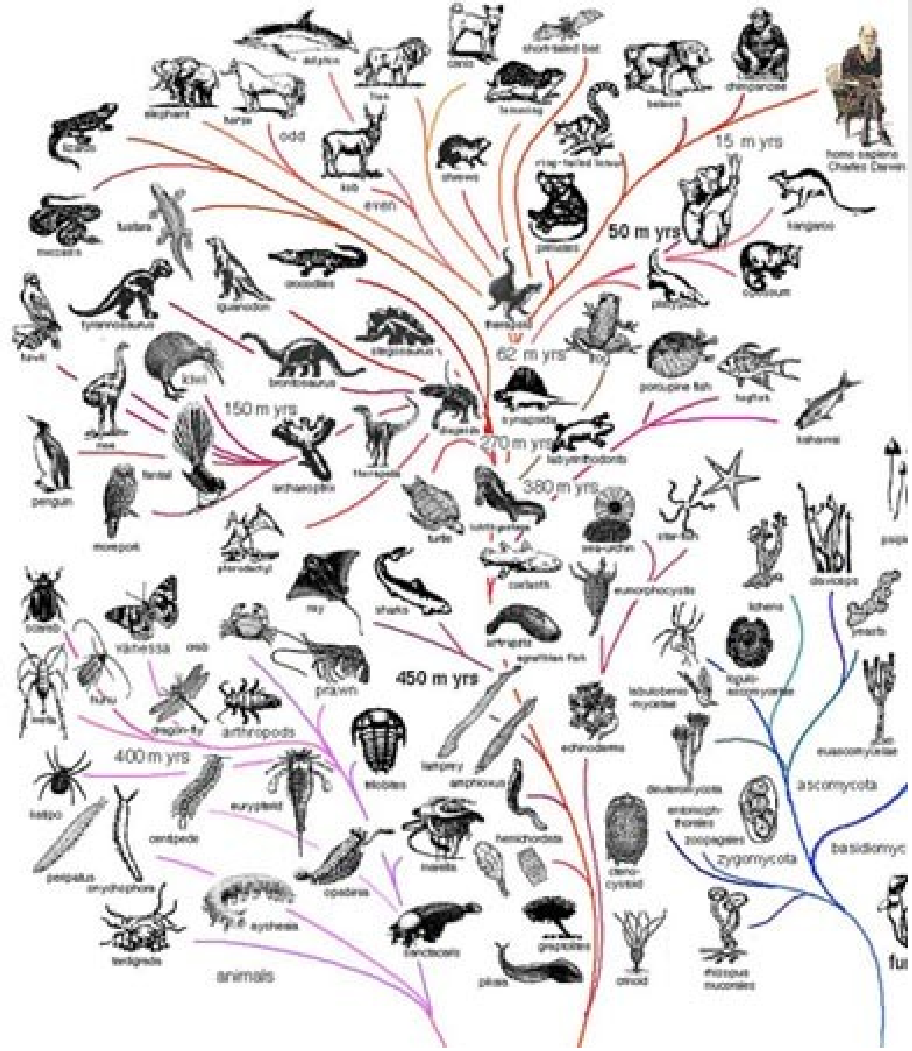




Replication



Replication

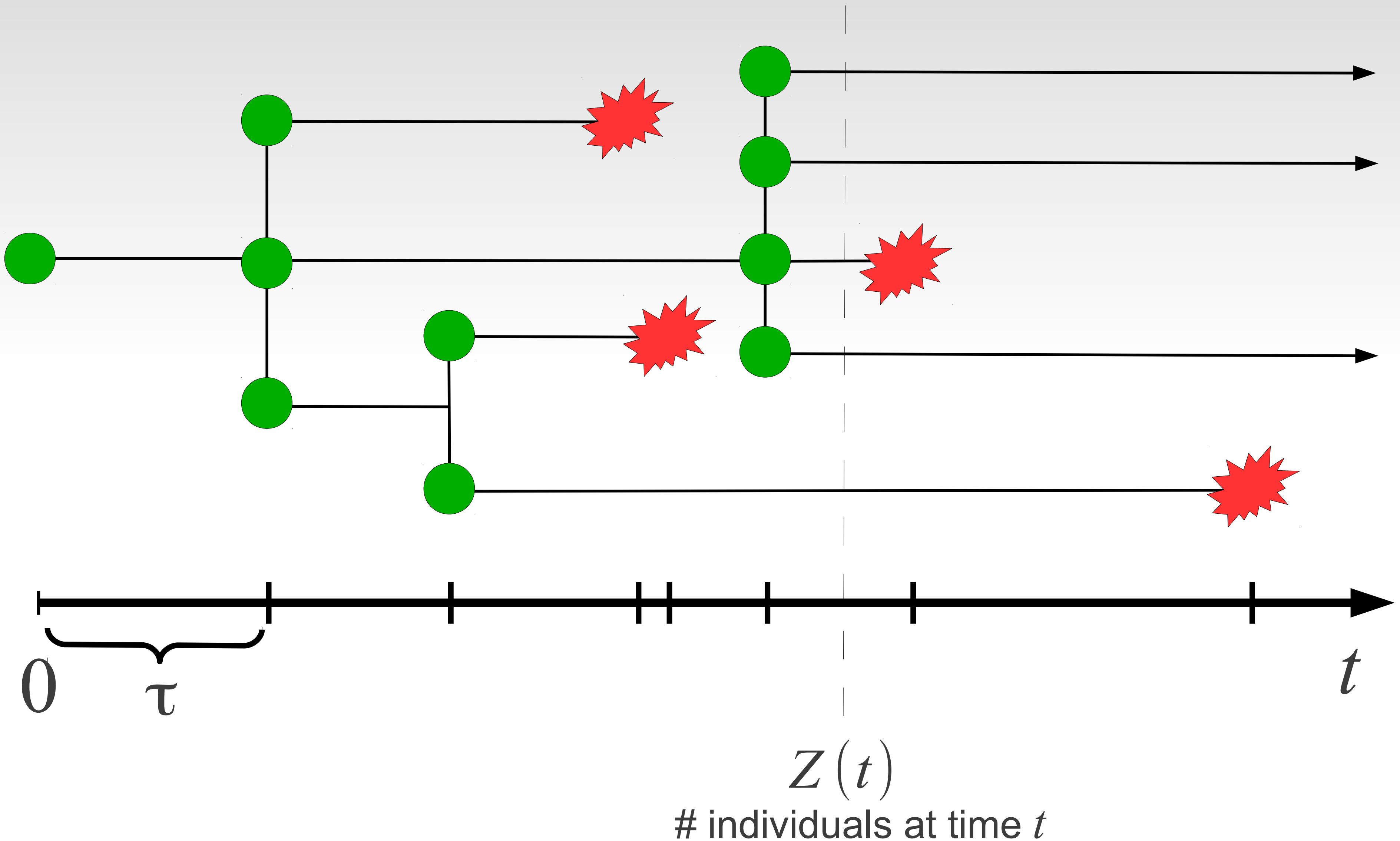


Replication

replication rate sets the speed of evolution

Branching processes

Branching processes



Branching processes

Event time distribution:

$$G(t) = \Pr\{\tau \leqslant t\}$$

Generating function of offspring distribution:

$$f(s) = \sum_{k=0}^{\infty} p_k s^k \qquad p_k = \Pr\{X = k \mid \text{event}\}$$

Generating function of the process:

$$F(s,t) \equiv \sum_{k=0}^{\infty} P_k(t) s^k \qquad P_k(t) = \Pr\{Z(t) = k \mid Z(0) = 1\}$$

Branching processes

Constitutive equation:

$$Z(t) = \begin{cases} 1 & \text{if } t < \tau \\ \sum_{\mu=1}^{X} Z^{(\mu)}(t-\tau) & \text{if } t \geqslant \tau \end{cases}$$

$$F(s,t|t<\tau) = s \qquad F(s,t|t \geqslant \tau, X=j) = [F(s,t-\tau)]^j$$

$$F(s,t|t \geqslant \tau) = f(F(s,t-\tau))$$

$$F(s,t) = s[1-G(t)] + \int_0^t f(F(s,t-\tau))\,dG(\tau)$$

Extinction probability

$$q = \lim_{t \to \infty} F(0, t)$$

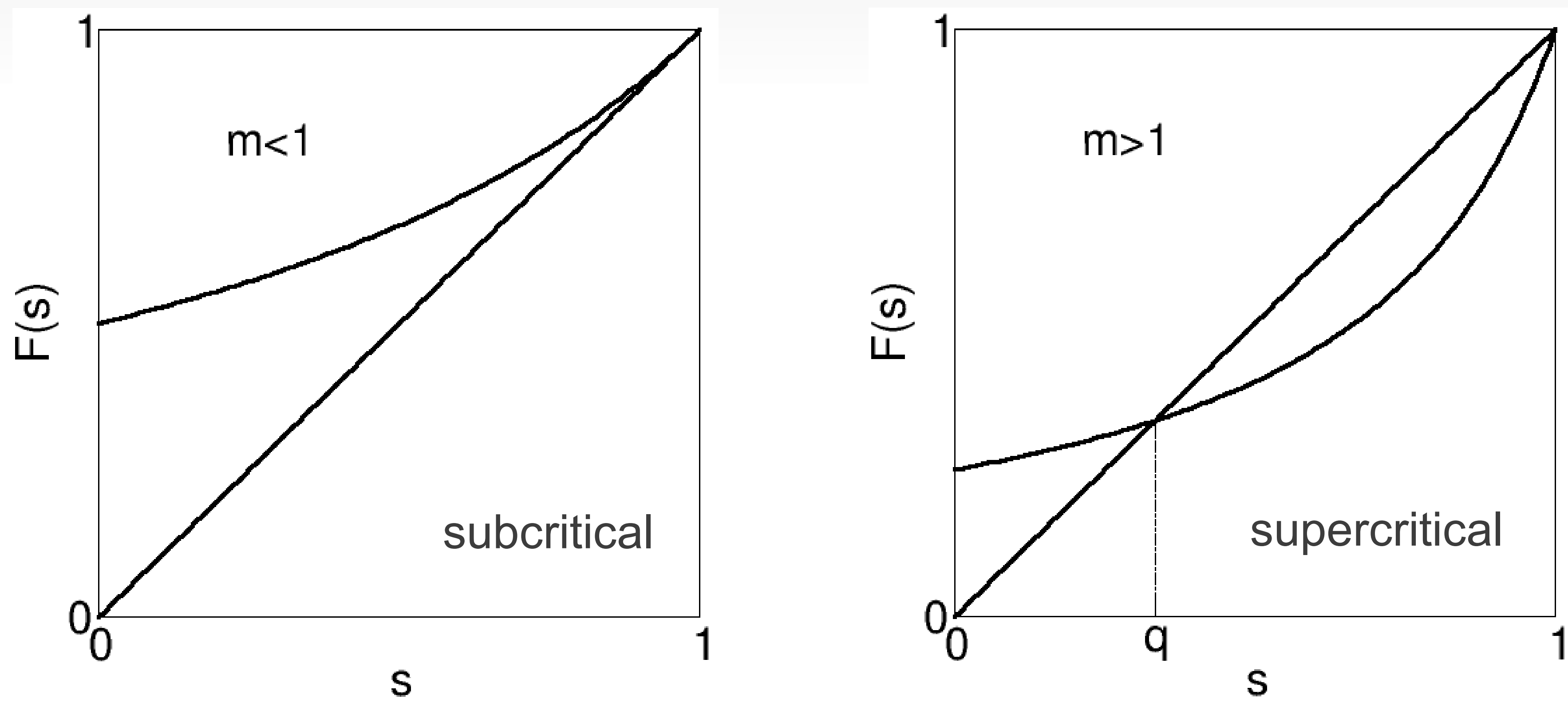
$$F(0, t) = \int_0^t f\left(F(0, t - \tau)\right) dG(\tau)$$

$$q = f(q)$$

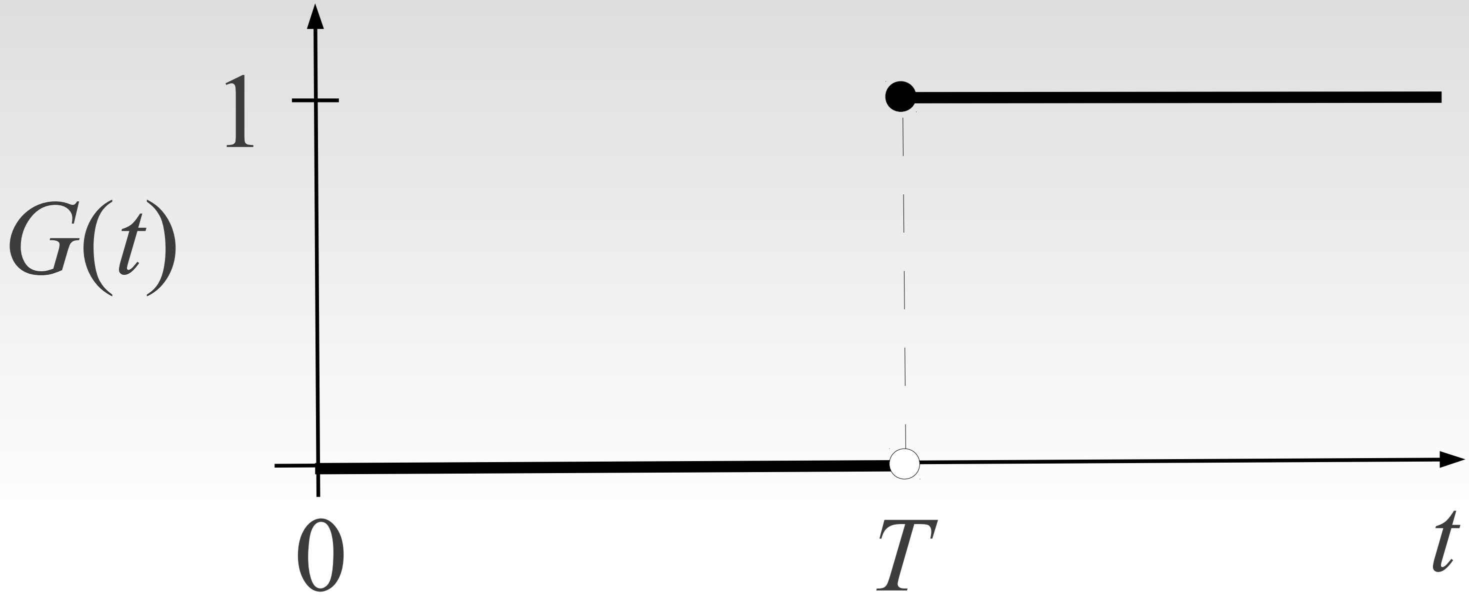
Extinction probability

$$p_0 > 0 \qquad p_0 + p_1 < 1$$

$$f(s) > 0 \qquad f'(s) > 0 \qquad f''(s) > 0 \qquad s \in [0,1]$$



Galton-Watson process



$$F_n(s) \equiv F(s, nT)$$

$$F_0(s) = s \qquad F_{n+1}(s) = f(F_n(s))$$

Galton-Watson process

$$f(1)=1 \qquad f'(1)=m \qquad f''(1)=\sigma^2+m^2-m$$

$$F'_n(1)=f'(1)F'_{n-1}(1)=mF'_{n-1}(1)$$

$$m_n=m^n$$

Galton-Watson process

$$f(1)=1 \qquad f'(1)=m \qquad f''(1)=\sigma^2+m^2-m$$

$$F''_n(1)=f''(1)\left[F'_{n-1}(1)\right]^2+f'(1)F''_{n-1}(1)$$
$$=f''(1)m^{2n-2}+mF''_{n-1}(1)$$

$$\sigma_n^2=\sigma^2\frac{m^{n-1}(m^n-1)}{m-1} \qquad m\neq 1$$
$$\sigma_n^2=n\sigma^2 \qquad m=1$$

Exponential life-times

$$G(t)=1-e^{-\lambda t}$$

$$F(s,0)=s \qquad \frac{\partial}{\partial t}F(s,t)=u(F(s,t))$$

$$u(s)\equiv\lambda[f(s)-s]$$

Markovian process

Exponential life-times

$$m_k(t) \equiv \langle Z(t)[Z(t)-1]\cdots[Z(t)-k+1]\rangle$$

$$\dot{m}_1(t) = u'(1)\, m_1(t)$$

$$m_1(t) = e^{u'(1)t}$$

Malthus law

Exponential life-times

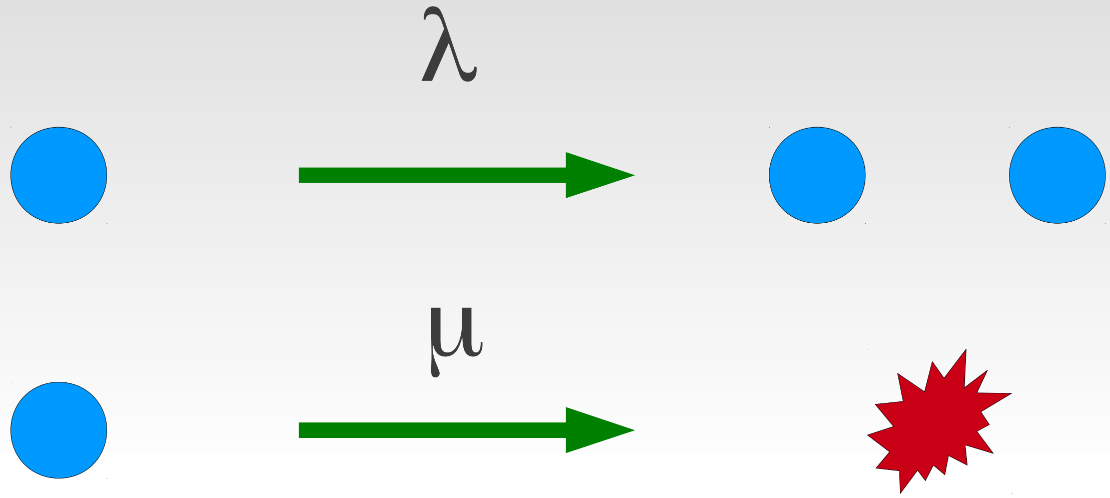
$$m_k(t) \equiv \langle Z(t)[Z(t)-1]\cdots[Z(t)-k+1]\rangle$$

$$\dot{m}_2(t) = u'(1)\, m_2(t) + u''(1)\, m_1(t)^2$$

$$\sigma^2(t) = \left(\frac{u''(1)}{u'(1)} - 1\right) e^{u'(1)t}\left(e^{u'(1)t} - 1\right) \qquad u'(1) \neq 0$$

$$\sigma^2(t) = u''(1)\, t \qquad u'(1) = 0$$

Ex.: birth-death process



$$G(t) = 1 - e^{-(\lambda+\mu)t}$$

$$u(s) = \mu - (\lambda+\mu)s + \lambda s^2$$

Ex.: birth-death process

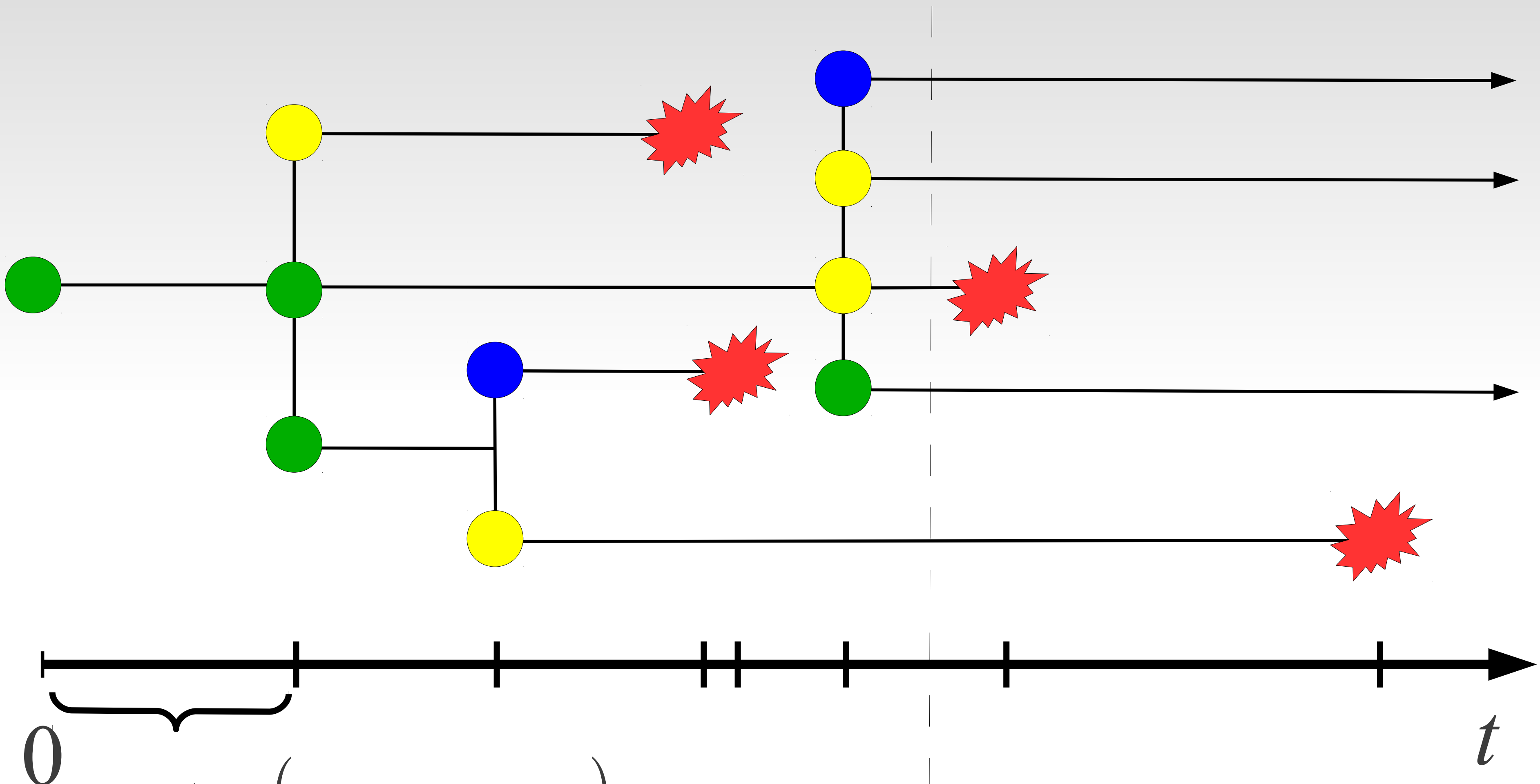
$$F(s,t)=\frac{\mu(1-s)+(\lambda s-\mu)e^{(\mu-\lambda)t}}{\lambda(1-s)+(\lambda s-\mu)e^{(\mu-\lambda)t}} \qquad \lambda\neq\mu$$

$$F(s,t)=\frac{s+(1-s)\lambda t}{1+(1-s)\lambda t} \qquad \lambda=\mu$$

$$\lambda>\mu \qquad F(0,t)=\frac{\mu-\mu e^{(\mu-\lambda)t}}{\lambda-\mu e^{(\mu-\lambda)t}}$$

$$q=\lim_{t\to\infty}F(0,t)=\frac{\mu}{\lambda}$$

Multi-type processes



$\boldsymbol{\tau} = (\tau_1, \ldots, \tau_r)$

$\boldsymbol{Z}_i(t) = (Z_{i,1}(t), \ldots, Z_{i,r}(t))$

individuals at time t

generated by one i individual

Branching processes

Event time distribution for type i:

$$G_i(t) = \Pr\{\tau_i \leqslant t\}$$

Generating function of offspring distribution for type i:

$$f_i(\boldsymbol{s}) = \sum_{\boldsymbol{k}=\boldsymbol{0}}^{\infty} p_{i,\boldsymbol{k}} \boldsymbol{s}^{\boldsymbol{k}} \qquad p_{i,\boldsymbol{k}} = \Pr\{\boldsymbol{X}_i = \boldsymbol{k} | \text{event}\} \qquad \boldsymbol{s}^{\boldsymbol{k}} \equiv \prod_{l=1}^{r} s_l^{k_l}$$

Generating function of the process for type i:

$$F_i(\boldsymbol{s}, t) \equiv \sum_{k=0}^{\infty} P_{i,\boldsymbol{k}}(t) \boldsymbol{s}^{\boldsymbol{k}} \qquad P_{i,\boldsymbol{k}}(t) = \Pr\{\boldsymbol{Z}_i(t) = \boldsymbol{k} | \boldsymbol{Z}_i(0) = \boldsymbol{e}_i\}$$

$$(i = 1, \ldots, r)$$

Branching processes

Constitutive equation:

$$\boldsymbol{Z}_i(t)=\begin{cases} \boldsymbol{e}_i & \text{if } t<\tau_i \\ \sum_{l=1}^{r}\sum_{\mu=1}^{X_l} \boldsymbol{Z}_l^{(\mu)}(t-\tau_i) & \text{if } t\geqslant\tau_i \end{cases}$$

$$F_i(\boldsymbol{s},t|t<\tau_i)=s_i \qquad F_i(\boldsymbol{s},t|t\geqslant\tau_i,\boldsymbol{X}=\boldsymbol{j})=[\boldsymbol{F}(\boldsymbol{s},t-\tau_i)]^{\boldsymbol{j}}$$

$$F_i(\boldsymbol{s},t|t\geqslant\tau_i)=f_i(\boldsymbol{F}(\boldsymbol{s},t-\tau_i))$$

$$F_i(\boldsymbol{s},t)=s_i[1-G_i(t)]+\int_0^t f_i(\boldsymbol{F}(\boldsymbol{s},t-\tau))\,dG_i(\tau)$$

Special cases

Multi-type Galton-Watson process:

$$\boldsymbol{F}_n(\boldsymbol{s}) \equiv \boldsymbol{F}(\boldsymbol{s}, nT)$$

$$\boldsymbol{F}_0(\boldsymbol{s}) = \boldsymbol{s} \qquad \boldsymbol{F}_{n+1}(\boldsymbol{s}) = \boldsymbol{f}(\boldsymbol{F}_n(\boldsymbol{s}))$$

Multi-type exponential process:

$$G_i(t) = 1 - e^{-\lambda_i t}$$

$$\boldsymbol{F}(\boldsymbol{s}, 0) = \boldsymbol{s} \qquad \frac{\partial}{\partial t}\boldsymbol{F}(\boldsymbol{s}, t) = \boldsymbol{u}(\boldsymbol{F}(\boldsymbol{s}, t))$$

$$u_i(\boldsymbol{s}) \equiv \lambda_i [f_i(\boldsymbol{s}) - s_i]$$

Exponential process

$$m_{i,j}(t) = \langle Z_{i,j}(t) \rangle = \frac{\partial F_i}{\partial s_j}(\mathbf{1}, t) \qquad \boldsymbol{M}(t) = \left(m_{i,j}(t) \right)$$

$$\frac{\partial u_i}{\partial s_j}(\mathbf{1}) = \lambda_i \left[\frac{\partial f_i}{\partial s_j}(\mathbf{1}) - \delta_{i,j} \right] \equiv a_{i,j} \qquad \boldsymbol{A} = \left(a_{i,j} \right)$$

$$\dot{\boldsymbol{M}} = \boldsymbol{A}\,\boldsymbol{M} \qquad \boldsymbol{M}(0) = \boldsymbol{I}$$

$$\boldsymbol{M}(t) = \exp(\boldsymbol{A}\,t)$$

Asymptotic behavior

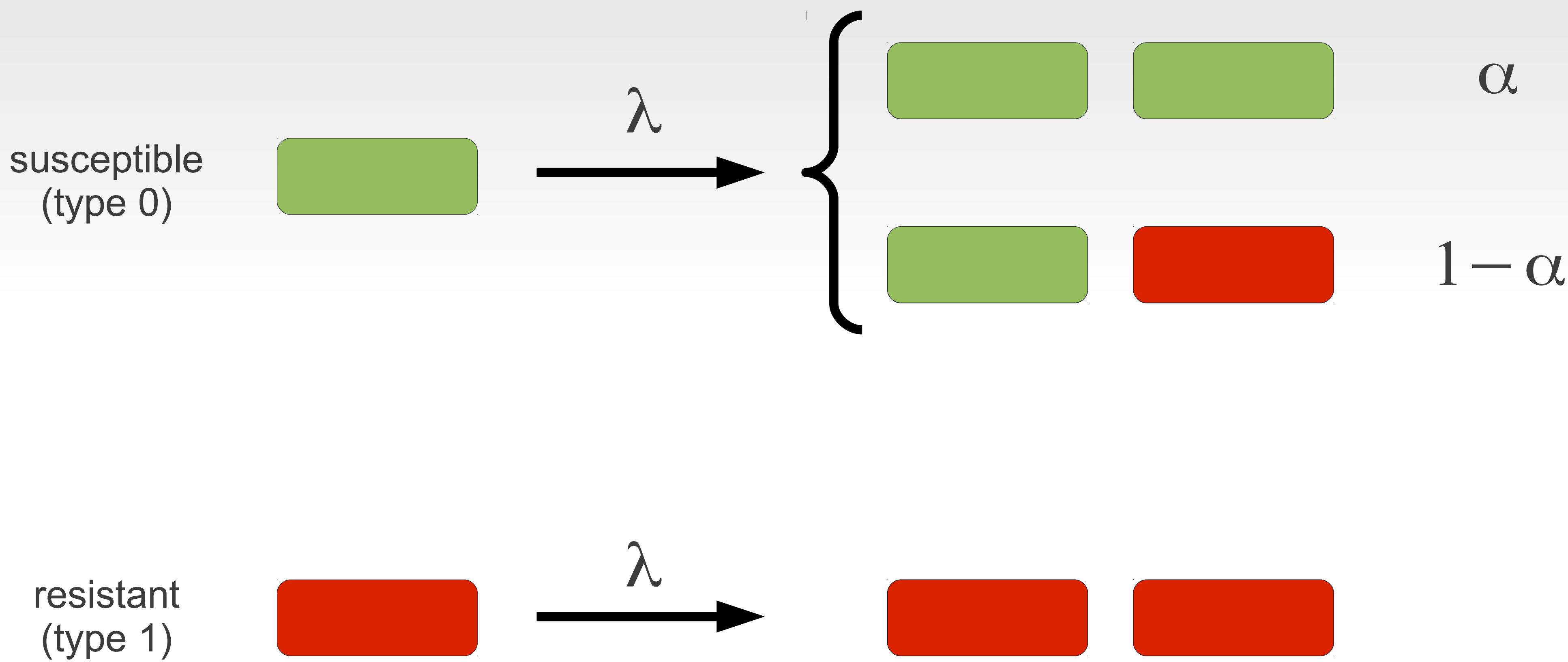
$$\boldsymbol{B} \equiv \left(\frac{\partial f_i}{\partial s_j}(\mathbf{1}) \right)$$

- $\boldsymbol{B}$ primitive
- a, the largest eigenvalue of $\boldsymbol{A}$, is single
- $\boldsymbol{A}\,\boldsymbol{u} = a\,\boldsymbol{u} \quad (\boldsymbol{u} > \mathbf{0})$
- $\boldsymbol{v}\,\boldsymbol{A} = a\,\boldsymbol{v} \quad (\boldsymbol{v} > \mathbf{0})$
- $\boldsymbol{u} \cdot \boldsymbol{v} = \boldsymbol{u} \cdot \mathbf{1} = 1$

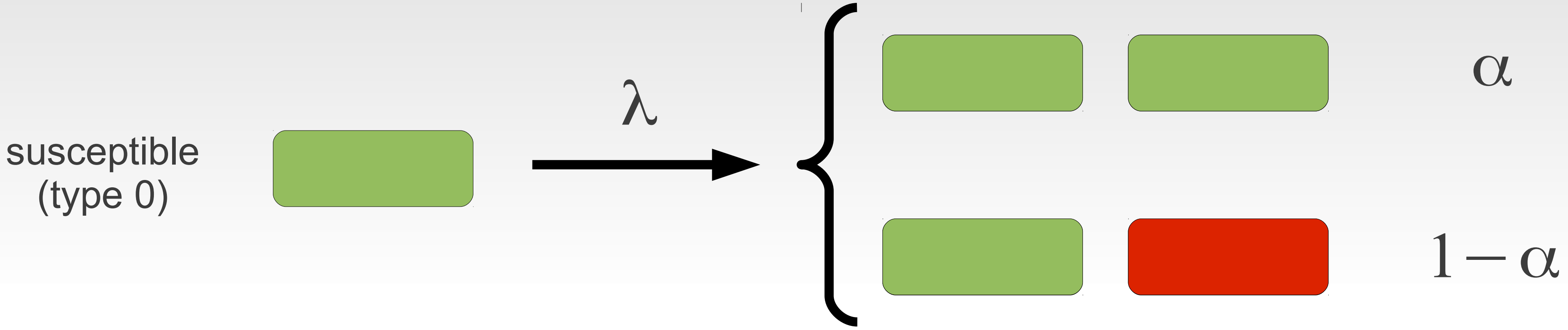
$$m_{i,j}(t) \sim e^{at} u_i v_j \qquad (t \to \infty)$$

$$\begin{cases} a > 0 & \text{supercritical} \\ a = 0 & \text{critical} \\ a < 0 & \text{subcritical} \end{cases}$$

Ex.: resistant cells

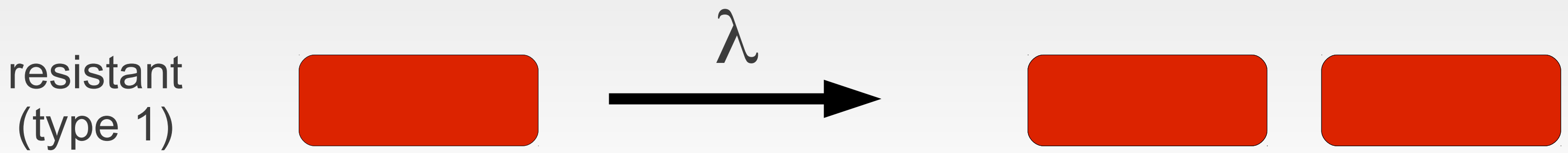


Ex.: resistant cells



$$f_0(s_0, s_1) = \alpha s_0^2 + (1-\alpha) s_0 s_1$$

Ex.: resistant cells



$$f_1(s_0, s_1) = s_1^2$$

Ex.: resistant cells

$$A=\lambda\begin{pmatrix}\alpha & 1-\alpha\\ 0 & 1\end{pmatrix} \qquad A^n=\lambda^n\begin{pmatrix}\alpha^n & 1-\alpha^n\\ 0 & 1\end{pmatrix}$$

$$M(t)=\begin{pmatrix}e^{\alpha\lambda t} & e^{\lambda t}-e^{\alpha\lambda t}\\ 0 & e^{\lambda t}\end{pmatrix}$$

$$=e^{\lambda t}\begin{pmatrix}e^{-(1-\alpha)\lambda t} & 1-e^{-(1-\alpha)\lambda t}\\ 0 & 1\end{pmatrix}\sim e^{\lambda t}\begin{pmatrix}0 & 1\\ 0 & 1\end{pmatrix}$$

resistant cells dominate the population

Ex.: resistant cells

$$\begin{cases} \frac{\partial}{\partial t} F_0 = \lambda F_0 [\alpha + (1-\alpha) F_1 - 1] \\ \frac{\partial}{\partial t} F_1 = \lambda F_1 (F_1 - 1) \\ F_0(s_0, s_1, 0) = s_0 \quad F_1(s_0, s_1, 0) = s_1 \end{cases}$$

$$F_1(s_0, s_1, t) = \frac{s_1 e^{-\lambda t}}{1 - s_1 + s_1 e^{-\lambda t}}$$

Ex.: resistant cells

$$\frac{\partial}{\partial t}\left(\frac{F_0}{F_1}\right)=\lambda\alpha\frac{F_0}{F_1}\left(\frac{F_0}{F_1}-1\right)F_1$$

$$F_1(s_0, s_1, t)=-\frac{\partial}{\partial t}\log\left(1-s_1+s_1 e^{-\lambda t}\right)$$

$$F_0(s_0, s_1, t)=\frac{s_0\left(1-s_1+s_1 e^{-\lambda t}\right)^{\alpha}}{s_1-s_0+\left(1-s_1+s_1 e^{-\lambda t}\right)^{\alpha}}F_1(s_0, s_1, t)$$