

Conference "Cooperation and major evolutionary transitions"
Kevli Institute for Theoretical Physics, U.C. Santa Barbara
February 8, 2013; 10:30-11:15

Self-Sacrificing of Social Amoeba

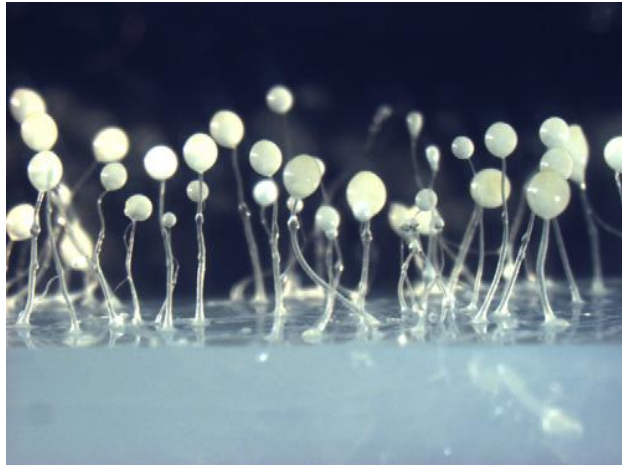
cell-to-cell interaction via a signaling chemical
shaped by cheating risk.

Yoh Iwasa

(Dept. Biology, Kyushu University)

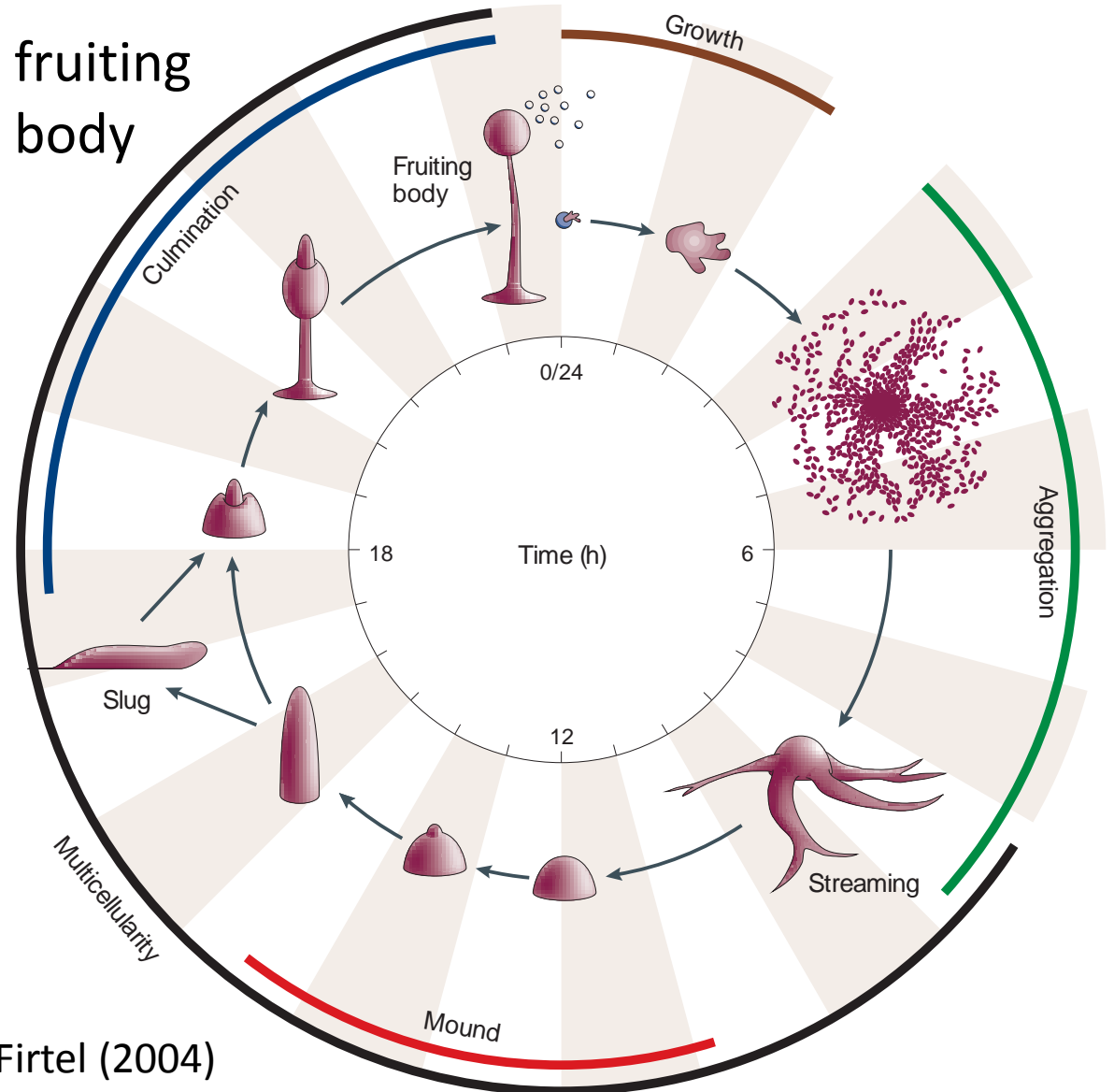
Collaborator: Kouki Uchinomiya

Dictyostelium discoideum



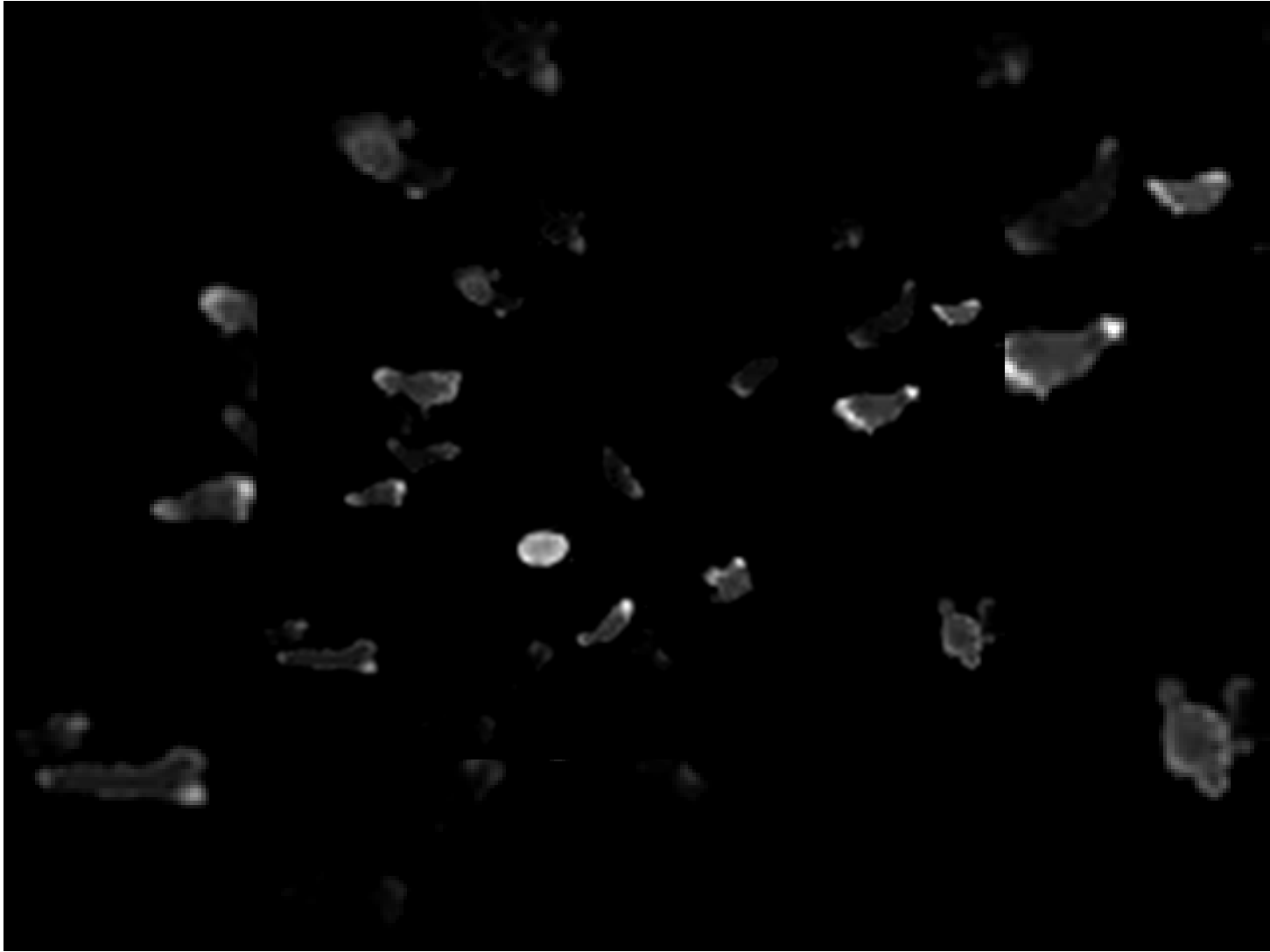
Strassmann & Queller (2011)

Slug



Chisholm & Firtel (2004)

Aggregation of cells



Formation of fruiting body

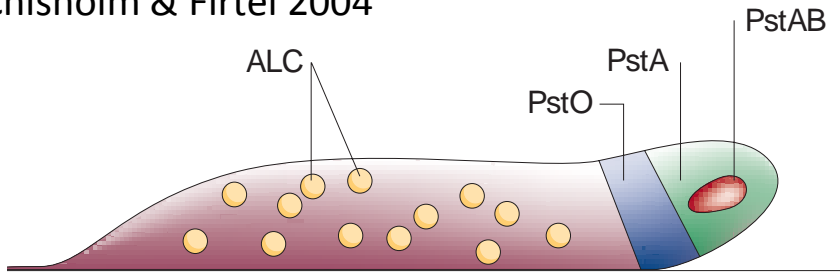


Becoming stalk is altruism.

assemblage

fruiting body

Chisholm & Firtel 2004



pre-spore cells



pre-stalk cells



Spore

Stalk

ation

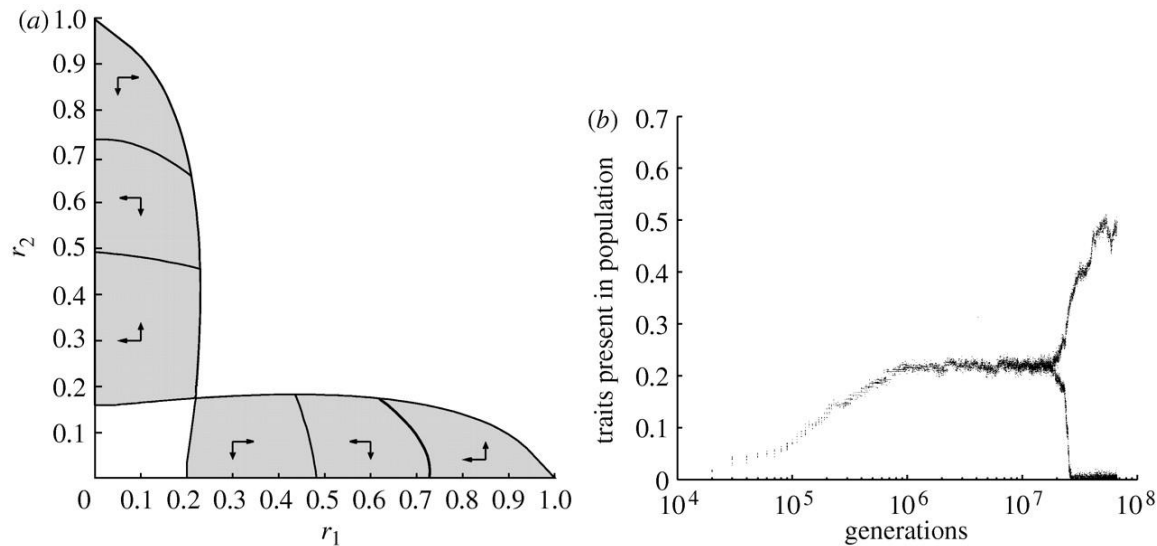


Aubry&Firtel (1999)

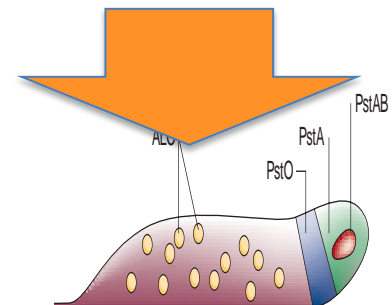
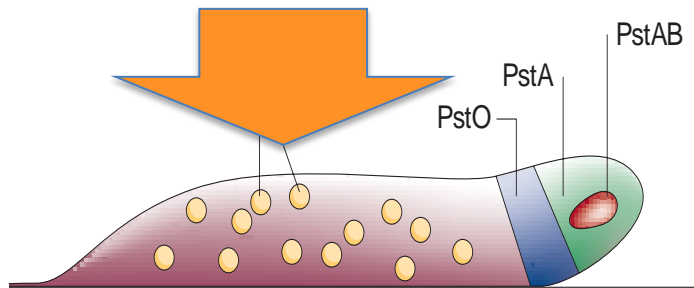
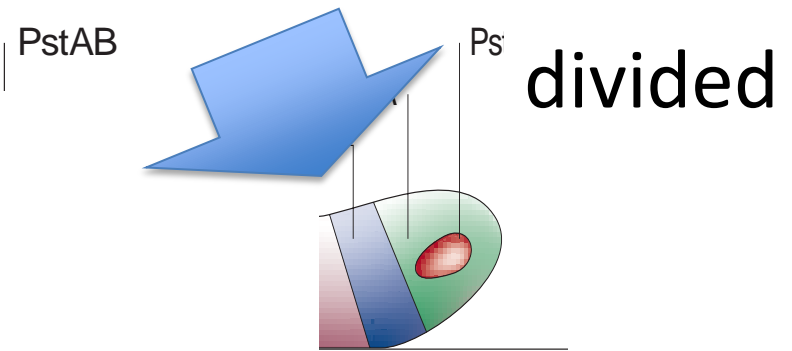
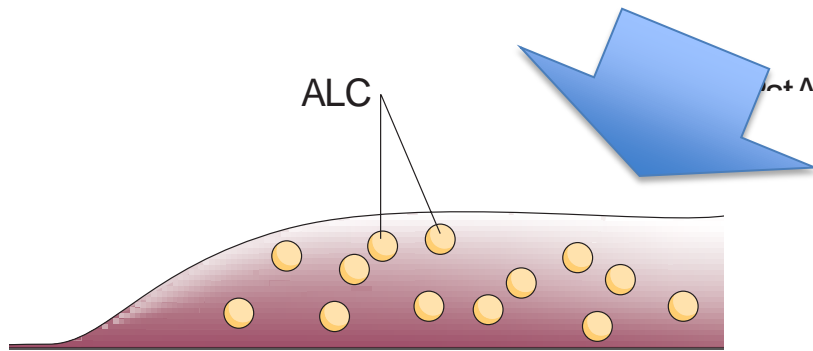
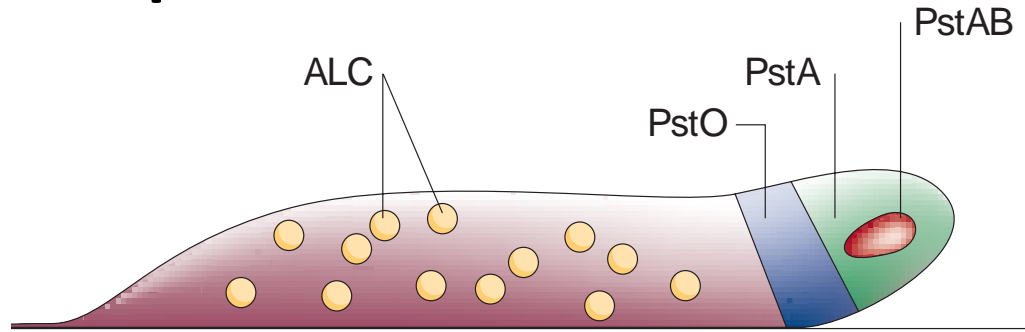
In evolutionary game models
on the stalk/spore ratio
each strain (genotype) has its own
value of contribution to stalk vs. spore.

for example

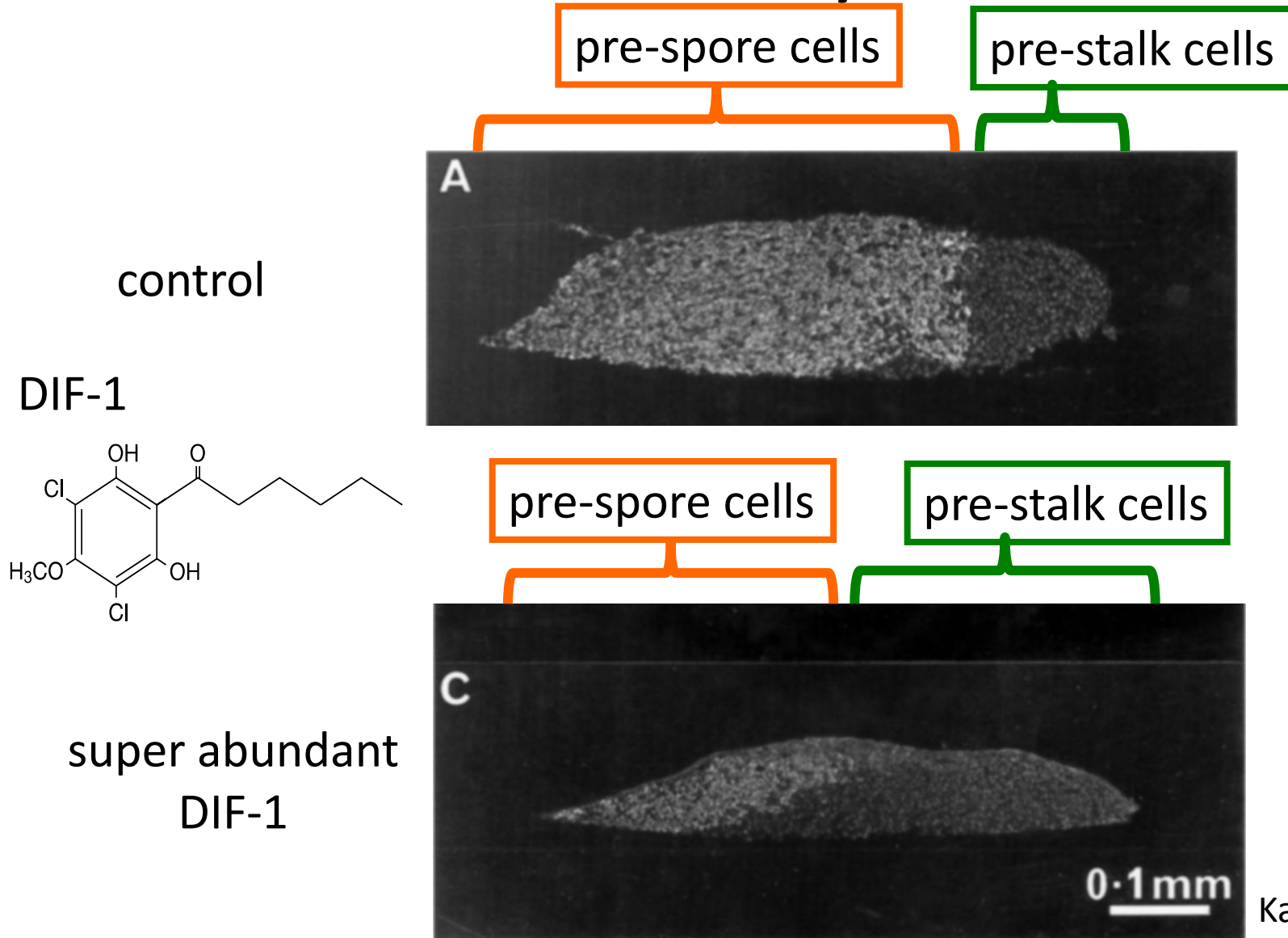
Brännström Å , & Dieckmann U 2005. Dimorphic evolutionary
dynamics after branching. Proc. R. Soc. B 2005;272:1609-1616



Ratio of pre-stalk cells is adjusted.



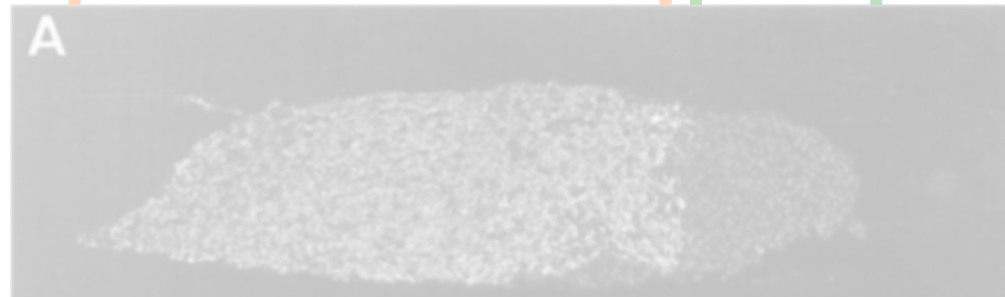
Fraction of Pre-stalk cells increases by DIF-1



Fraction of Pre-stalk cells increases by DIF-1

pre-spore cells

pre-stalk cells

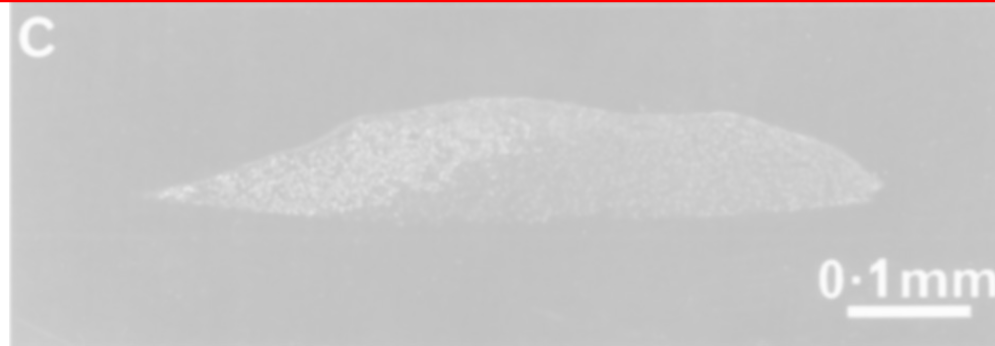


control

DIF-1

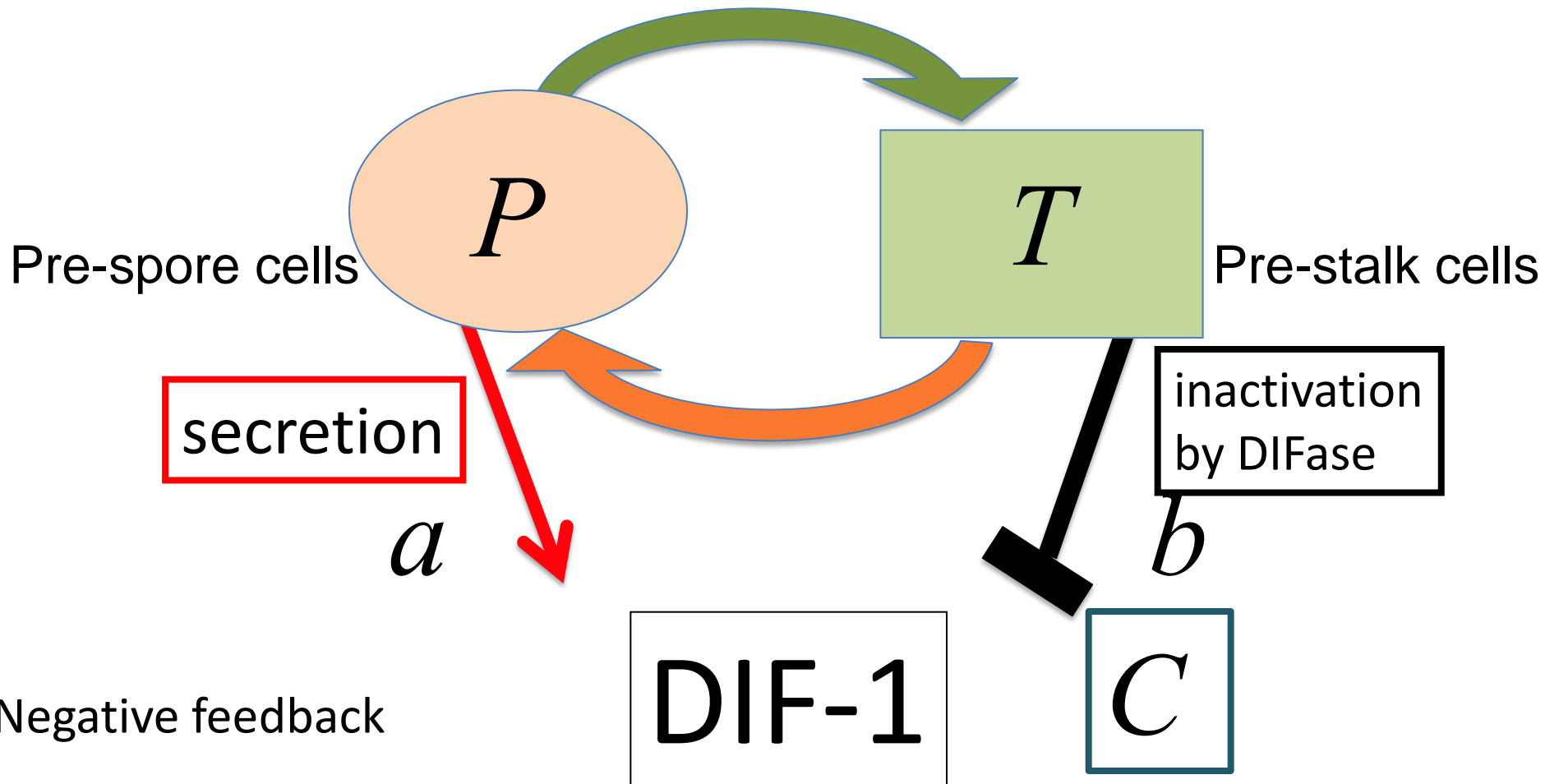


Cells become more altruistic
when they receive DIF-1.

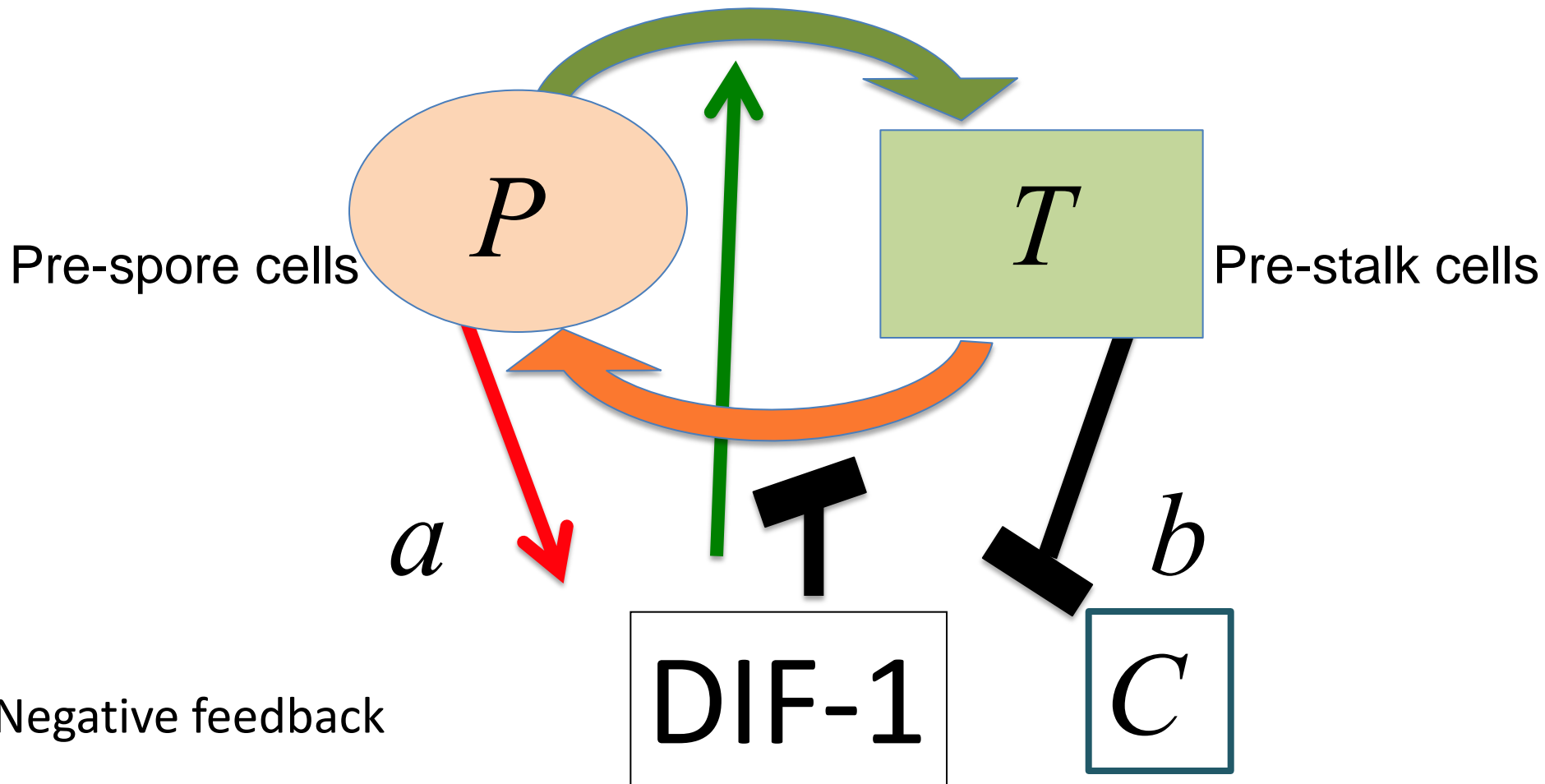


super abundant
DIF-1

Cell differentiation mediated by DIF-1

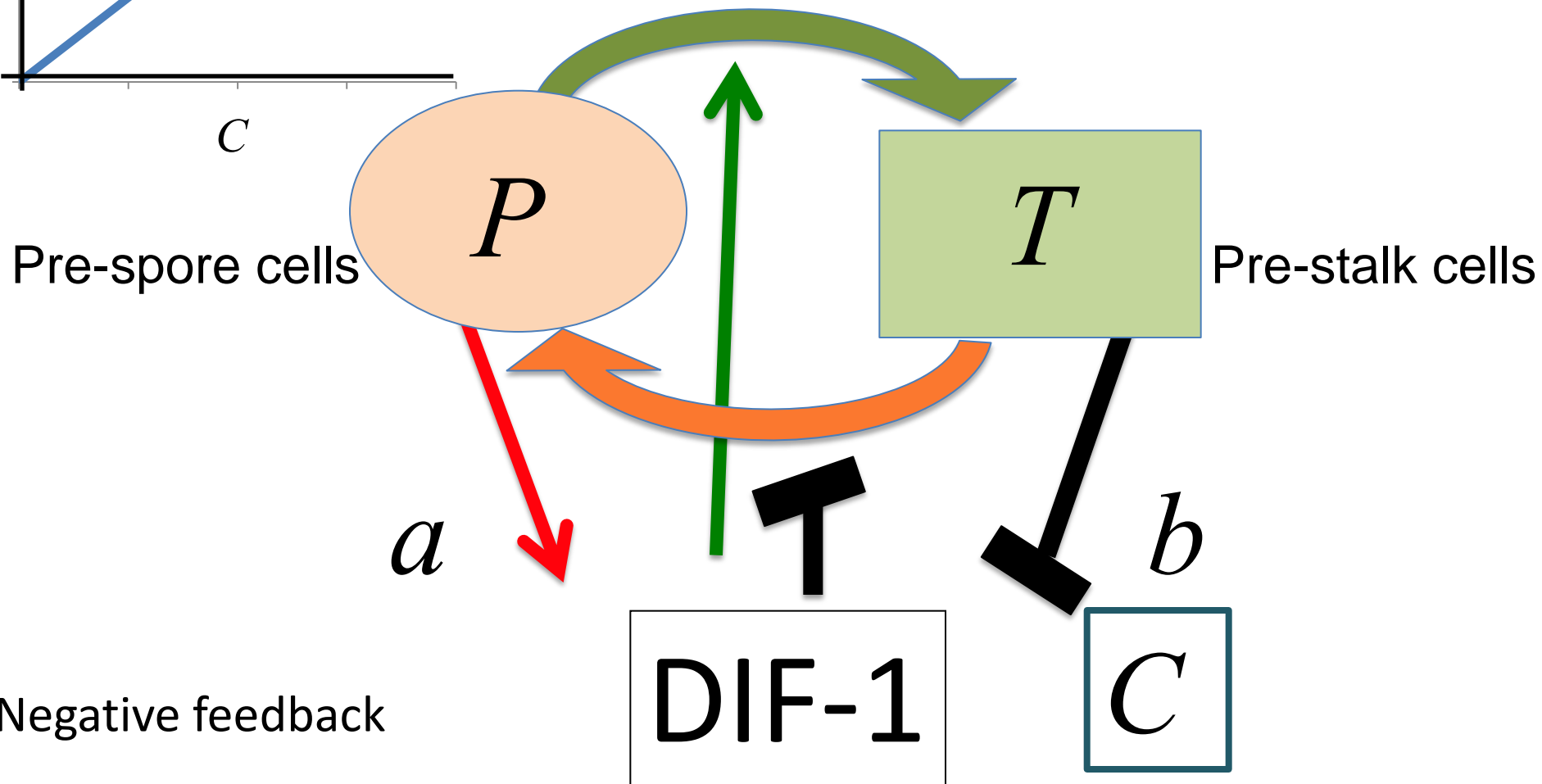
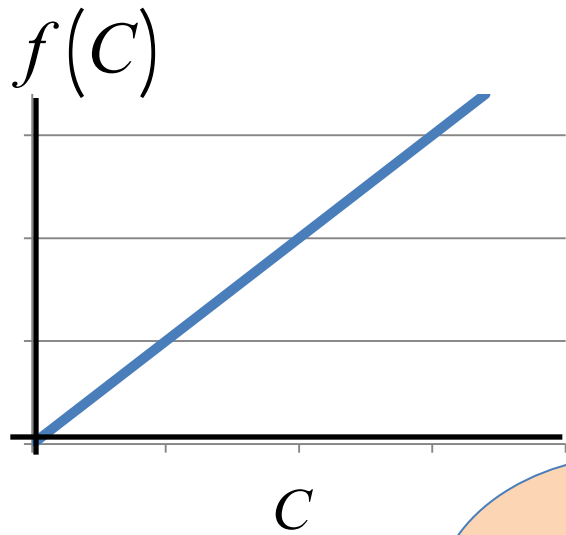


Cell differentiation mediated by DIF-1



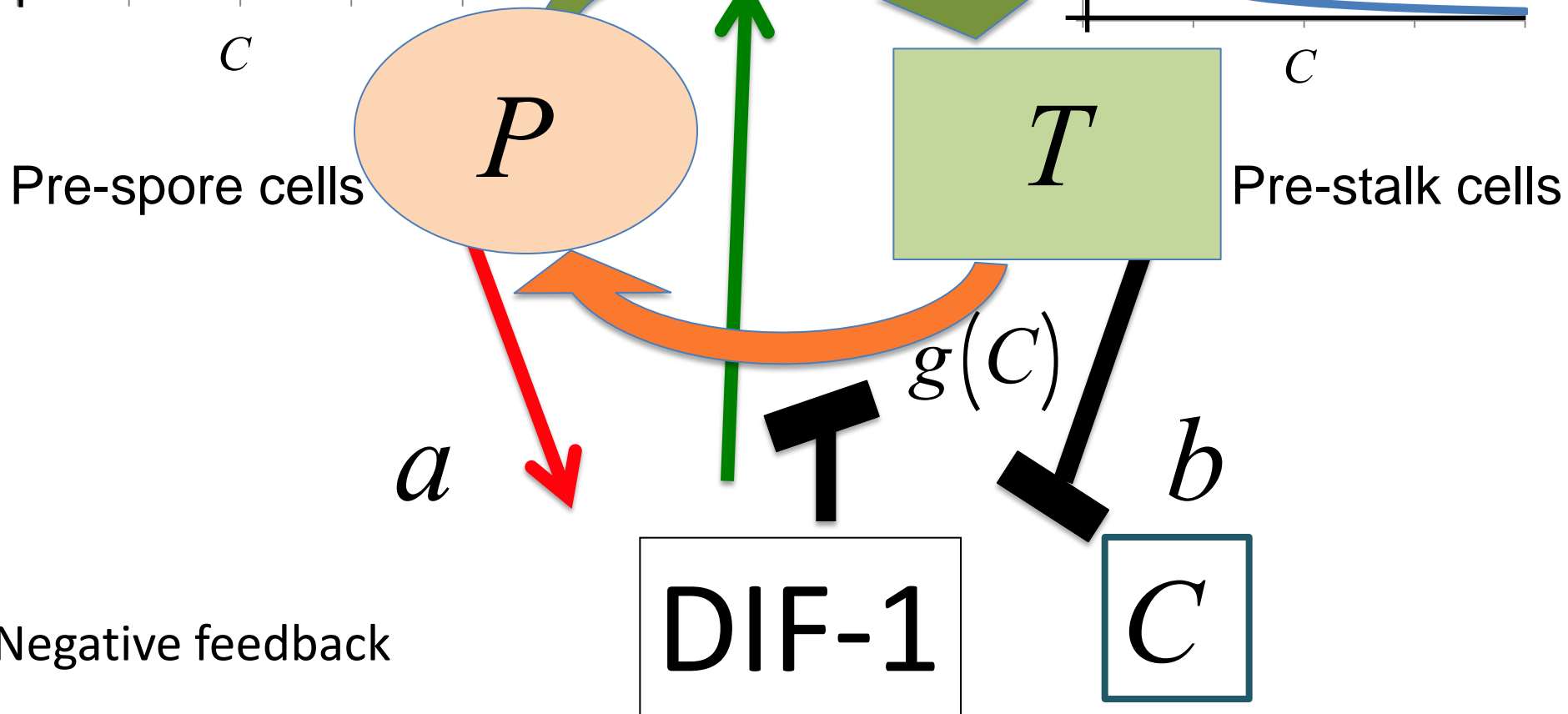
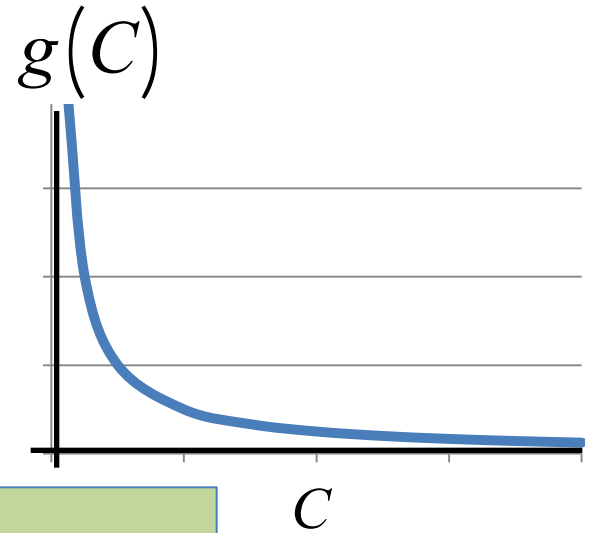
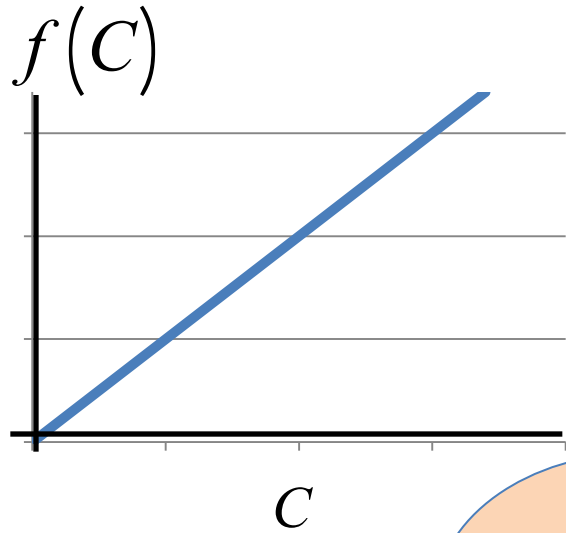
Cell differentiation mediated

by DIF-1



Cell differentiation mediated

by DIF-1



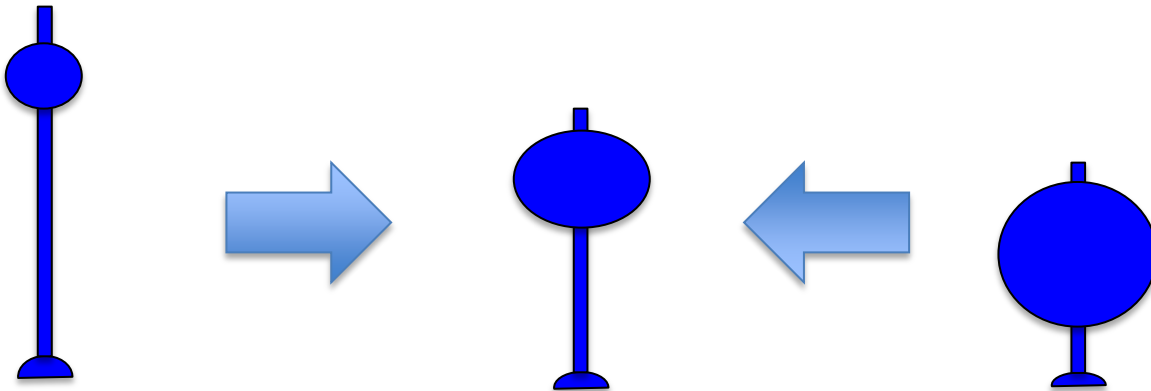
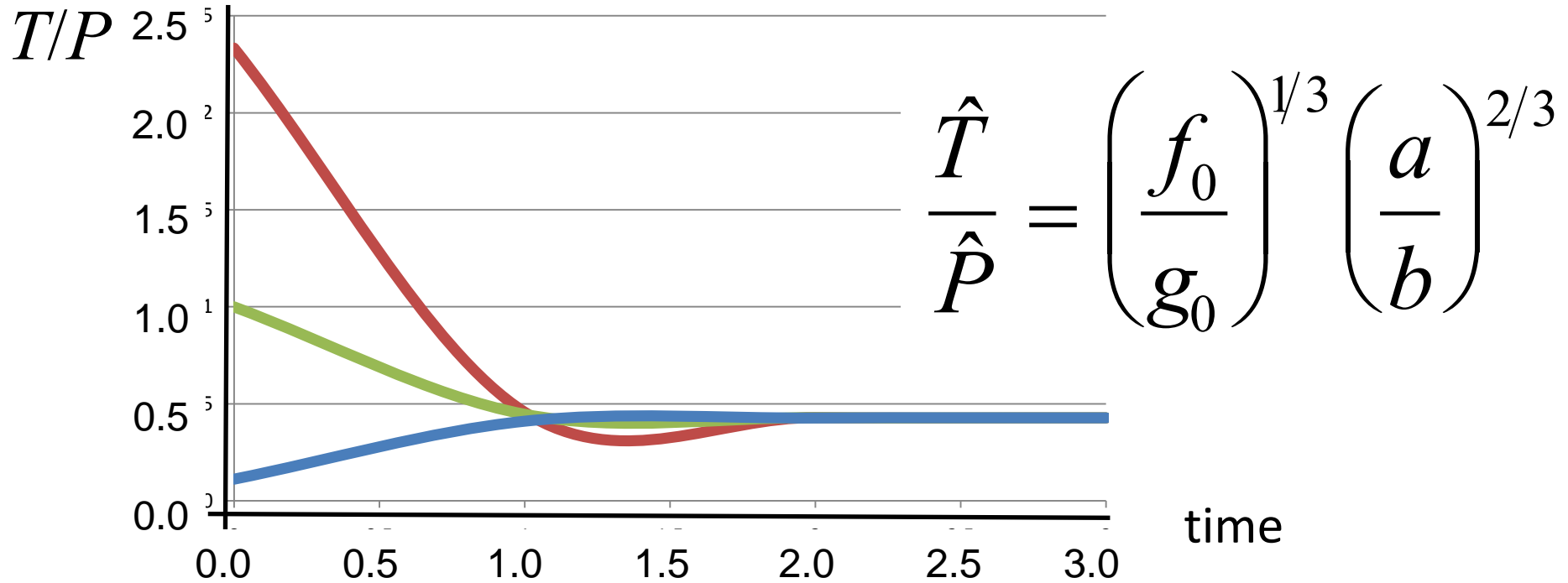
Kinetics of DIF-1 and cells

$$\frac{dT}{dt} = f(C)P - g(C)T \quad (\text{Pre-stalk cells})$$

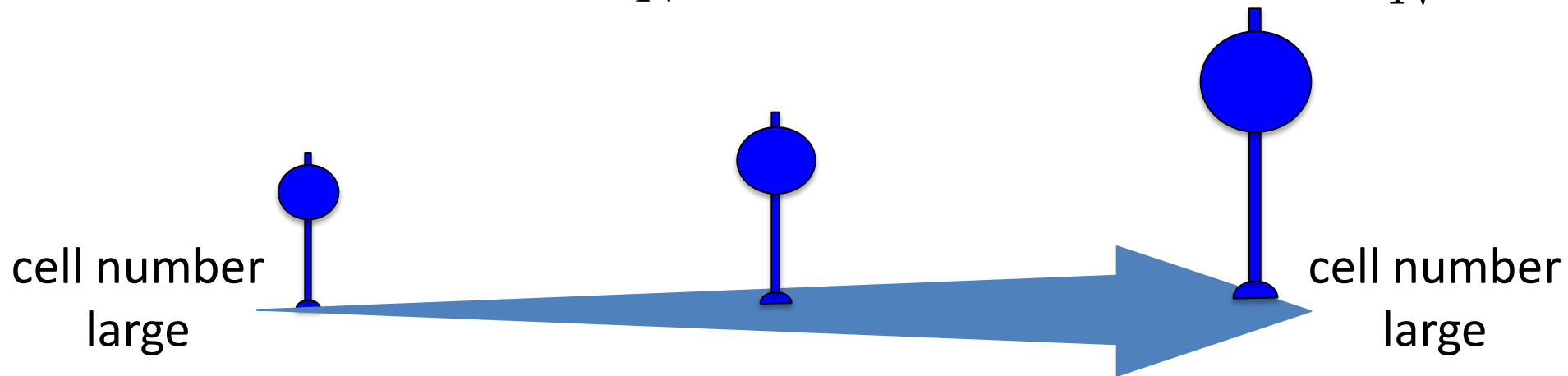
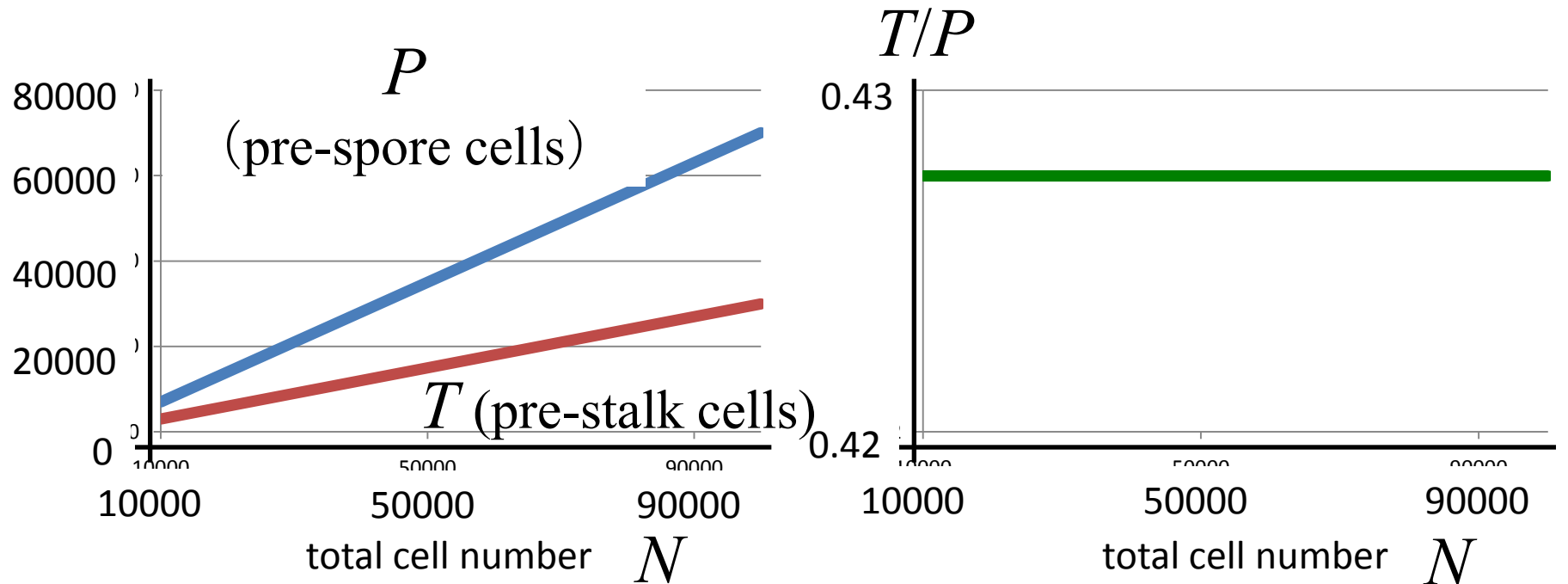
$$\frac{dC}{dt} = aP - bCT \quad (\text{DIF-1})$$

$$N = P + T \quad (\text{Total cell number})$$

T/P ratio converges to a constant

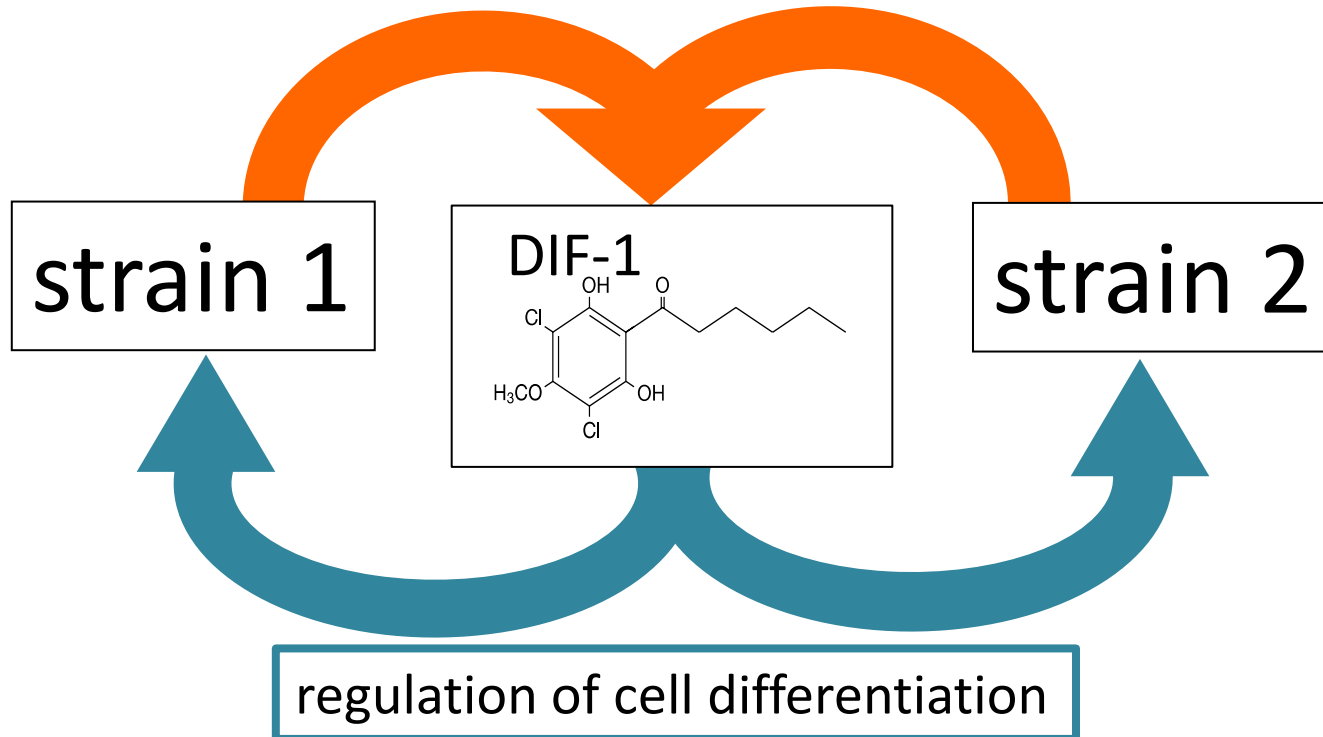


T/P ratio is independent of total cell number



A mixture of cells of two strains share DIF-1

Production and inactivation



In a mixture of multiple strains,

$$\frac{dT_1}{dt} = f_1(C)P_1 - g_1(C)T_1 \quad (\text{Pre-stalk cells})$$

$$\frac{dT_2}{dt} = f_2(C)P_2 - g_2(C)T_2 \quad (\text{Pre-stalk cells})$$

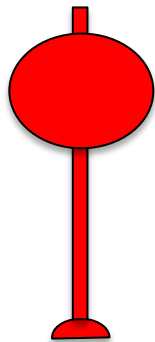
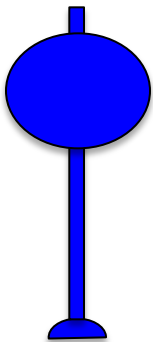
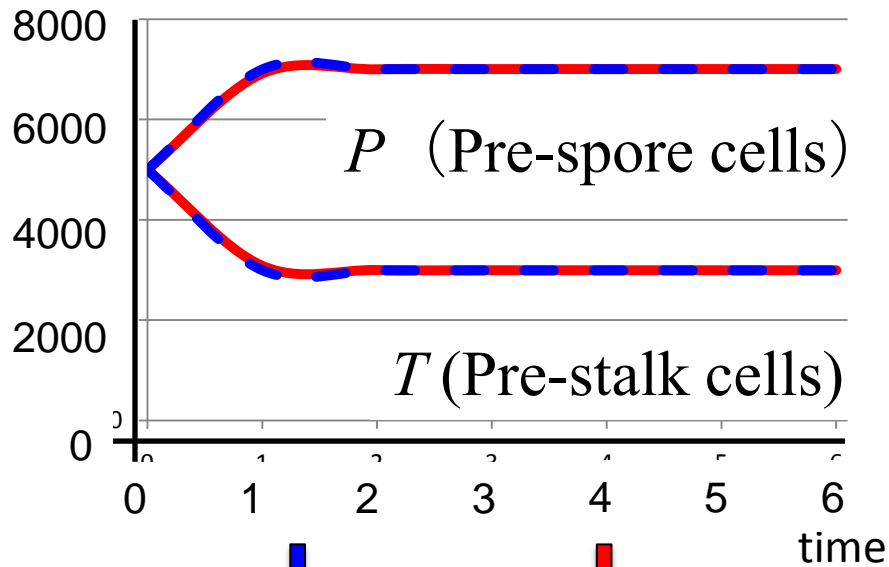
$$\frac{dC}{dt} = \sum_i (a_i P_i - b_i C T_i) \quad (\text{DIF-1})$$

$$N_i = P_i + T_i$$

Contribution to Stalk/Spore may differ between strains

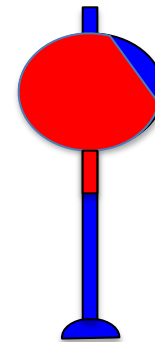
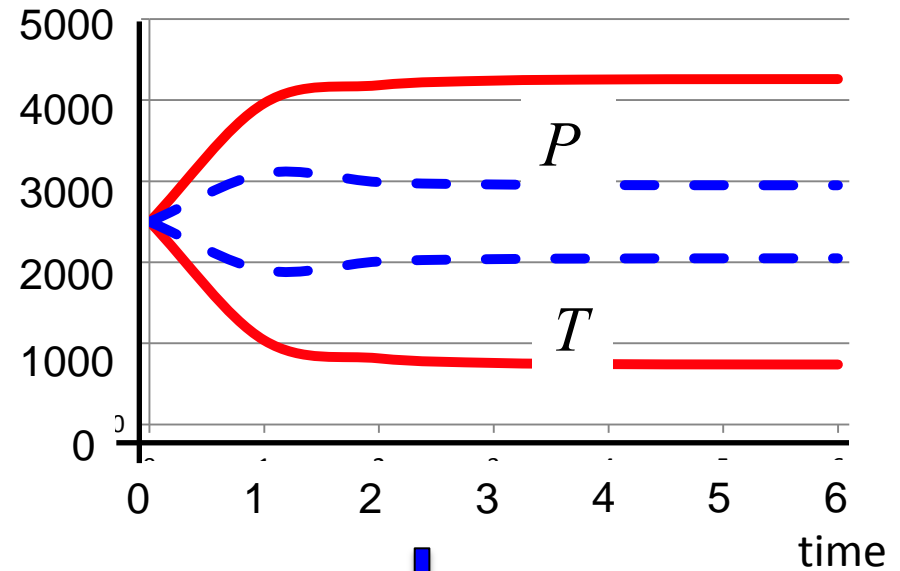
a single strain

cell number



a mixture of two strains

cell number



Red is a
Facultative
Cheater

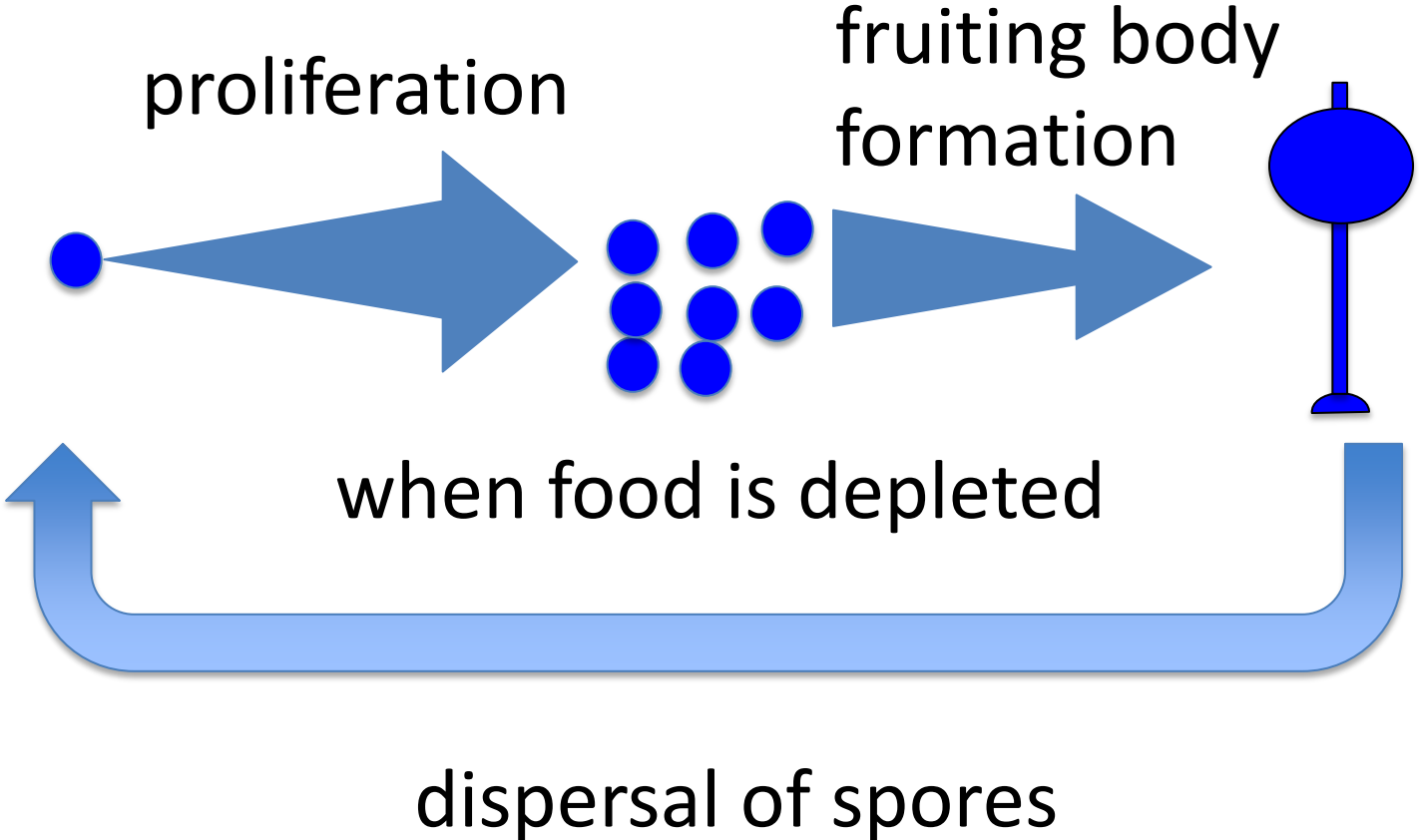
Stalk/spore ratio of each strain when mixed:

$$\frac{\hat{T}_i}{\hat{P}_i} = \frac{f_{0i}}{g_{0i}} \hat{C}^2 \quad i=1, 2 \quad \hat{C} = \frac{\sum_j a_j \hat{P}_j}{\sum_j b_j \hat{T}_j}$$

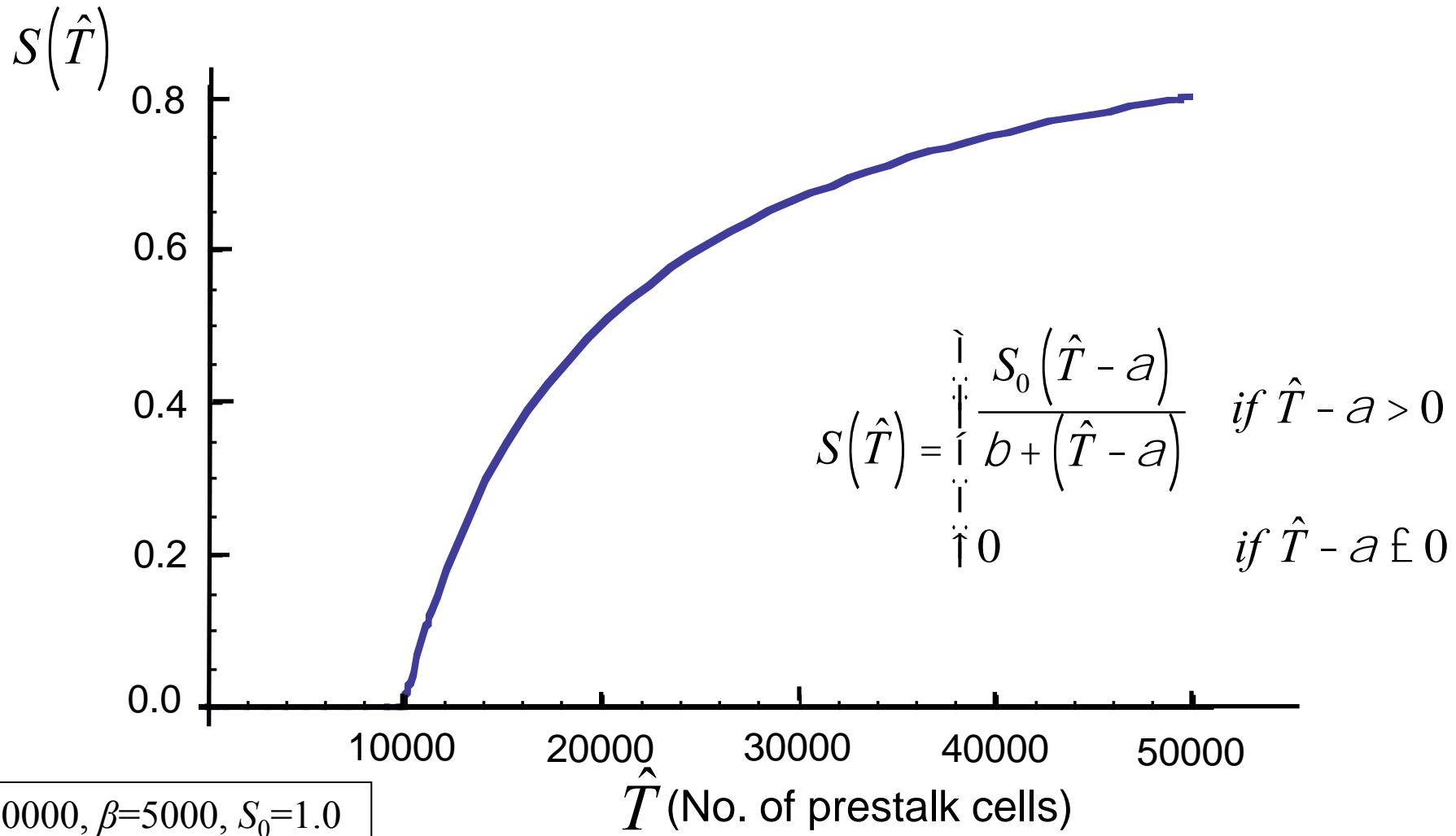
Stalk/spore ratio of a single strain fruiting body:

$$\frac{\hat{T}}{\hat{P}} = \left(\frac{f_0}{g_0} \right)^{1/3} \left(\frac{a}{b} \right)^{2/3}$$

Evolution



Dispersal and settlement success of spores



- f_0 Rate of transition
from prespore cell to prestalk cell
- g_0 Rate of transition
from prestalk cell to prespore cell
- a Rate of production of DIF-1 per prespore cell
- b Rate of decomposition of DIF-1 by prestalk
- k Cost of DIF-1 production

Fitness

Number of
Spores

Dispersal
success

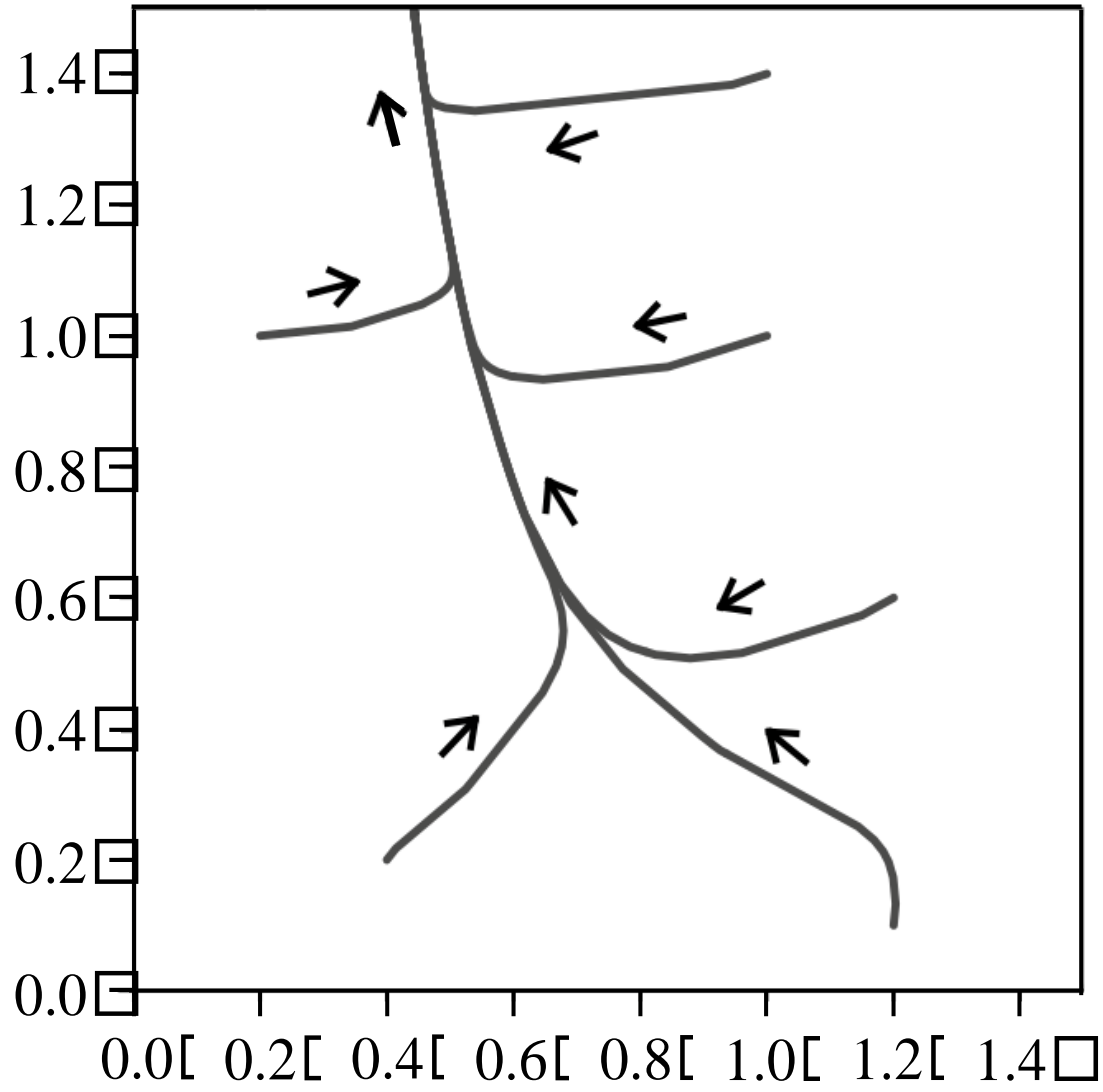
Cost of DIF-1
production

$$W_i = \hat{P}_i \cdot S(\hat{T}_i) e^{-k a_i}$$

A mutant who is close to their parental type invades, and it may replace the old type. After a long time, the species changes its property slowly.

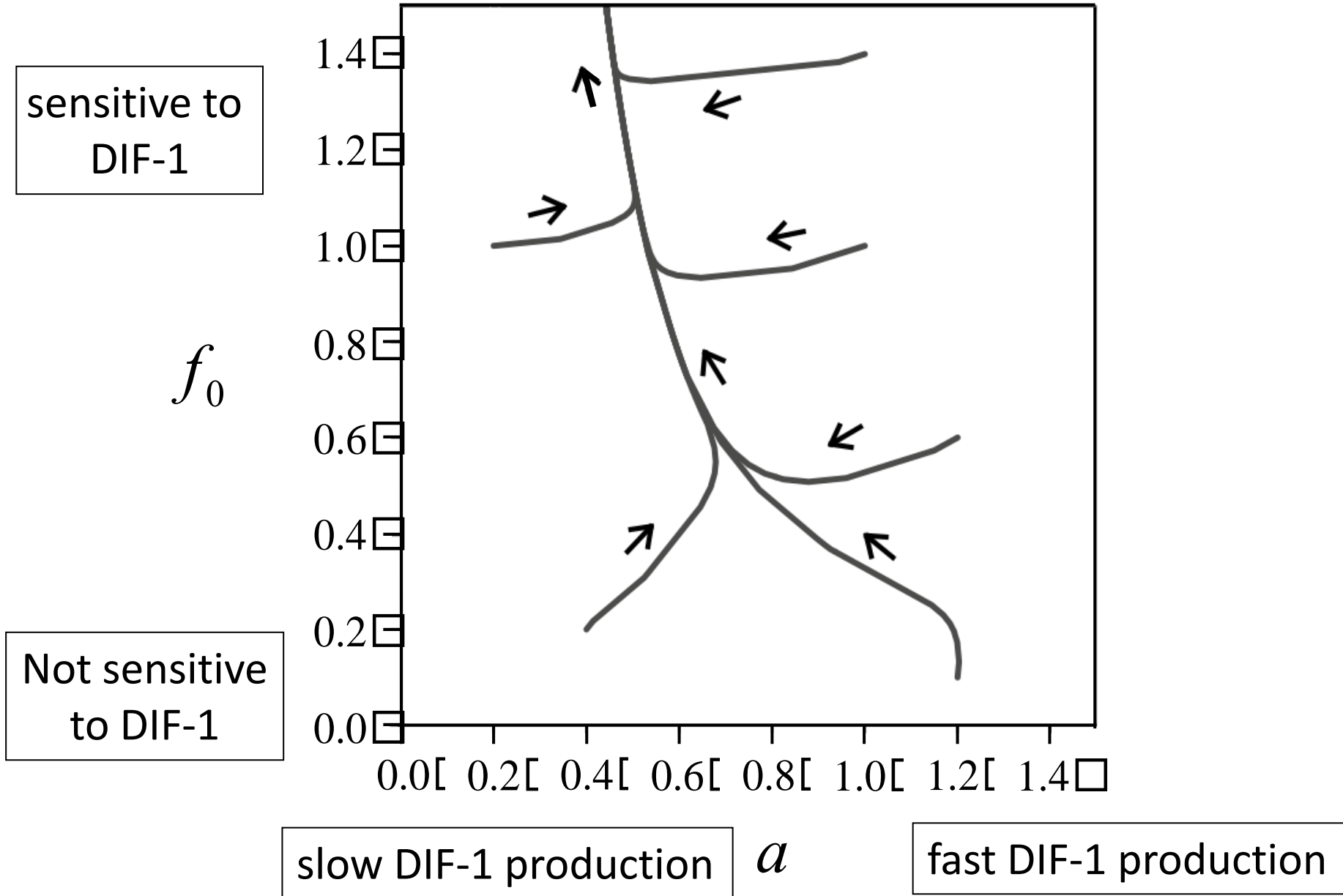
Evolutionary trajectory

Sensitivity for DIF-1
differentiating
prespore cell to pre
stalk cell (f_0)



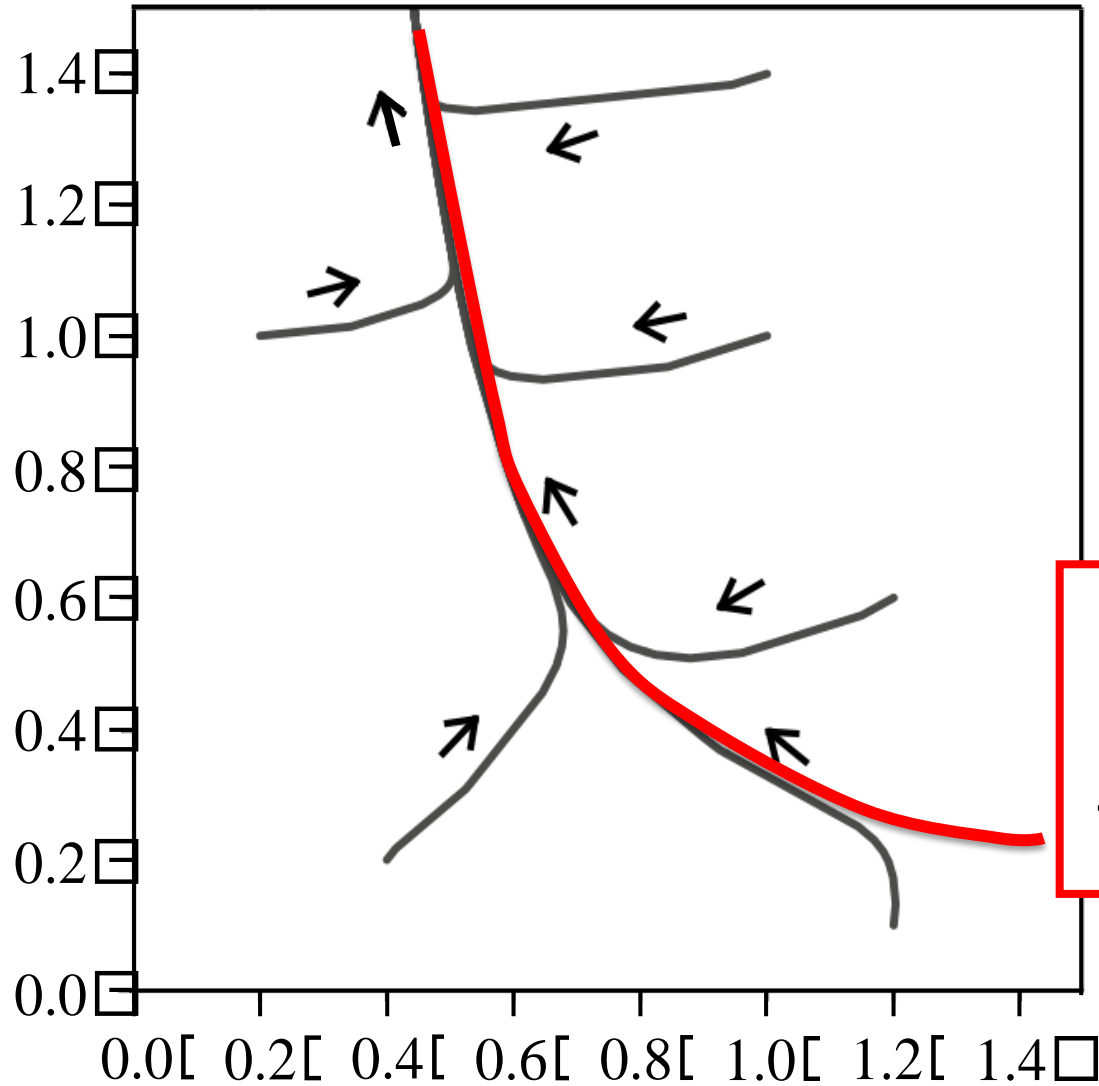
DIF-1 production rate (a)

Evolutionary trajectory



Evolutionary trajectory

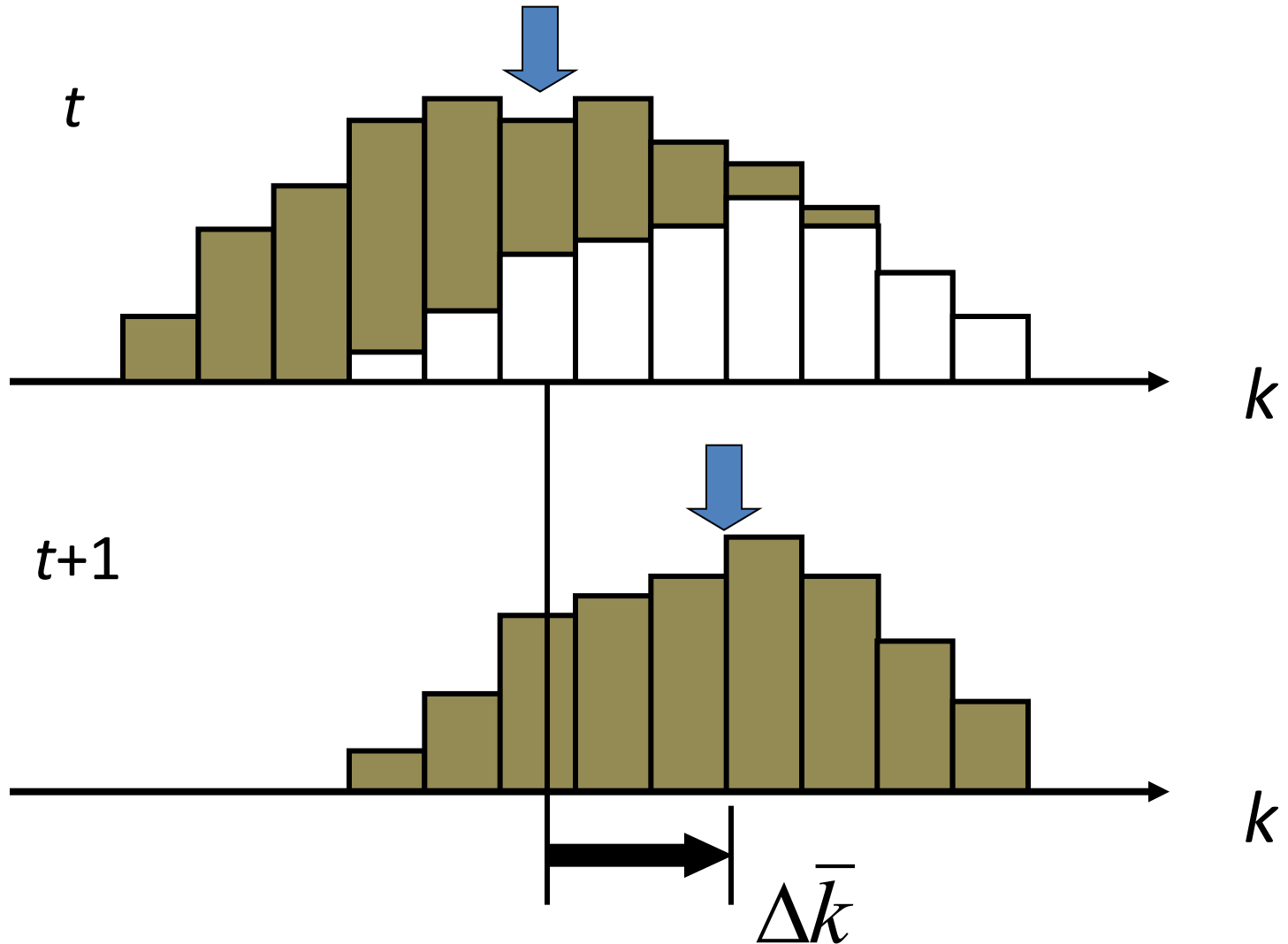
Sensitivity for DIF-1
differentiating
prespore cell to pre
stalk cell (f_0)

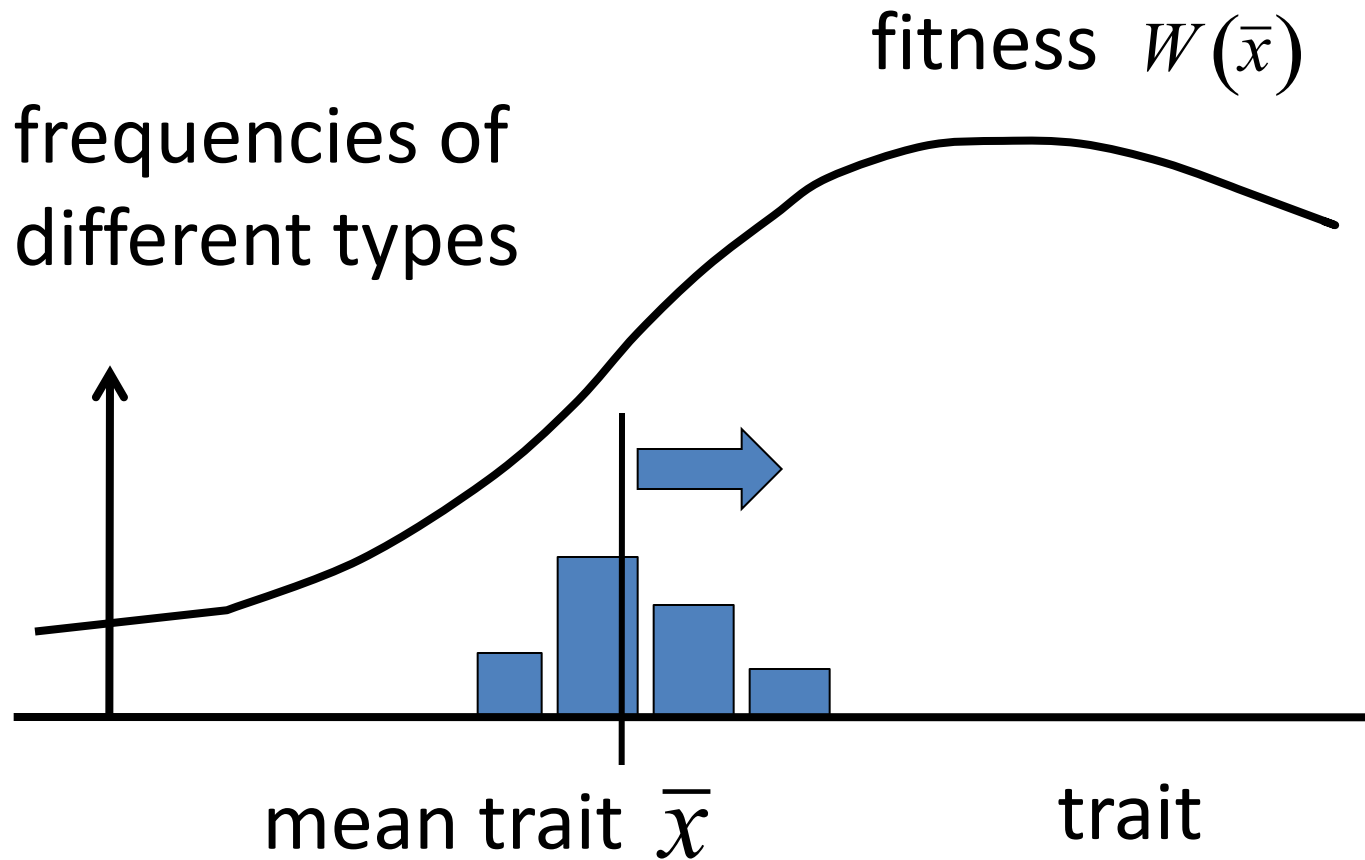


realizing
optimal
T/P ratio

DIF-1 production rate (a)

Response of a population to natural selection





Under weak selection,

change in the mean
trait in a generation

$$\Delta \bar{k} = \text{Var} [k_i] \bullet \frac{d \ln W}{dk}$$

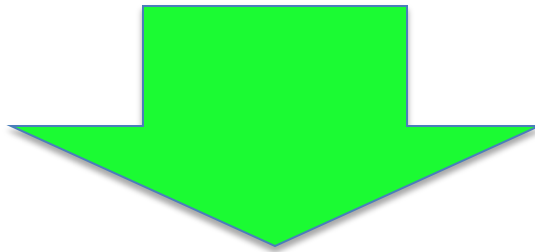
variance of the trait
within a population

selection
gradient

Strength of
Natural Selection

If there are two traits,

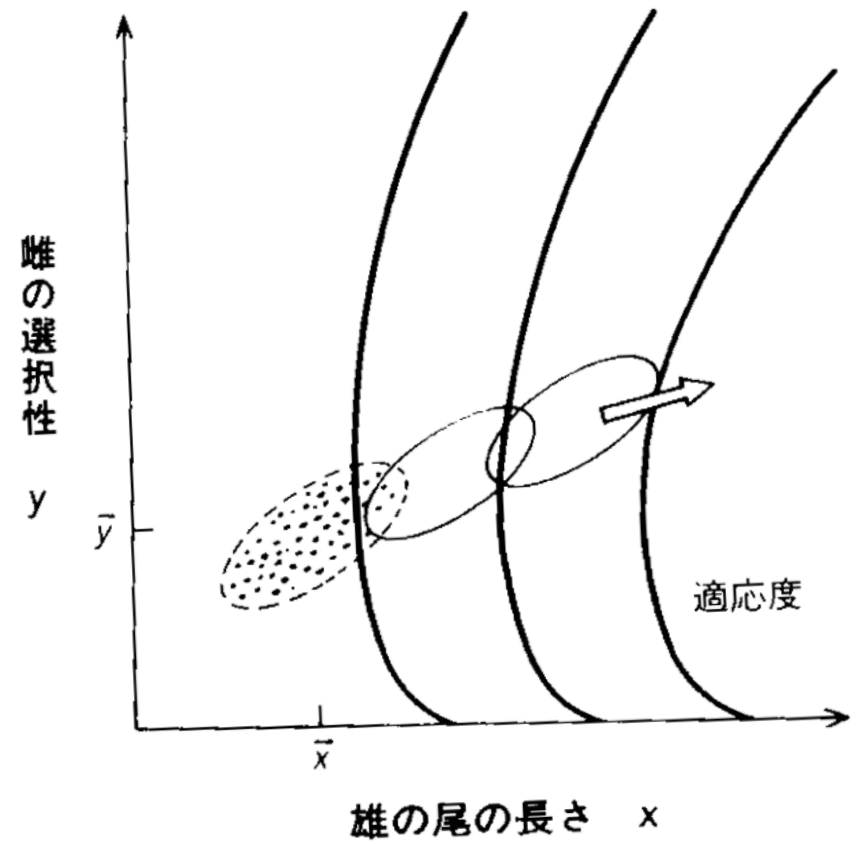
$$w(x,y) = w(\bar{x}, \bar{y}) + (x - \bar{x}) \frac{\partial w}{\partial x} + (y - \bar{y}) \frac{\partial w}{\partial y} + \dots$$



$$\Delta \bar{x} = \text{Var}[x] \frac{\partial \ln W}{\partial x} + \text{Cov}[x,y] \frac{\partial \ln W}{\partial y}$$

$$\Delta \bar{y} = \text{Cov}[x,y] \frac{\partial \ln W}{\partial x} + \text{Var}[y] \frac{\partial \ln W}{\partial y}$$

One generation change when there are two traits



$$\begin{pmatrix} \Delta \bar{x} \\ \Delta \bar{y} \end{pmatrix} = \begin{pmatrix} \text{Var}[x] & \text{Cov}[x,y] \\ \text{Cov}[x,y] & \text{Var}[y] \end{pmatrix} \begin{pmatrix} \frac{\partial \ln W}{\partial x} \\ \frac{\partial \ln W}{\partial y} \end{pmatrix}$$

Evolutionary Dynamics

$$\begin{pmatrix} \Delta \bar{a} \\ \Delta f_0 \end{pmatrix} = \begin{pmatrix} G & B \end{pmatrix} \begin{pmatrix} \beta_a \\ \beta_{f_0} \end{pmatrix}$$

Selection to realize the optimal stalk size

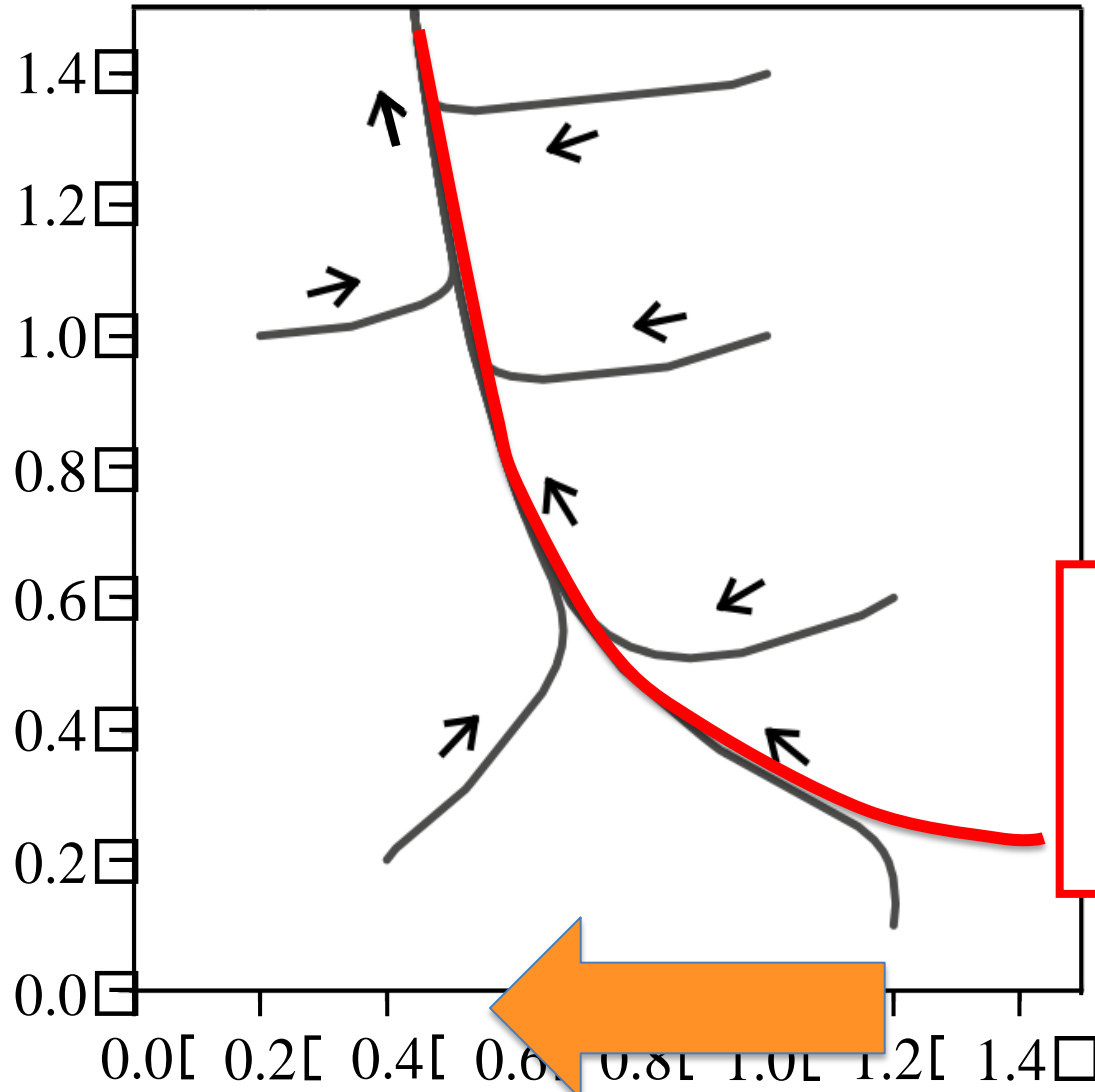
Selection to reduce the DIF-1 production

$$\beta_a = \frac{\partial \ln W}{\partial a} = \left(\frac{1}{S} \frac{dS}{dT} - \frac{1}{N-T} \right) \frac{\partial T}{\partial a} - k$$

$$\beta_{f_0} = \frac{\partial \ln W}{\partial f_0} = \left(\frac{1}{S} \frac{dS}{dT} - \frac{1}{N-T} \right) \frac{\partial T}{\partial f_0}$$

Evolutionary trajectory

Sensitivity for DIF-1
differentiating
prespore cell to pre
stalk cell (f_0)



realizing
optimal
T/P ratio

DIF-1 production rate (a)

When a fruiting body consists of cells of a single strain

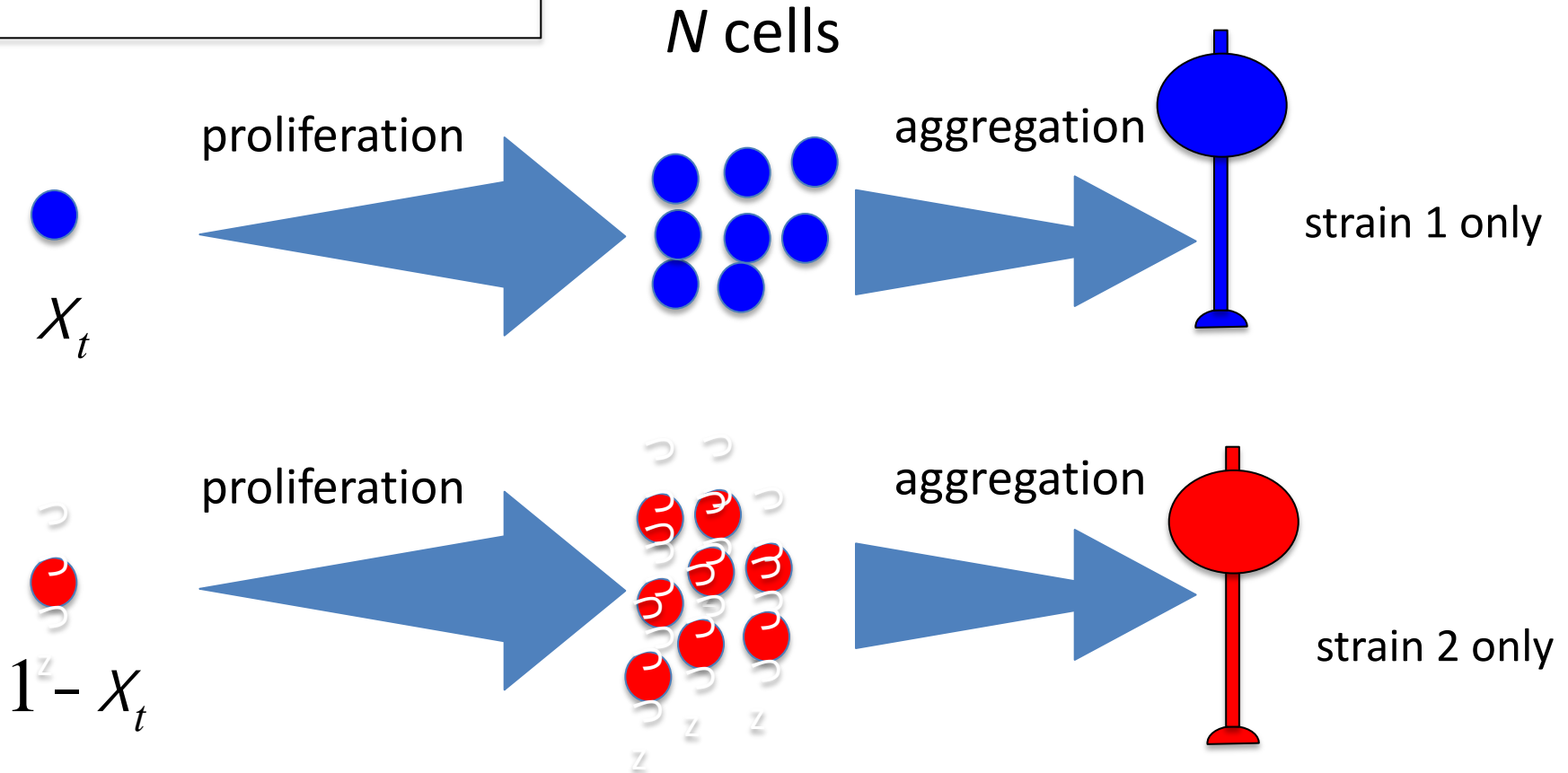
evolution of the **optimal stalk/spore ratio** that maximizes the number of successfully dispersed spores.

followed by a slow evolution toward **reduced DIF-1 production** and **enhanced sensitivity to DIF-1**

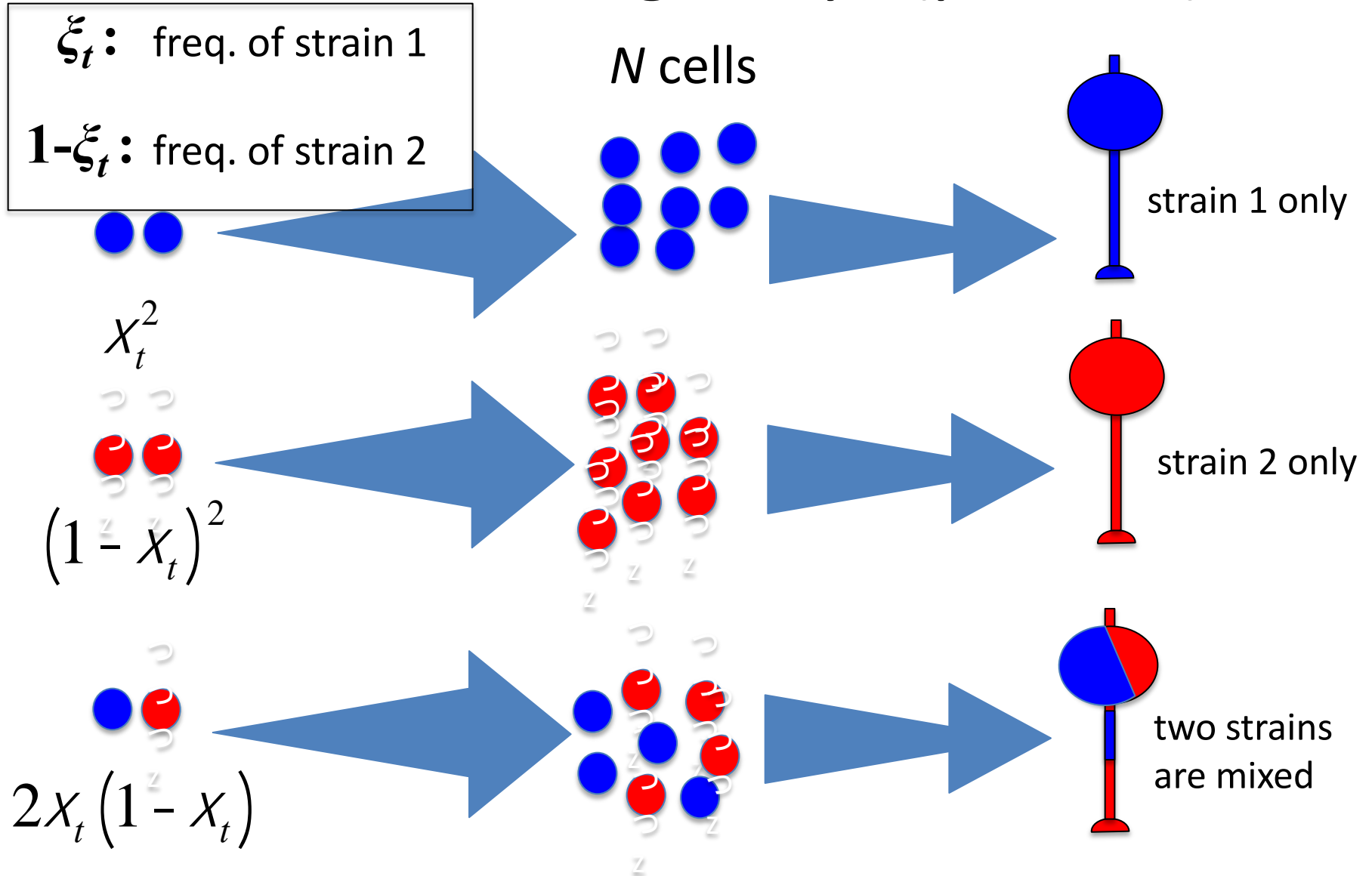
When some fruiting bodies are mixtures of multiple strains,

When cells originated from a single spore form a fruiting body (prob. $1-m$)

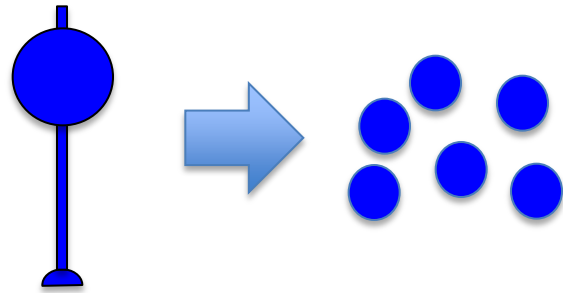
ξ_t : freq. of strain 1
 $1-\xi_t$: freq. of strain 2



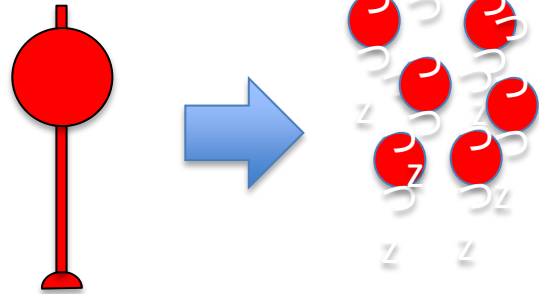
When cells originated from two spores form a fruiting body (prob. m)



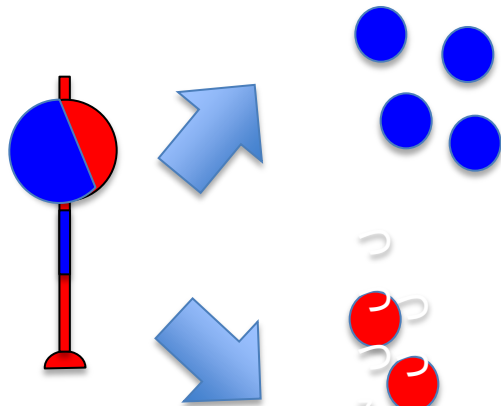
No. of spores from a fruiting body



$$W_1 = S(\hat{T}_1) \hat{P}_1 e^{-k a_1}$$



$$W_2 = S(\hat{T}_2) \hat{P}_2 e^{-k a_2}$$



$$W_1^{mix} = S(\hat{T}_1^* + \hat{T}_2^*) \hat{P}_1^{mix} e^{-k a_1}$$

$$W_2^{mix} = S(\hat{T}_1^* + \hat{T}_2^*) \hat{P}_2^{mix} e^{-k a_2}$$

No. of spores of strain 1

$$R_1 = \underbrace{\{(1-m)\xi + m\xi^2\}}_{\text{freq. of fruiting body of strain 1 only}} X_1 + \underbrace{\{2m\xi(1-\xi)\}}_{\text{freq. of fruiting body with both strains}} X_1^{mix}$$

freq. of fruiting body of strain 1 only

freq. of fruiting body with both strains

No. of spores of strain 2

$$R_2 = \underbrace{\{(1-m)(1-\xi) + m(1-\xi)^2\}}_{\text{freq. of fruiting body of strain 2 only}} X_2 + \underbrace{\{2m\xi(1-\xi)\}}_{\text{freq. of fruiting body with both strains}} X_2^{mix}$$

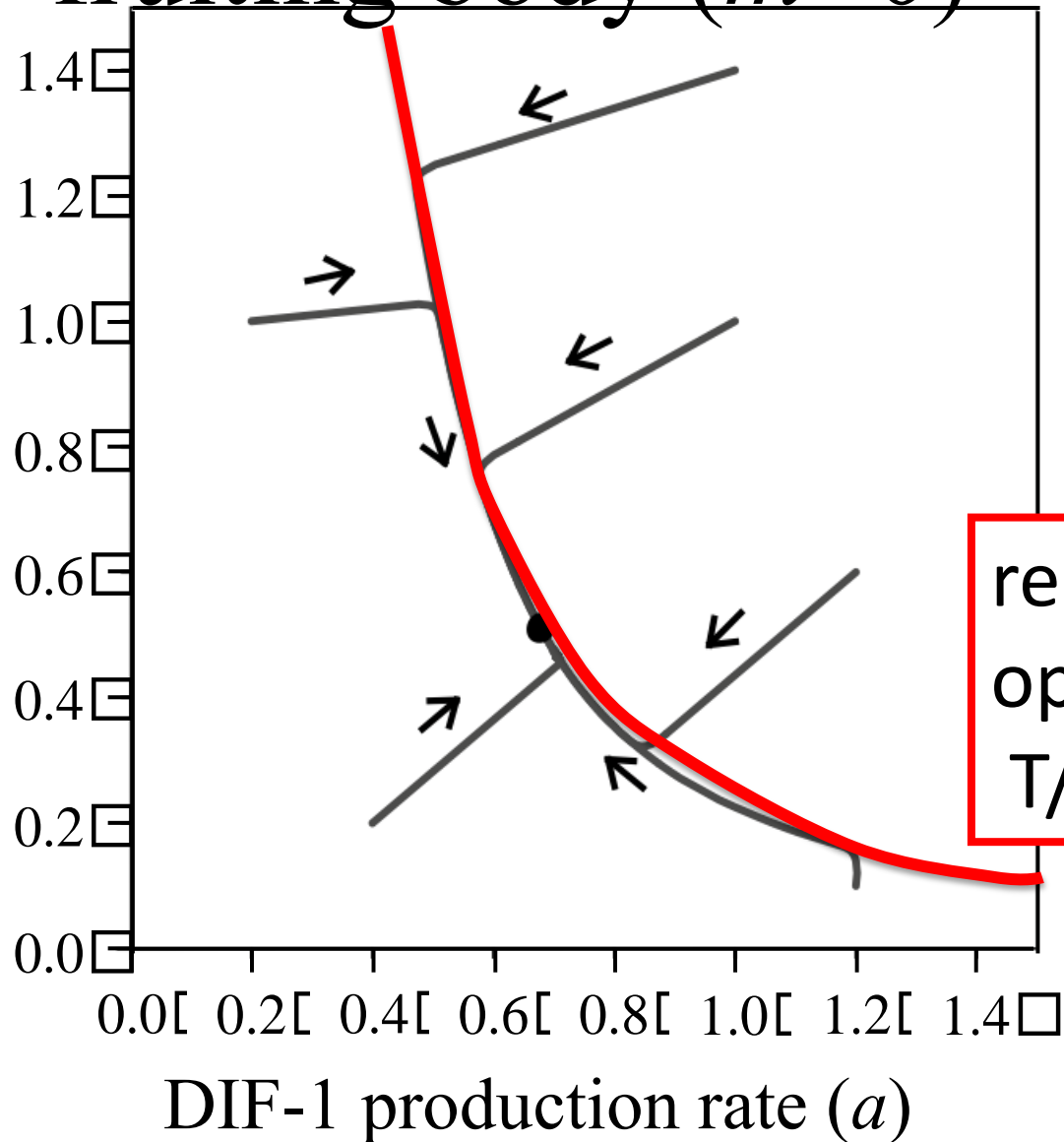
freq. of fruiting body of strain 2 only

freq. of fruiting body with both strains

$$\xi^{next} = \frac{R_1}{R_1 + R_2}$$

When two strains are mixed in a fruiting body ($m > 0$)

Sensitivity for DIF-1
differentiating
prespore cell to pre
stalk cell (f_0)



Selection gradients when cells of two strains can be mixed

Selection reducing DIF-1 production rate

$$\beta_a = \left(\frac{1}{S} \frac{dS}{dT} - \frac{1}{N-T} \right) \left\{ (1-m+m\xi) \frac{\partial T_1}{\partial a} + m(1-2\xi) \left(\frac{\partial T_1^*}{\partial a} + \frac{\partial T_2^*}{\partial a} \right) \right\} - k$$

$$\beta_{f_0} = \left(\frac{1}{S} \frac{dS}{dT} - \frac{1}{N-T} \right) \left\{ (1-m+m\xi) \frac{\partial T_1}{\partial f_0} + m(1-2\xi) \left(\frac{\partial T_1^*}{\partial f_0} + \frac{\partial T_2^*}{\partial f_0} \right) \right\} - \frac{2mN}{T(N-T)^2} \frac{1}{f_0}$$

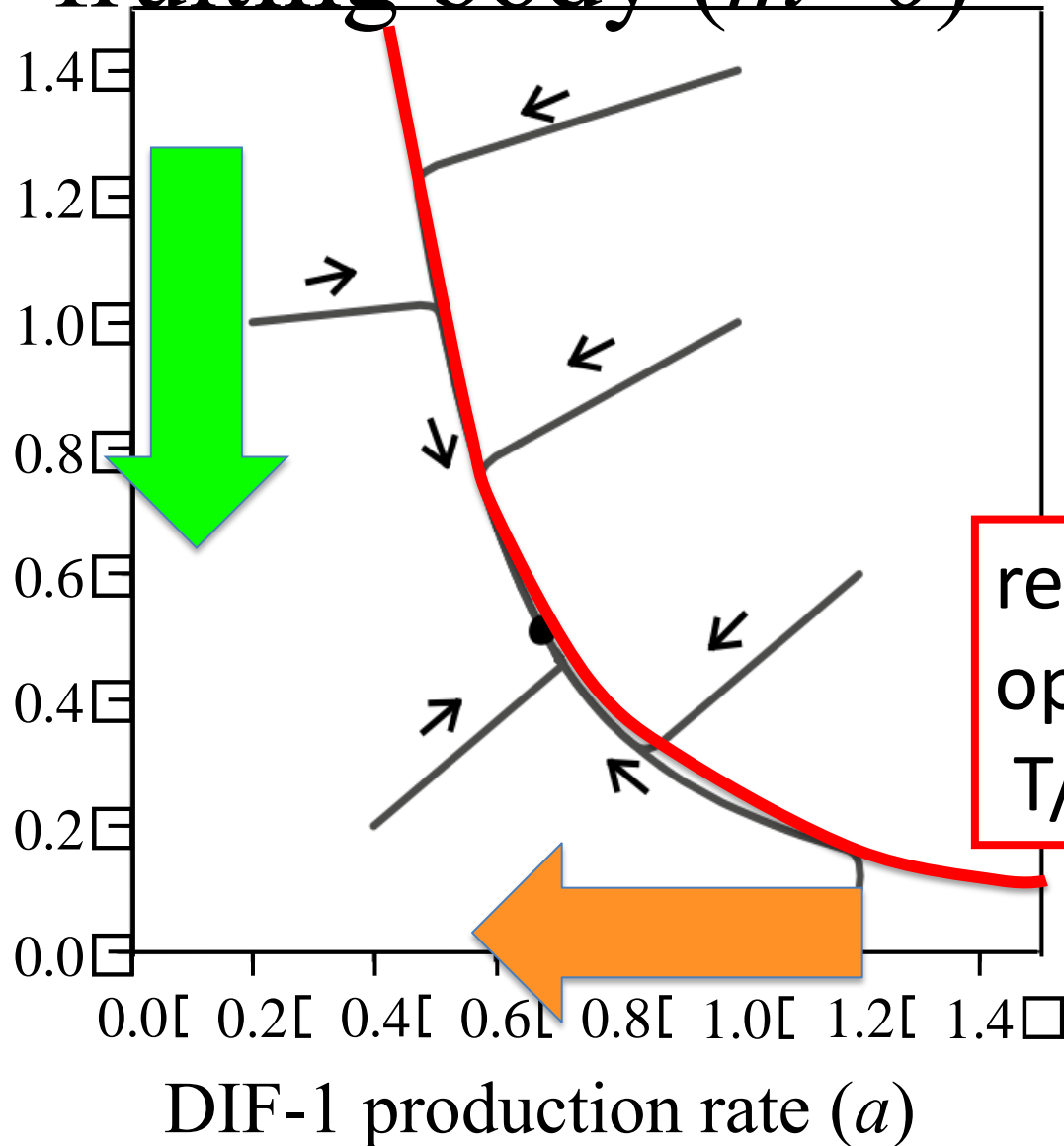
Selection realizing the optimal stalk size

Selection reducing sensitivity to DIF-1

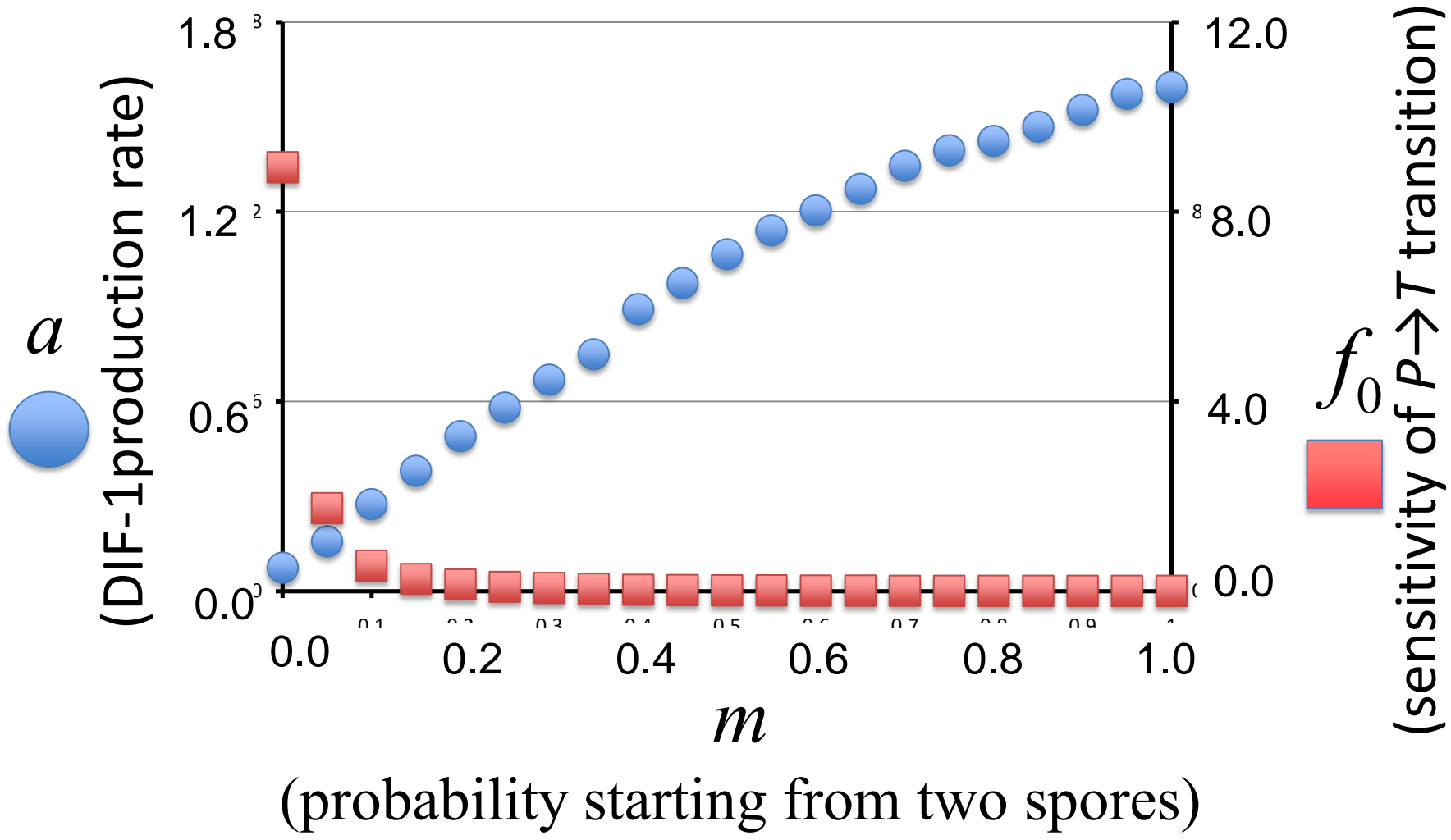
When two strains are mixed in a fruiting body ($m > 0$)

Sensitivity for DIF-1
differentiating

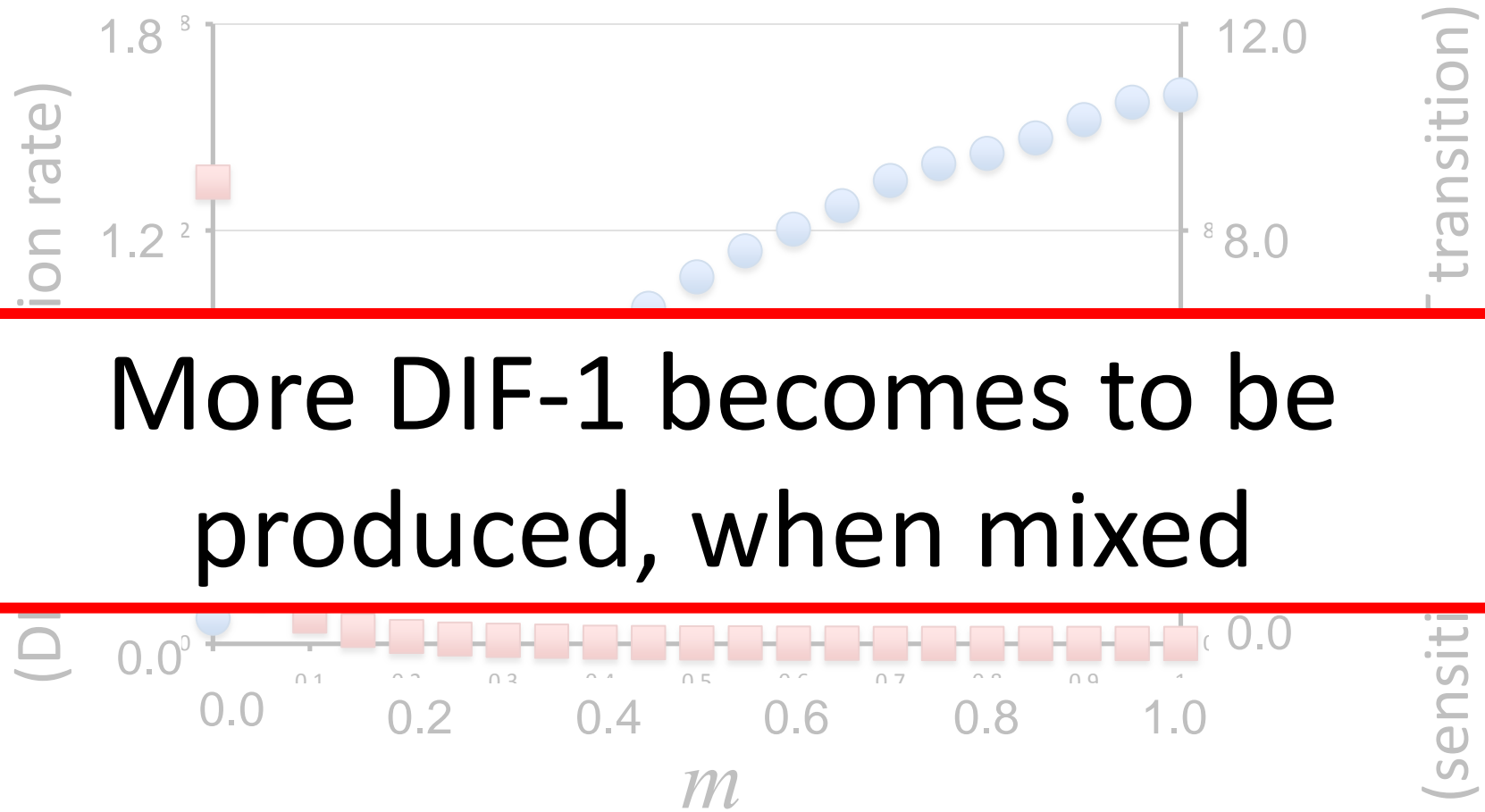
prespore cell to pre
stalk cell (f_0)



When two strains are mixed in a fruiting body ($m \neq 0$)



When two strains are mixed in a fruiting body ($m \neq 0$)



More DIF-1 becomes to be produced, when mixed

(probability starting from two spores)

Conclusion

- When not mixed, DIF-1 production evolves smaller with the optimal stalk/spore ratio maintained.
- When multiple strains are mixed, more DIF-1 will be produced.
- But the stalk/spore ratio remains close to the optimal.

ecology, behavior,
evolutionary biology

potential
phenotypes



the observed
phenotype

natural & sexual
selection,
random drift

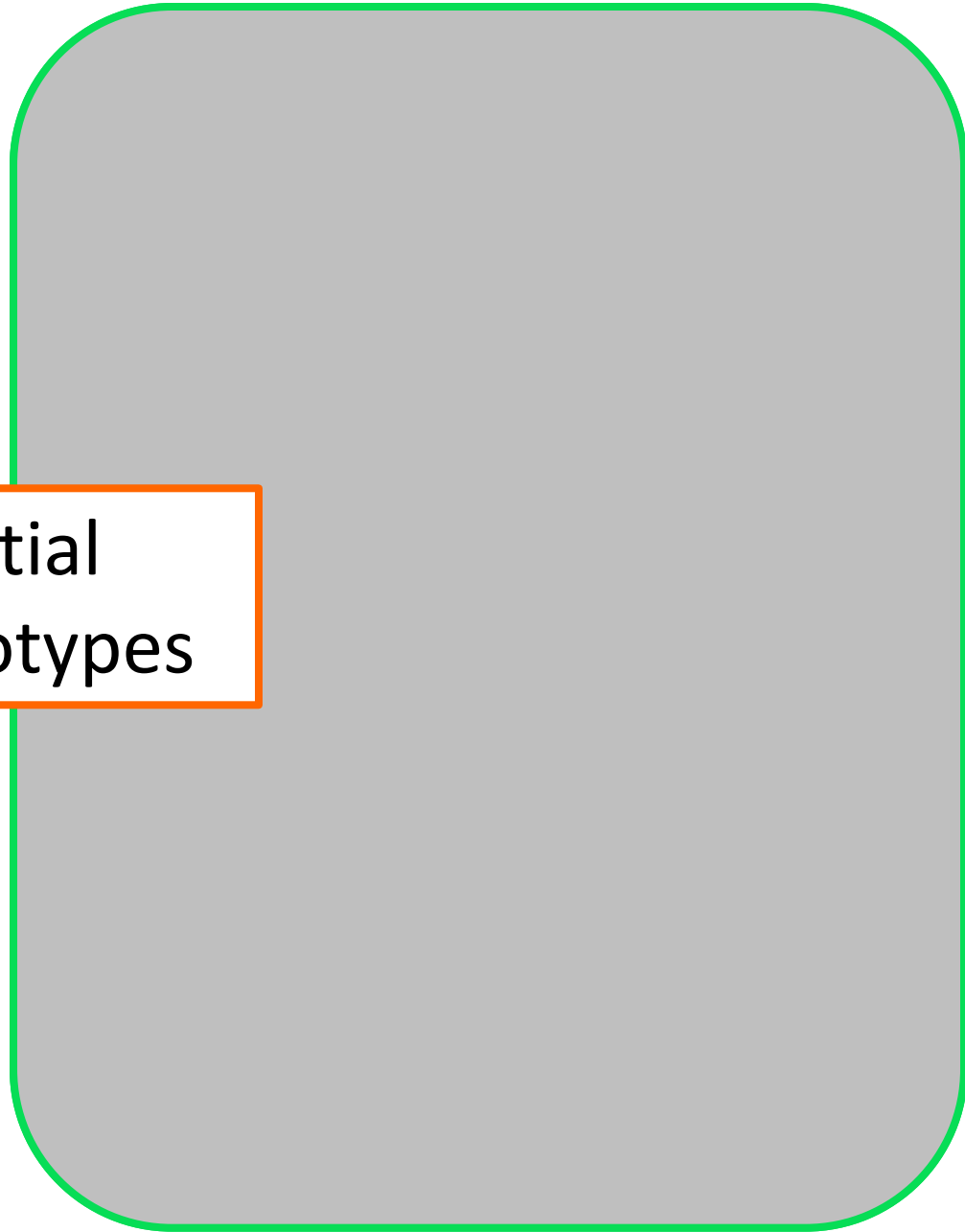
cellular &
molecular biology

genes,
proteins,
pathways



potential
phenotypes

development,
control,
regulation



cellular &
molecular biology

genes,
proteins,
pathways

development,
control,
regulation



potential
phenotypes

ecology, behavior,
evolutionary biology

the observed
phenotype



natural & sexual
selection,
random drift

When gene network / molecular mechanisms of the trait expression and social interactions are known, evolutionary models incorporating them may provide more useful/testable predictions.

Thank you.