ECO-EVOLUTIONARY FEEDBACK & *RUNAWAY* COOPERATION EVOLUTION

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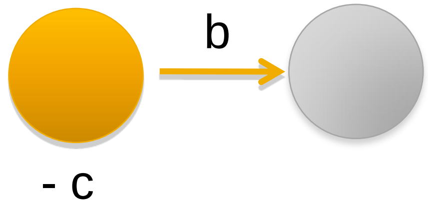
www.spectrosciences.com

Modeling social evolution

Fitness Model



Social partners can add or subtract **fitness** from one-another

Effects determined by payoff matrix

Dynamical Model

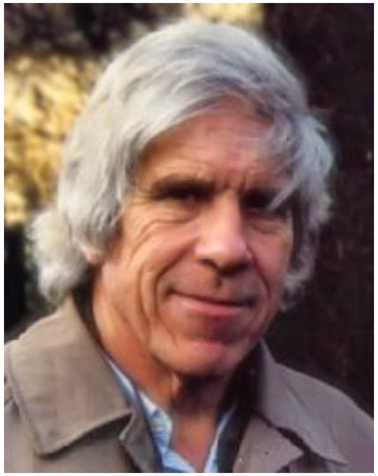
Toolbox

Classical population genetics
Inclusive fitness theory
Partial differentiation methods
Covariance methods (Price)
Branching processes
Replicator equation
etc.

→ Partition dynamics into within- and among-groups

Modeling social evolution

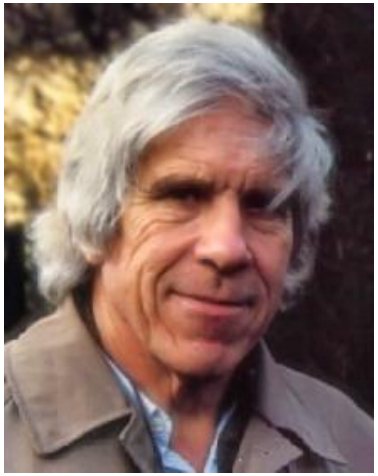
- Hamilton's Rule



$$B\rho - C > 0$$

Modeling social evolution

Hamilton's Rule



?

Where's the Ecology?

When should I build a nest and when should I provision resources?

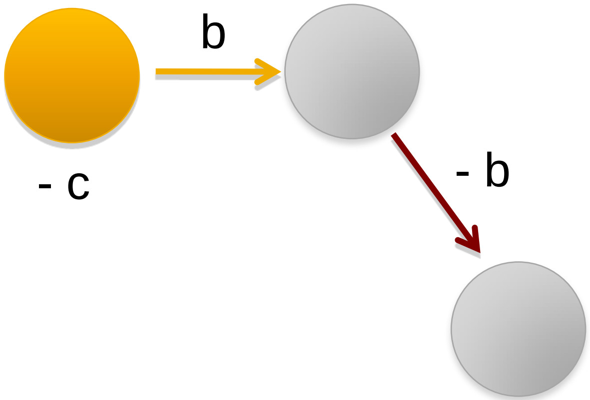
$$B\rho - C > 0$$

Degree of assortment: How much more likely are you to cooperate with an individual of your type than expected by chance?

Genetic relatedness (population structure)
Kin discrimination
Greenbeards
Repeated encounters
Conformity
Enforcement

Modeling social evolution

Fitness Model
with "Ecology"



$$\sum W_{ij} = C$$

Ecology is an external constraint: Density regulation makes cooperation a Zero-Sum Game

Local Competition Constrains Cooperation

Van Dyken 2010 *Evolution*

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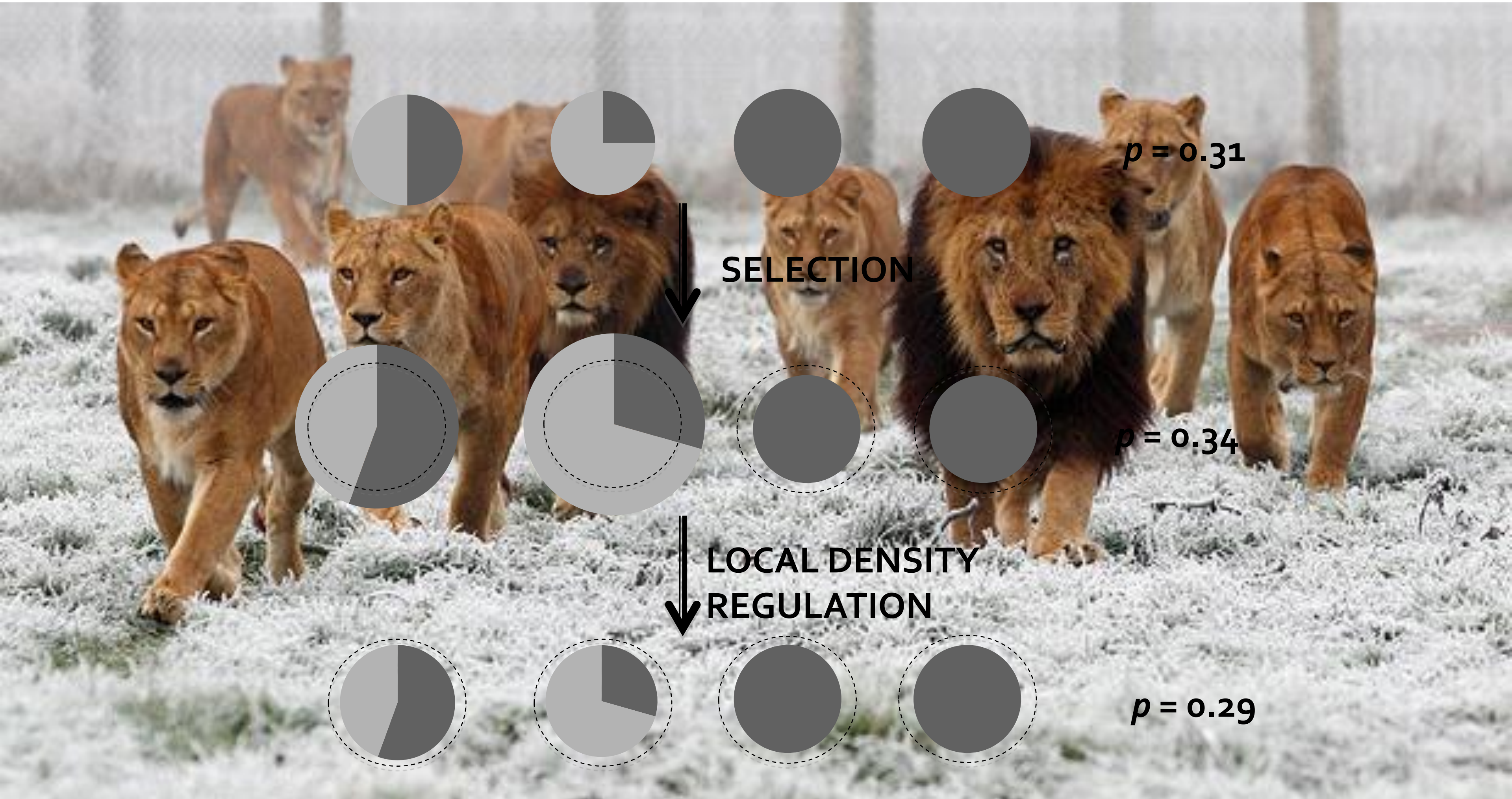
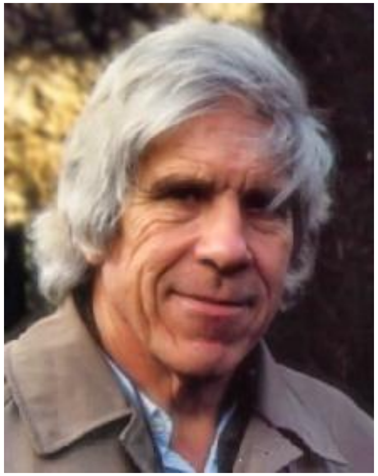
Local Competition Constrains Cooperation



Van Dyken 2010 *Evolution*

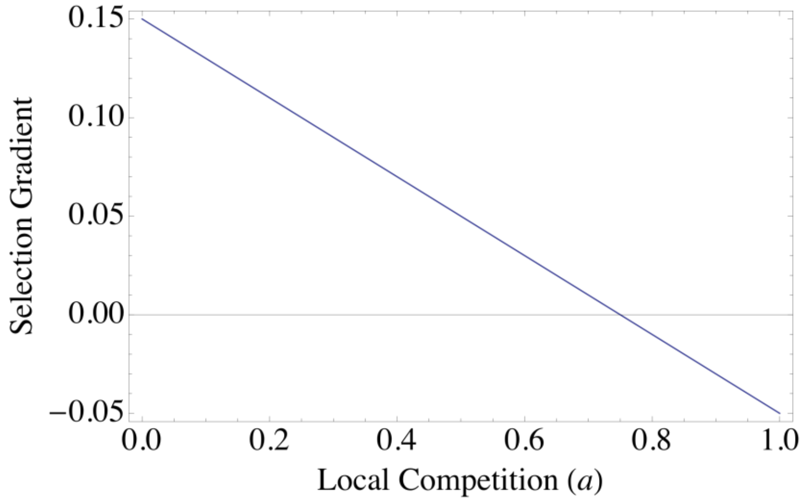
Modeling Social Evolution

Hamilton's Rule with Density Regulation



$$(1-a)br-(1-ar)c>0$$

Intensity of Local Competition



Local Competition inhibits cooperation

Problems with the Problem

But . . .

What does "local density regulation" mean?

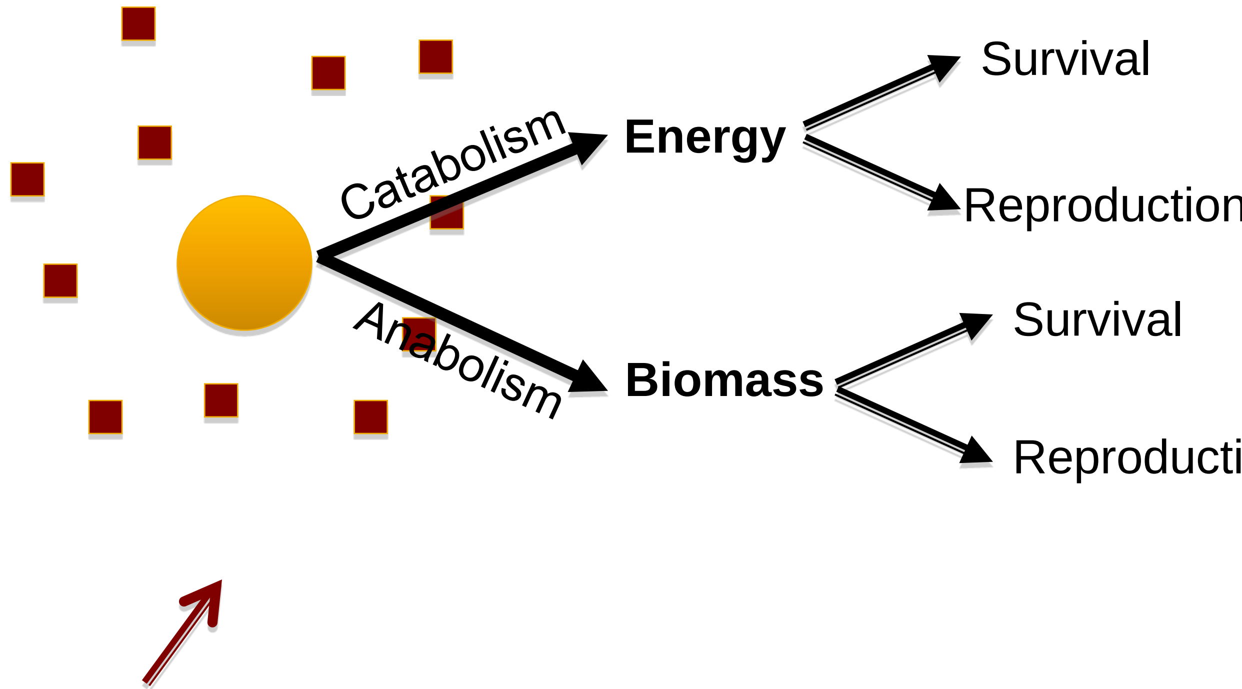
- Can we even measure it?
- Can we predict when it will occur?

Density regulation is a **consequence** of competition not its **cause**

What about cooperative traits that modify competition?

Solution: Start over from first principles

Mechanistic Fitness Model

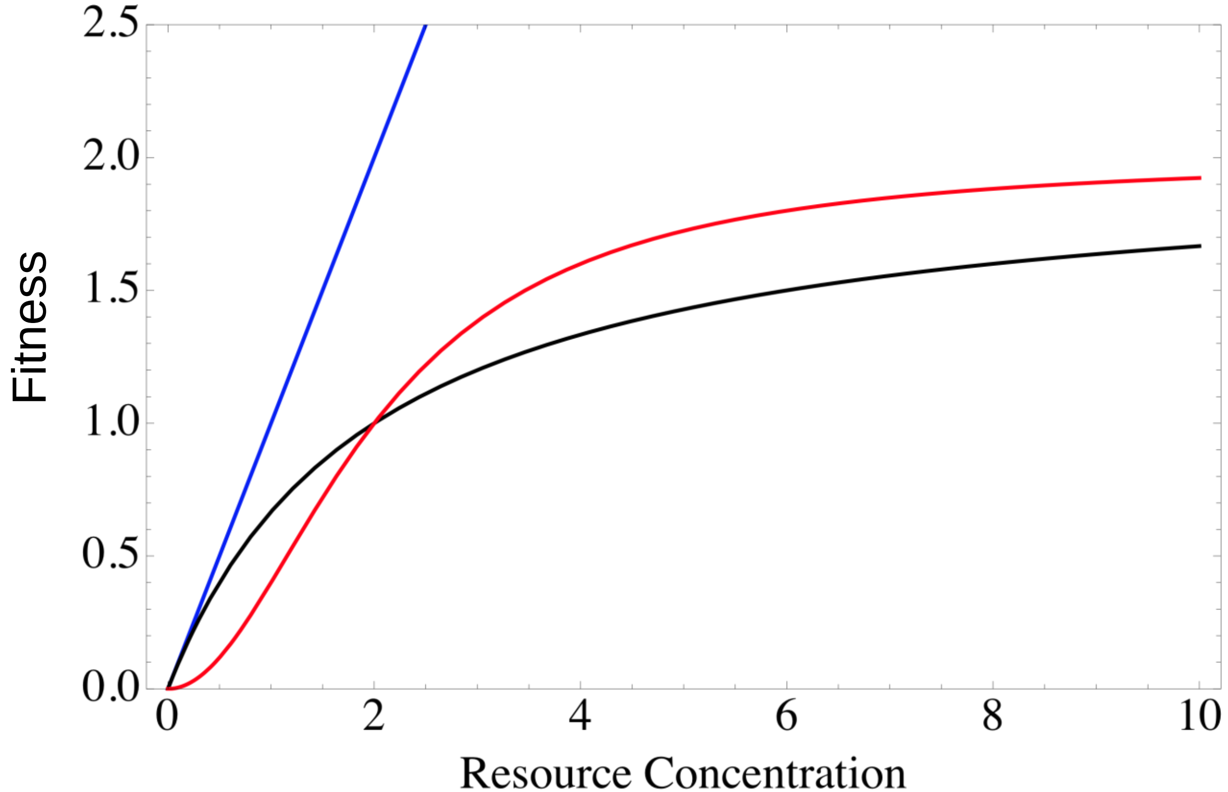


Sociality

Mechanistic Fitness Model

$$I + S \underset{k_2}{\overset{k_1}{\rightleftharpoons}} IS \xrightarrow{k_3} I + P$$

Individuals catalyze the conversion of **resources** into **offspring**

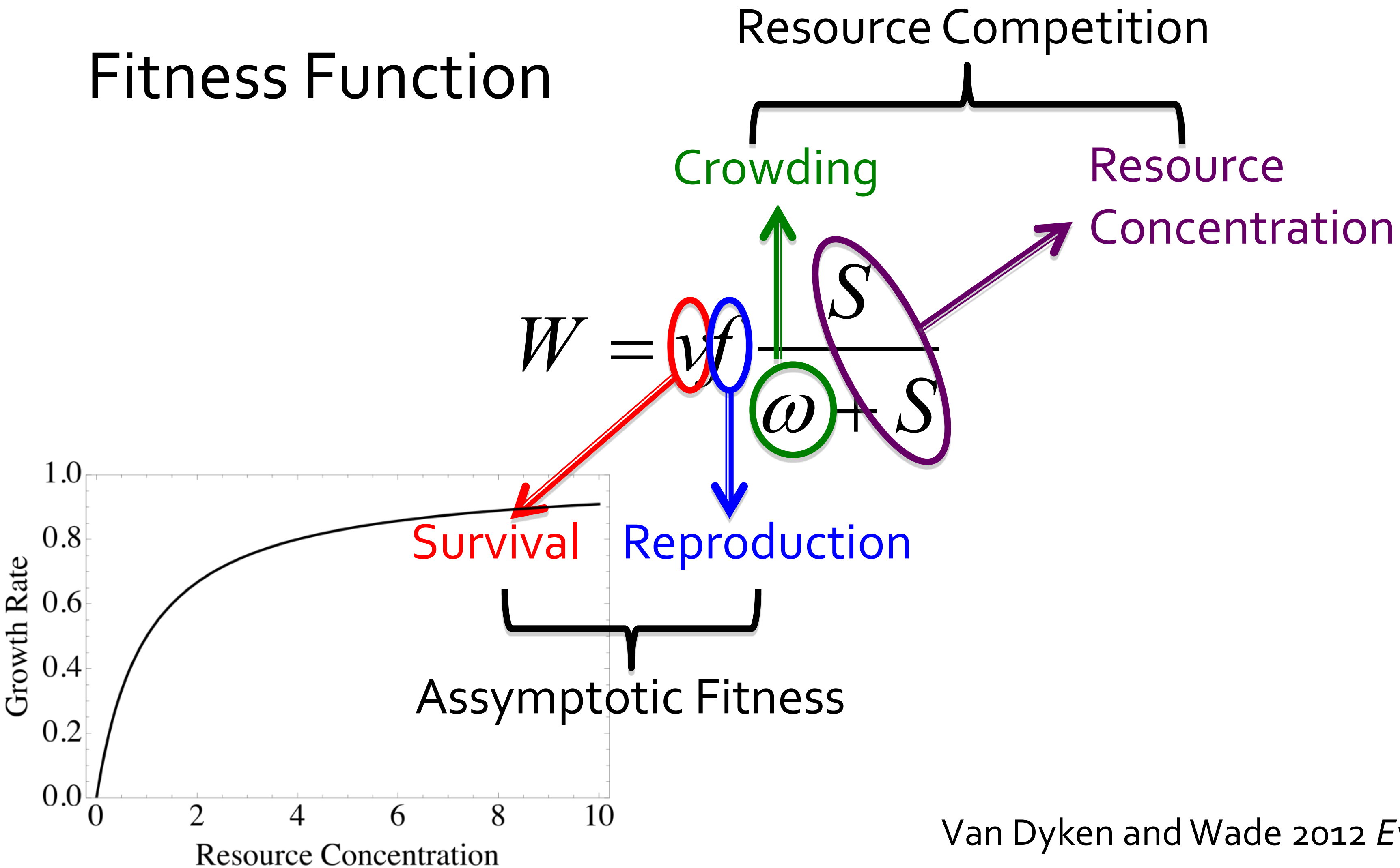


Type I
Type II
Type III

Mechanistic Fitness Model

Fitness Function

$$W = vf\frac{S}{\omega + S}$$



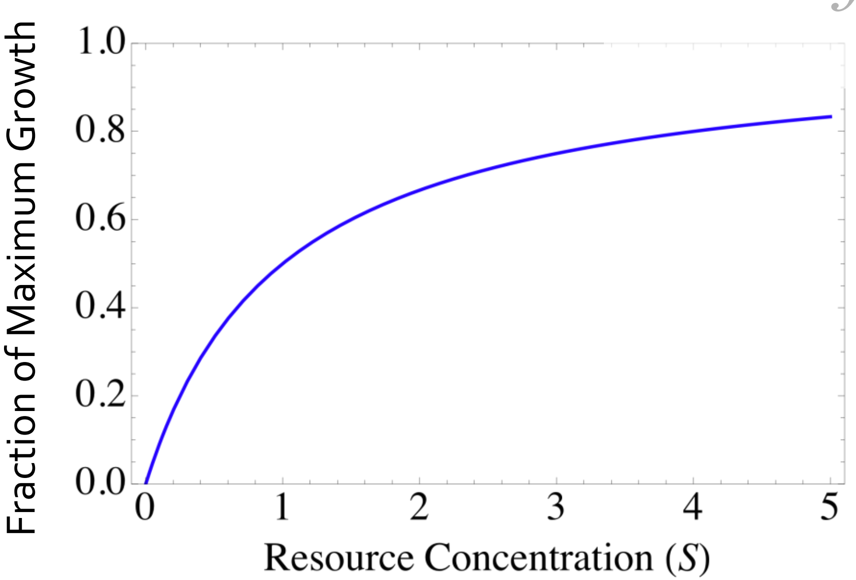
Van Dyken and Wade 2012 *Evolution*

Mechanistic Fitness Model

Fitness Function

$$W = vf \frac{S}{\omega + S}$$

Per capita resources and fitness decline as crowding increases



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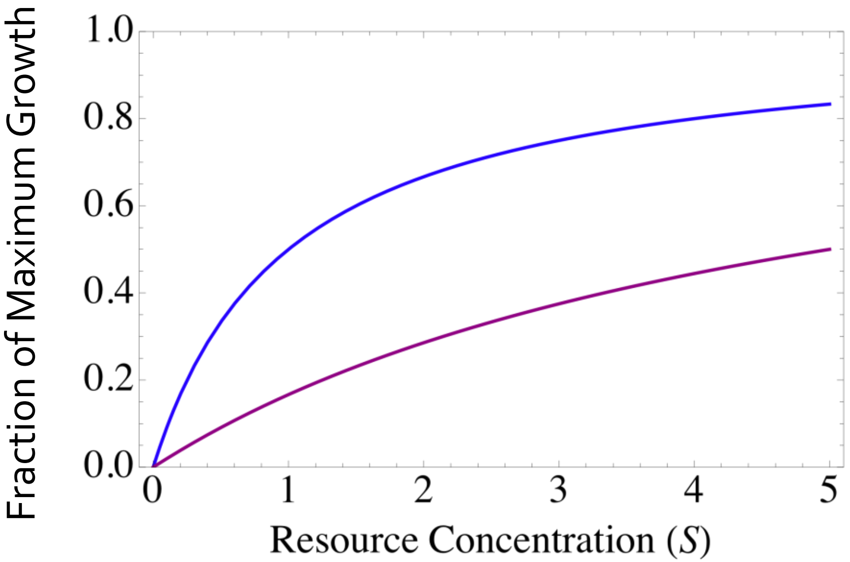

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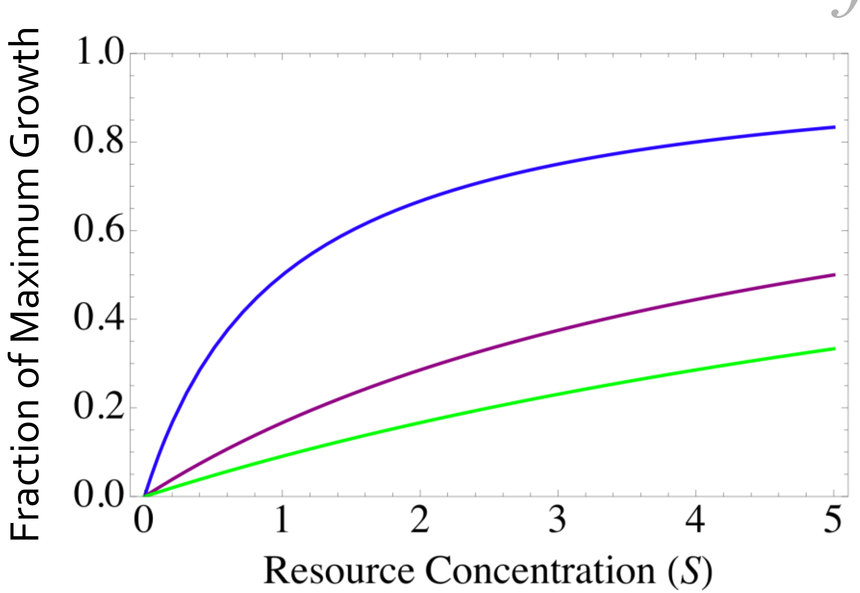

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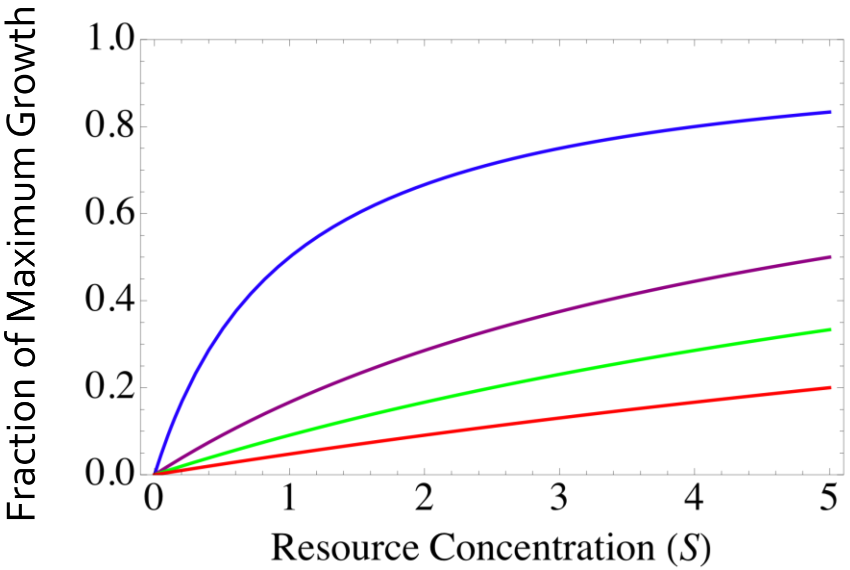

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Mechanistic Fitness Model

Fitness Function

$$W = vf\frac{S}{\omega + S}$$

Crowding and asymptotic fitness are correlated!

Greater Reproductive Output = Greater Crowding

Van Dyken and Wade 2012 *Evolution*

Modeling Cooperation

$$W = v f \frac{S}{\omega + S}$$

Survival Altruism




Modeling Cooperation

$$W = vf\frac{S}{\omega + S}$$

Fecundity Altruism

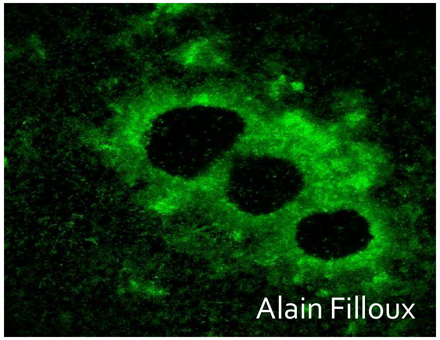
Allocation of Viability gains to Reproduction

Modeling Cooperation

$$W = vf \frac{S}{\omega + S}$$

Resource-Supply Altruism

Provisioning



Agriculture

Modeling Cooperation

$$W = vf\frac{S}{\omega + S}$$

Pack Hunting

Resource-Efficiency Altruism

$$S = \frac{S_{Total}}{NK_S}$$

Modeling Cooperation

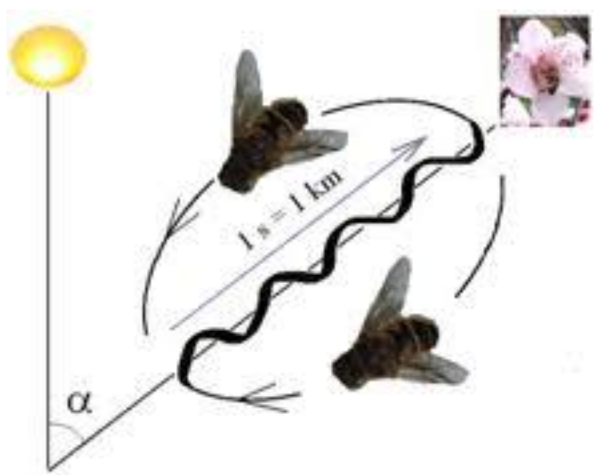
$$W = vf\frac{S}{\omega + S}$$

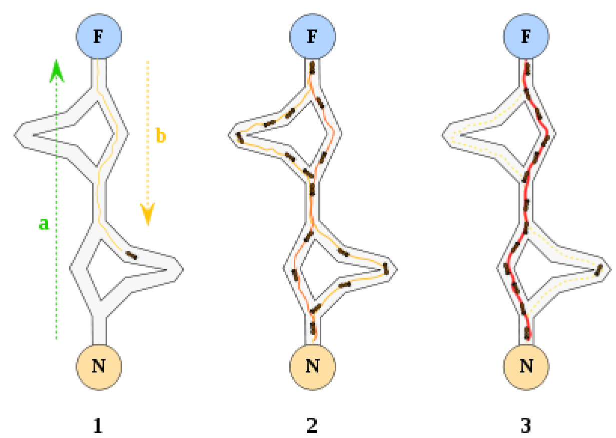
Resource-Efficiency

Altruism

$$S = \frac{S_{Total}}{NK_S}$$

Communication





http://lifeinwireframe.blogspot.com/2010/08/ant-algoithms.html

Modes of Cooperation

Instead of 2 ways to cooperate, we identify at least 4

- Survival Altruism
- Fecundity Altruism
- Resource-Supply Altruism
- Resource-Efficiency Altruism

Survival/Fecundity Altruism (Survival Altruism, Fecundity Altruism)

Resource Altruism (Resource-Supply Altruism, Resource-Efficiency Altruism)

Each has its own "Hamilton's Rule" and responds to resource competition in unique ways

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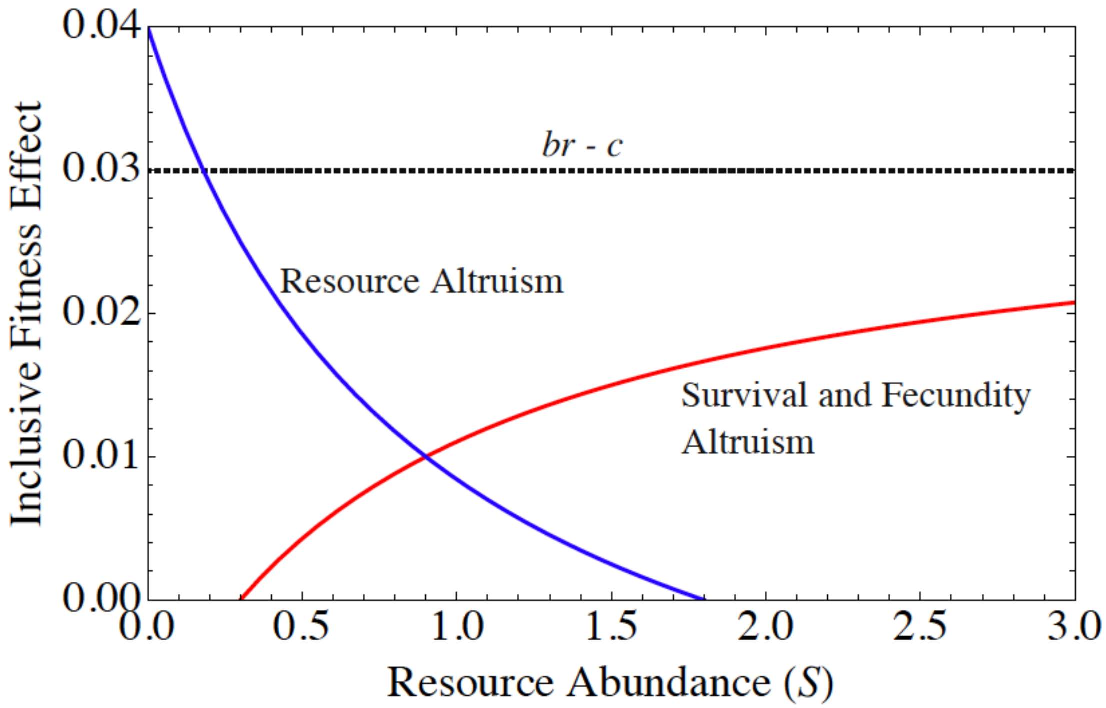
Evolution of Altruism Types



Resource Altruism ***requires*** **local competition!**

Survival/Fecundity Altruism

$$(1-a)br - c(1-ar) > 0$$

Resource Altruism

$$abr - c(1-ar) > 0$$

Intensity of Local Competition

$$a = \frac{\omega}{\omega + S}$$

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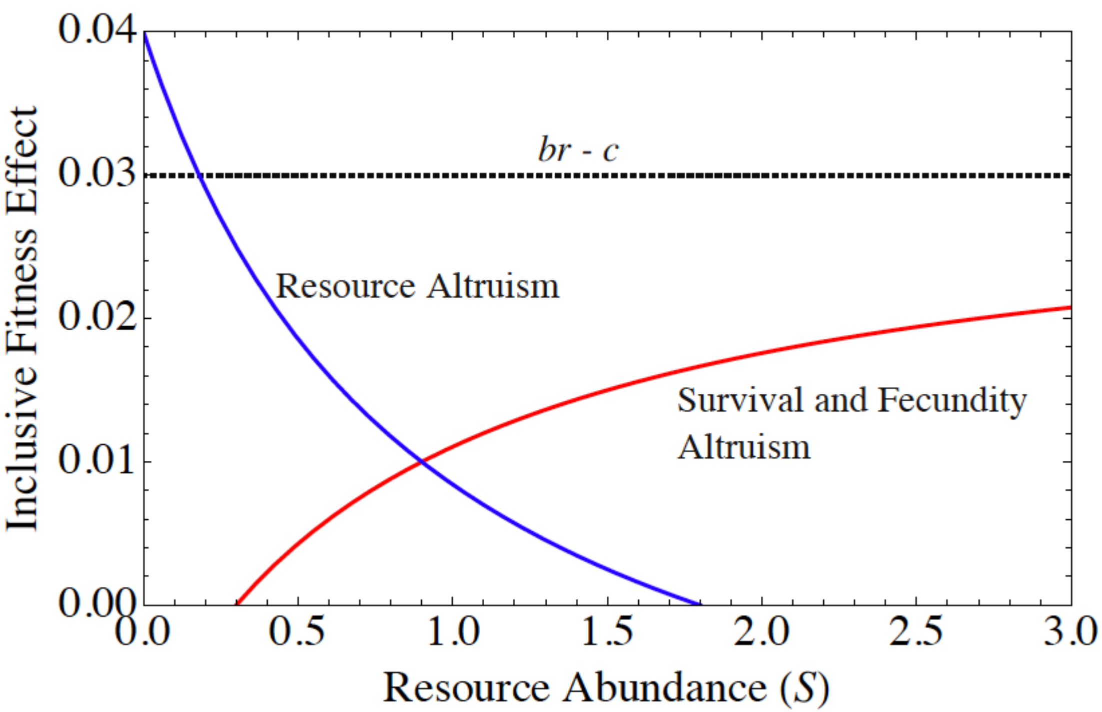

Survival/Fecundity Altruism

$$(1-a)br - c(1-ar) > 0$$

Resource Altruism

$$abr - c(1-ar) > 0$$

Intensity of Local Competition

$$a = \frac{\omega}{\omega + S}$$

Resource Altruism and Survival/Fecundity Altruism have complementary responses to resource pressure

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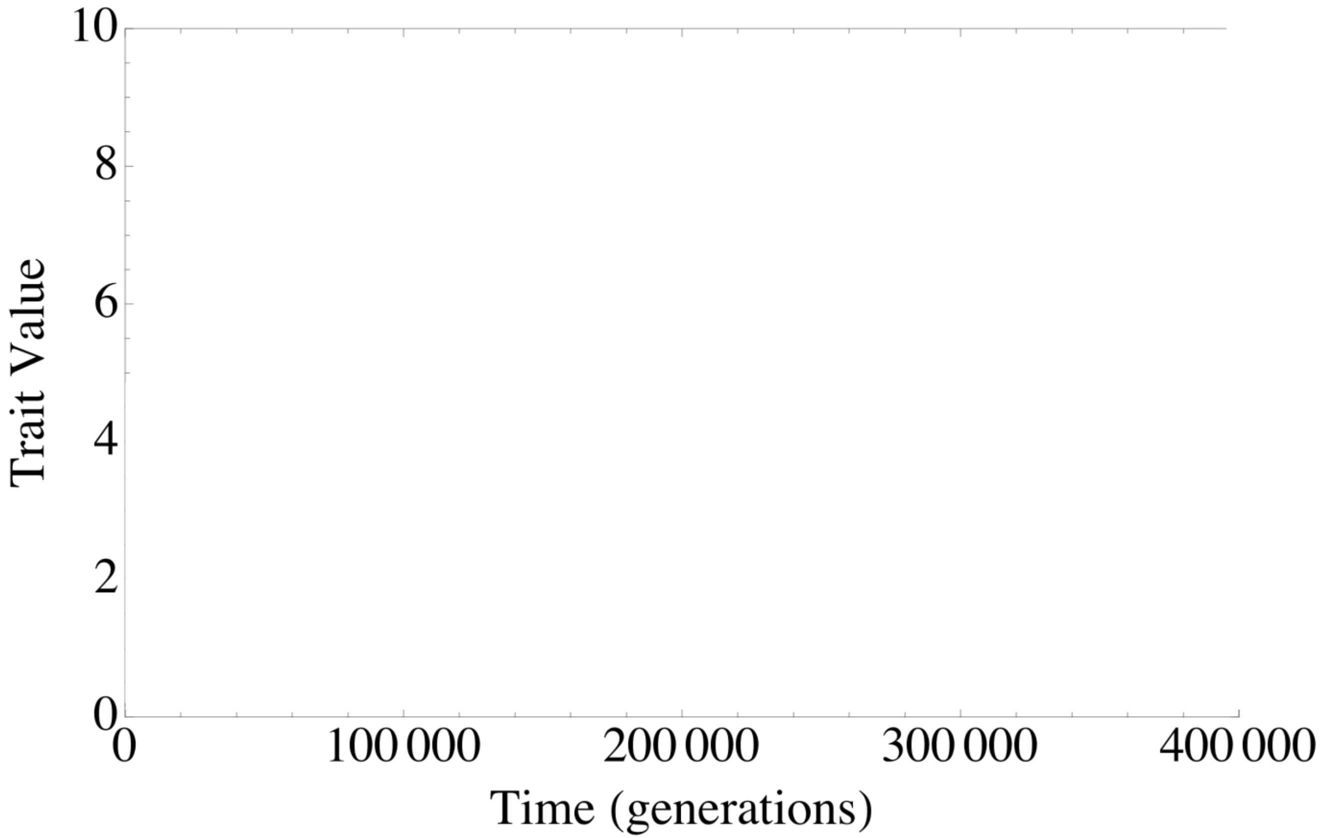
Long Term Evolution

Numerical Simulations with Recurrent Beneficial Mutations



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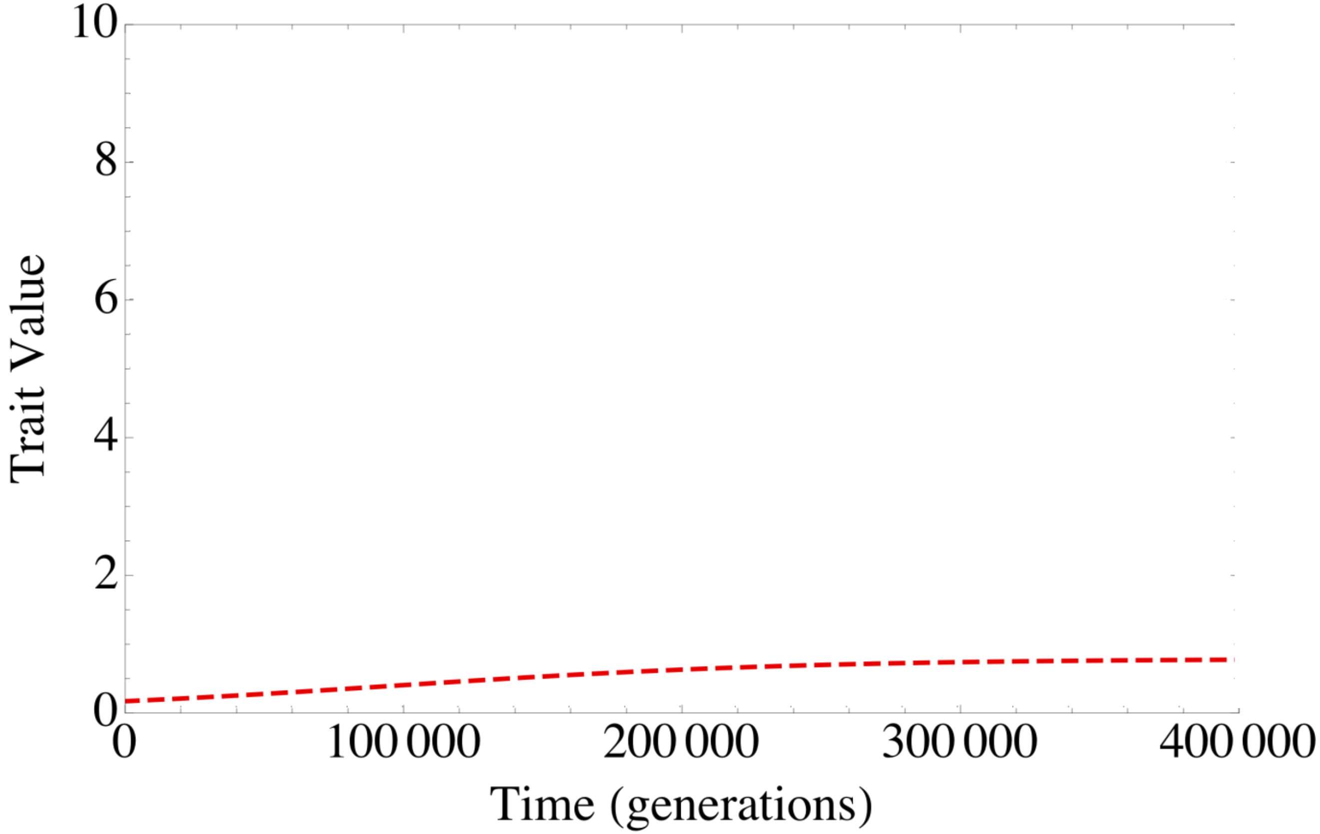

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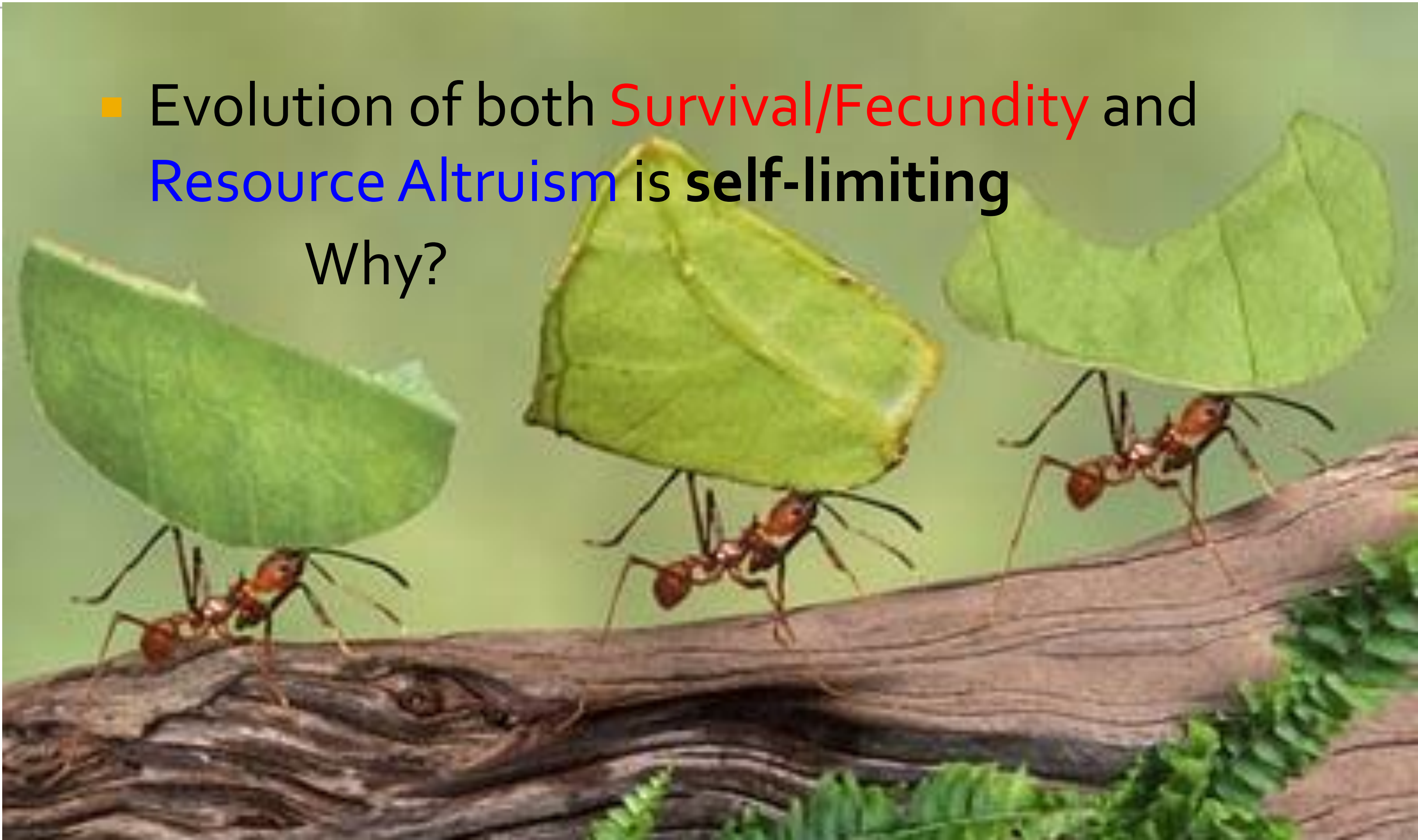
Long Term Evolution

- Evolution of both Survival/Fecundity and Resource Altruism is **self-limiting**

  Why?



Long Term Evolution

- Evolution of both Survival/Fecundity and Resource Altruism is **self-limiting**

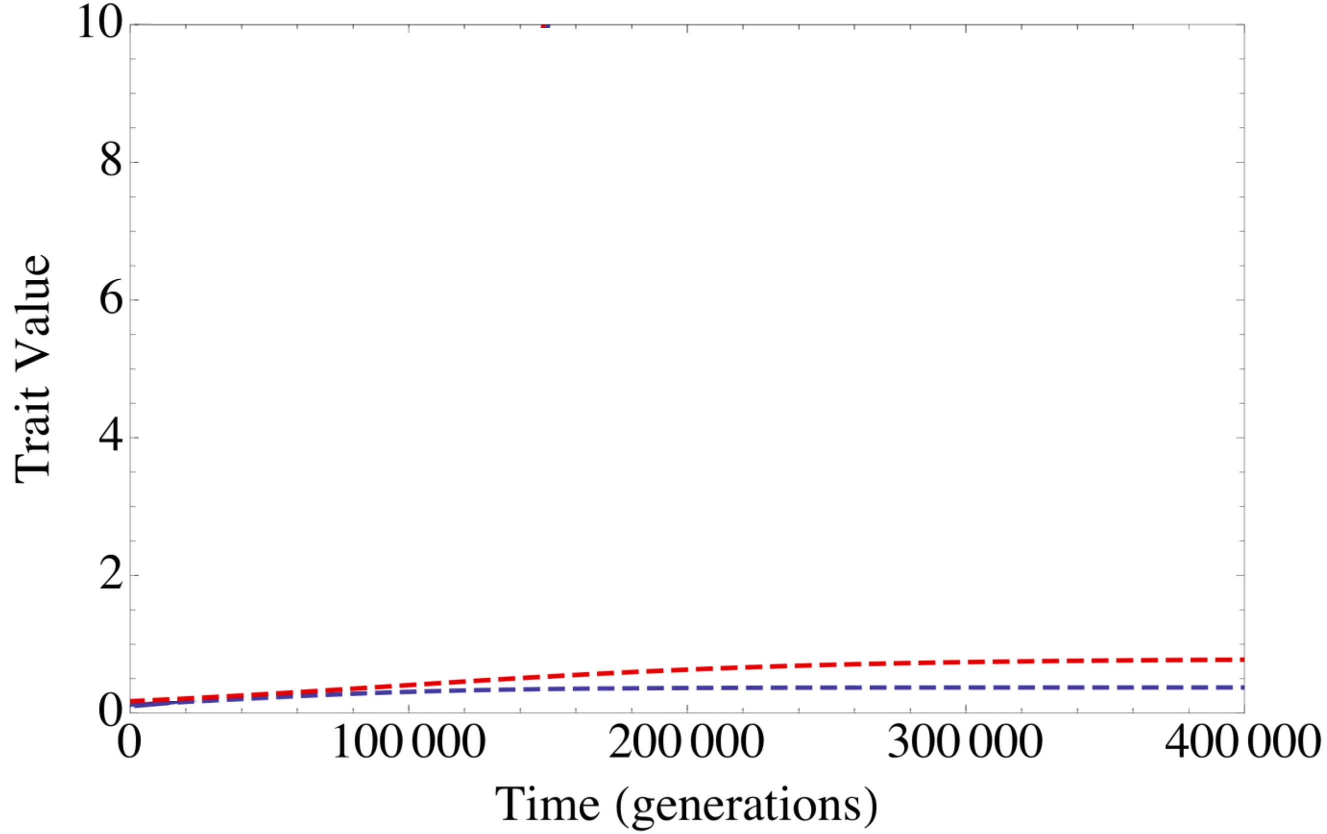
  Why?

- Because each alters the environment in a way that weakens its own selection
  - Survival/Fecundity Altruism **increases** local competition
  - Resource Altruism **reduces** local competition

Could these traits complement one another?

Long Term Evolution

Numerical Simulations with Recurrent Beneficial Mutations



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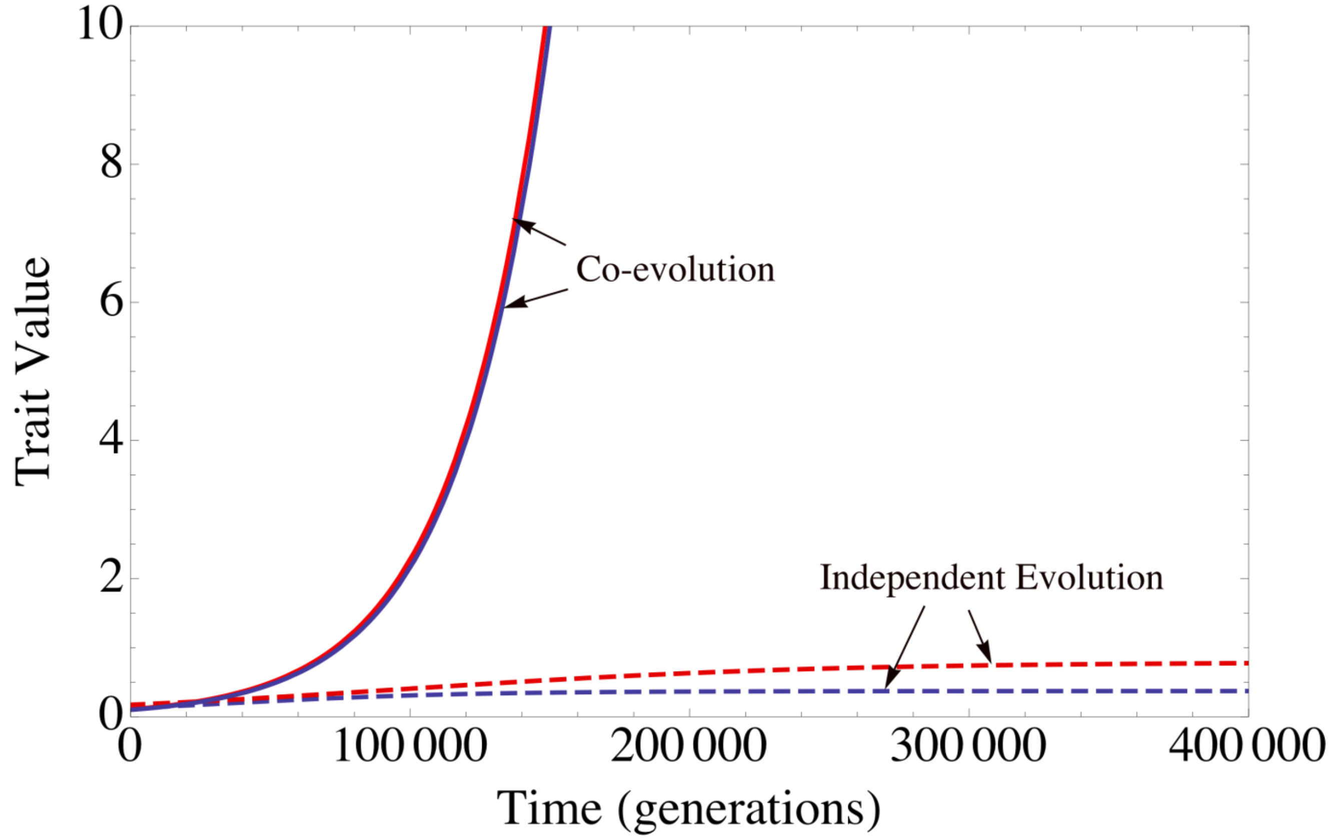

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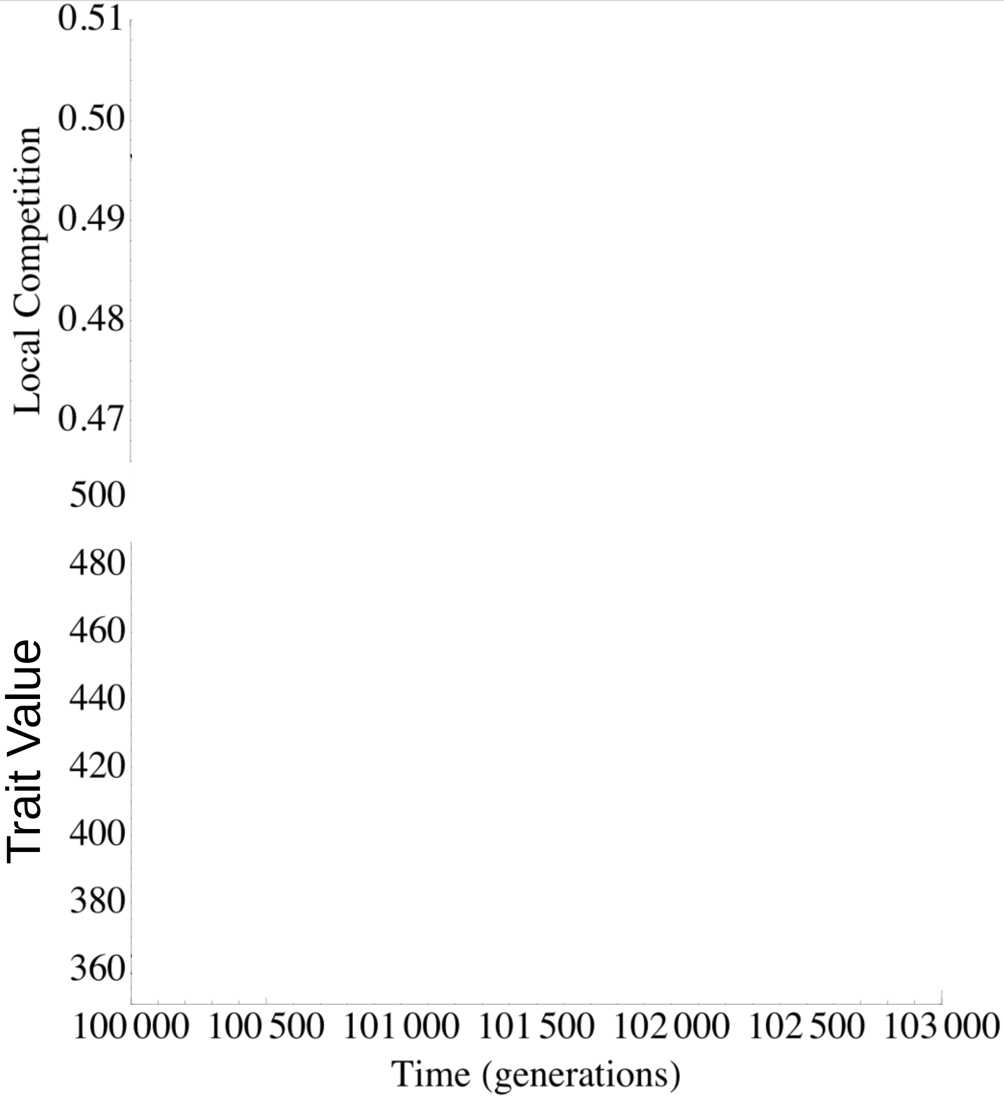
Reciprocal Niche-Construction

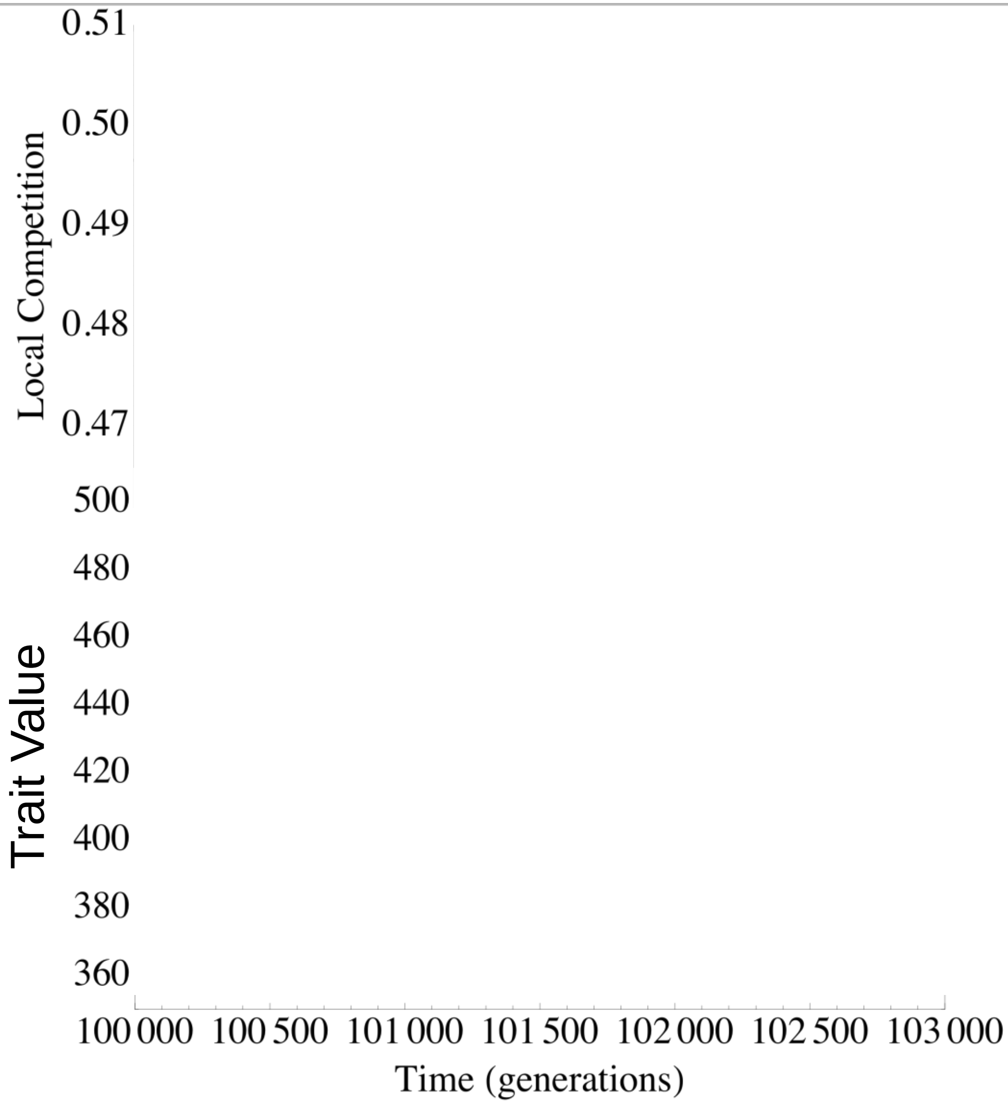
Provisioning



Defense

Reciprocal Niche-Construction

Provisioning



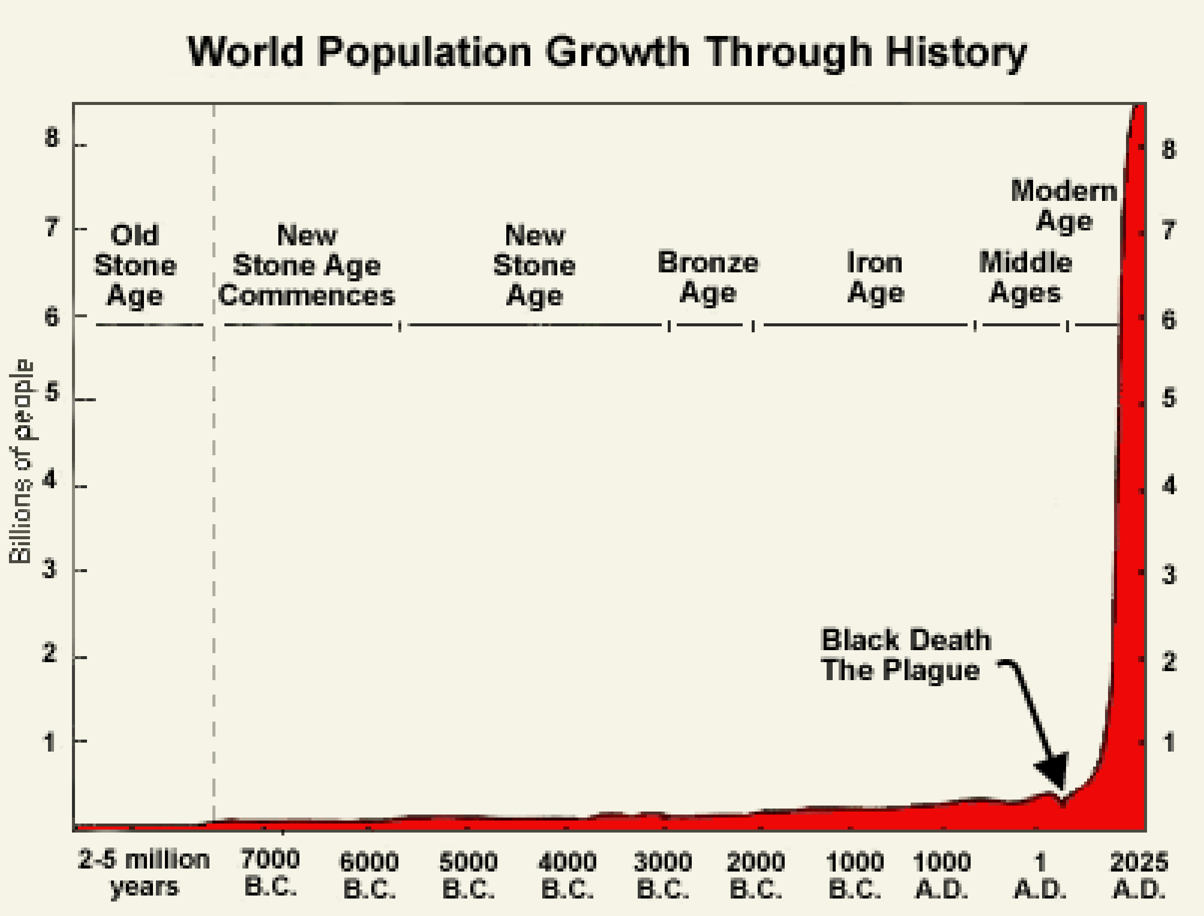
Defense

Extreme Sociality in Nature

Eusocial Hymenoptera, termites and humans each posses all 4 altruism types

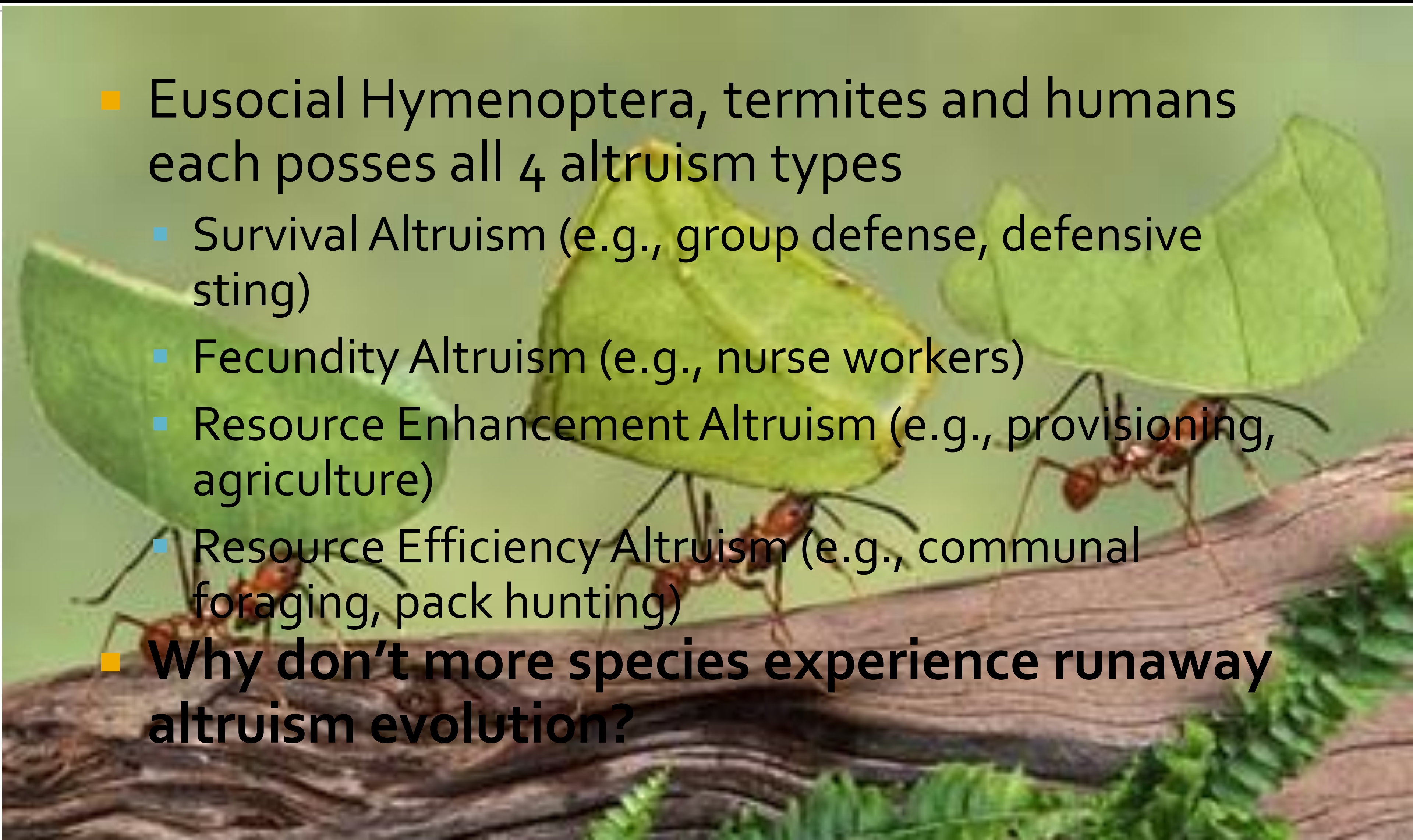
- Survival Altruism (e.g., group defense)
- Fecundity Altruism (e.g., nurse workers, nurses)
- Resource Enhancement Altruism (e.g., provisioning, agriculture)
- Resource Efficiency Altruism (e.g., communal foraging, pack hunting)

Reciprocal Niche-Construction and Runaway Co-Evolution in Humans



SavingtheEarth.net

Extreme Sociality in Nature



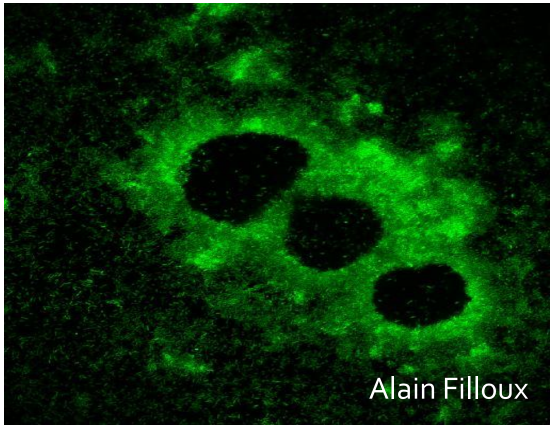
- Eusocial Hymenoptera, termites and humans each posses all 4 altruism types
  - Survival Altruism (e.g., group defense, defensive sting)
  - Fecundity Altruism (e.g., nurse workers)
  - Resource Enhancement Altruism (e.g., provisioning, agriculture)
  - Resource Efficiency Altruism (e.g., communal foraging, pack hunting)
- **Why don't more species experience runaway altruism evolution?**

Constraints on Runaway Altruism Co-Evolution

Availability of beneficial mutations

Limits on Resource Enhancement

- Provisioning is limited by availability of nearby resources



Constraints on Runaway Altruism Co-Evolution

Availability of beneficial mutations

Limits on Resource Enhancement

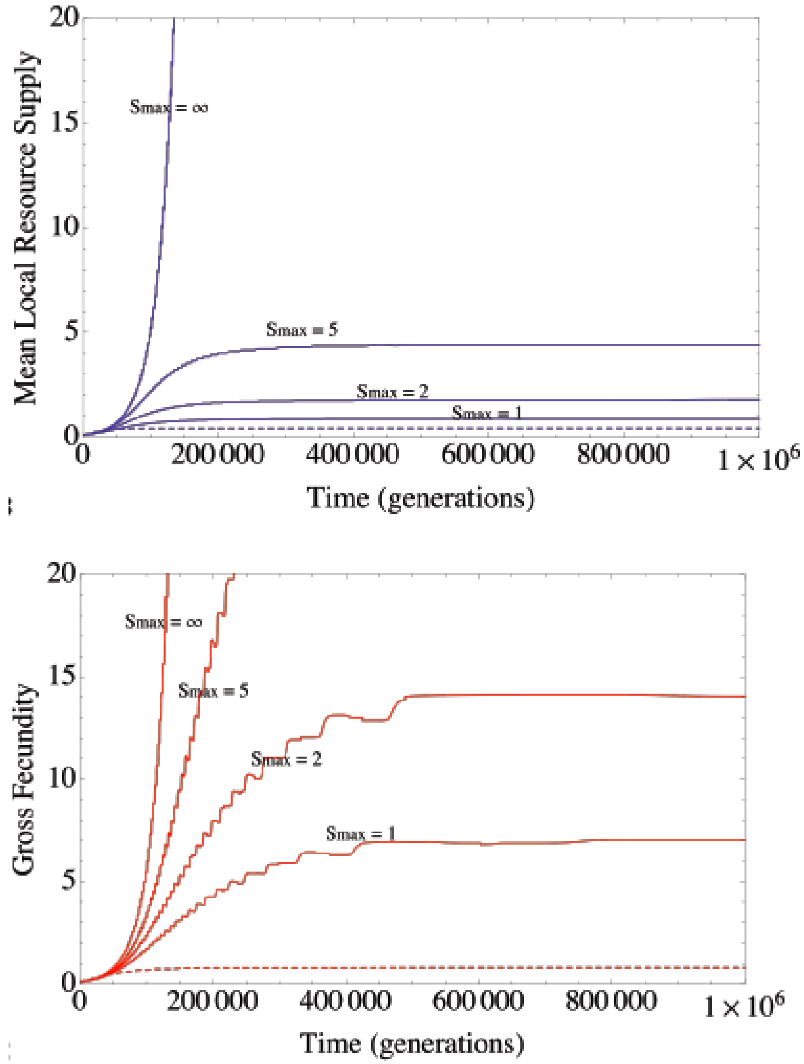
- Provisioning is limited by availability of nearby resources
- Agriculture is limited by water, nutrients, space, and increased pressure from other resource types

Agriculture

Crowding

Depleted Game Supply

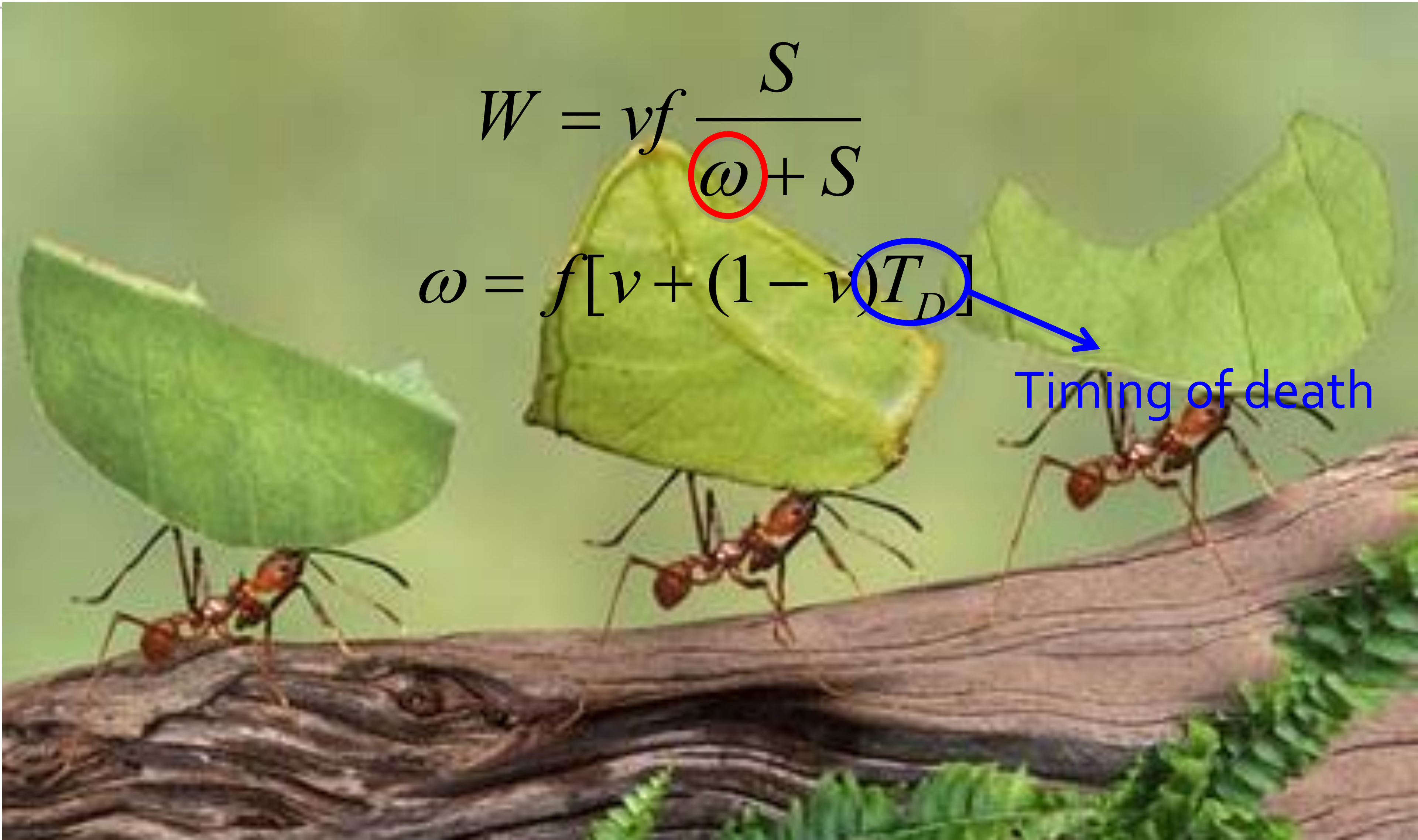
Constraints on Runaway Altruism Supply Co-Evolution



Timing of Death

$$W = vf\frac{S}{\omega + S}$$

$$\omega = f[v + (1 - v)T_D]$$



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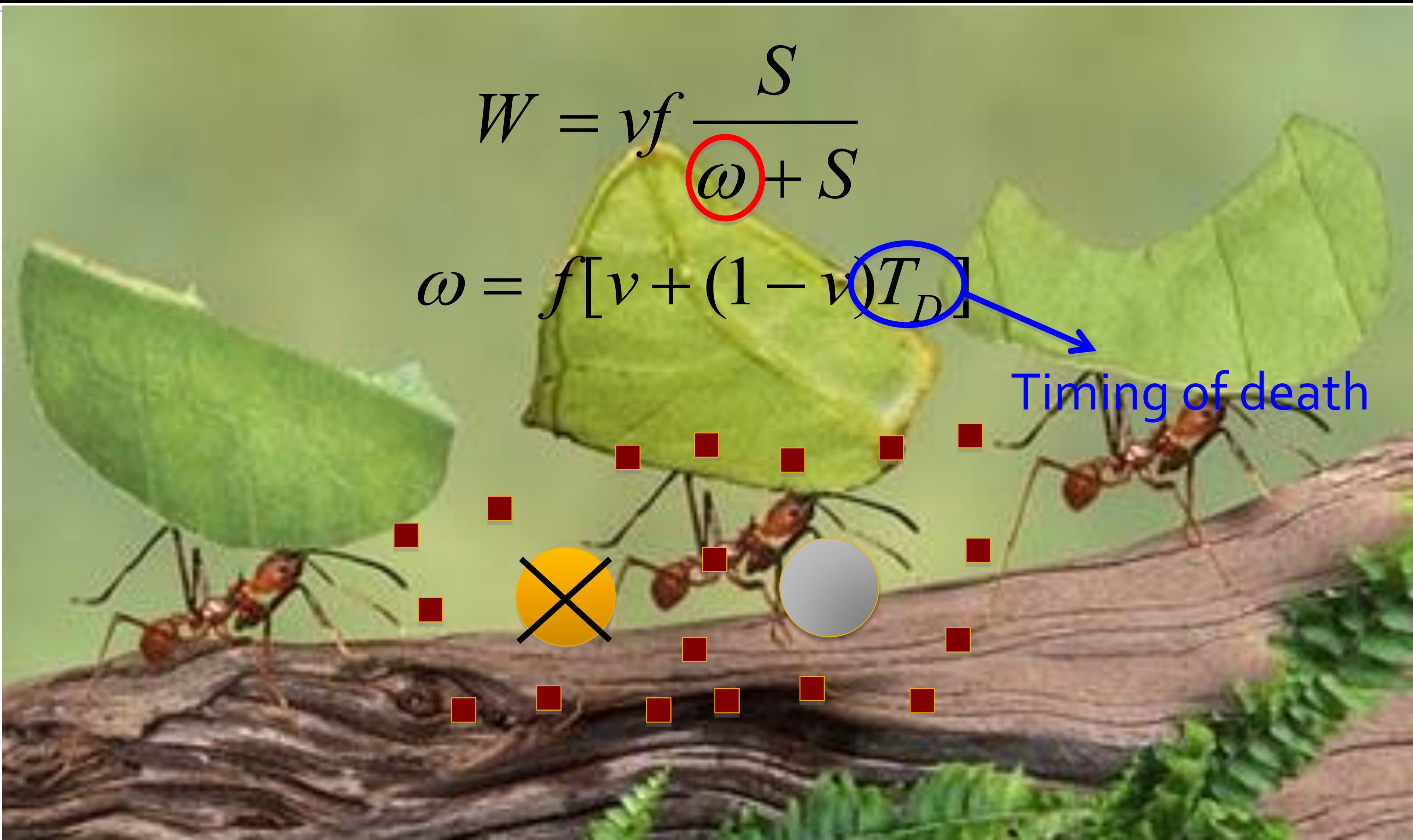

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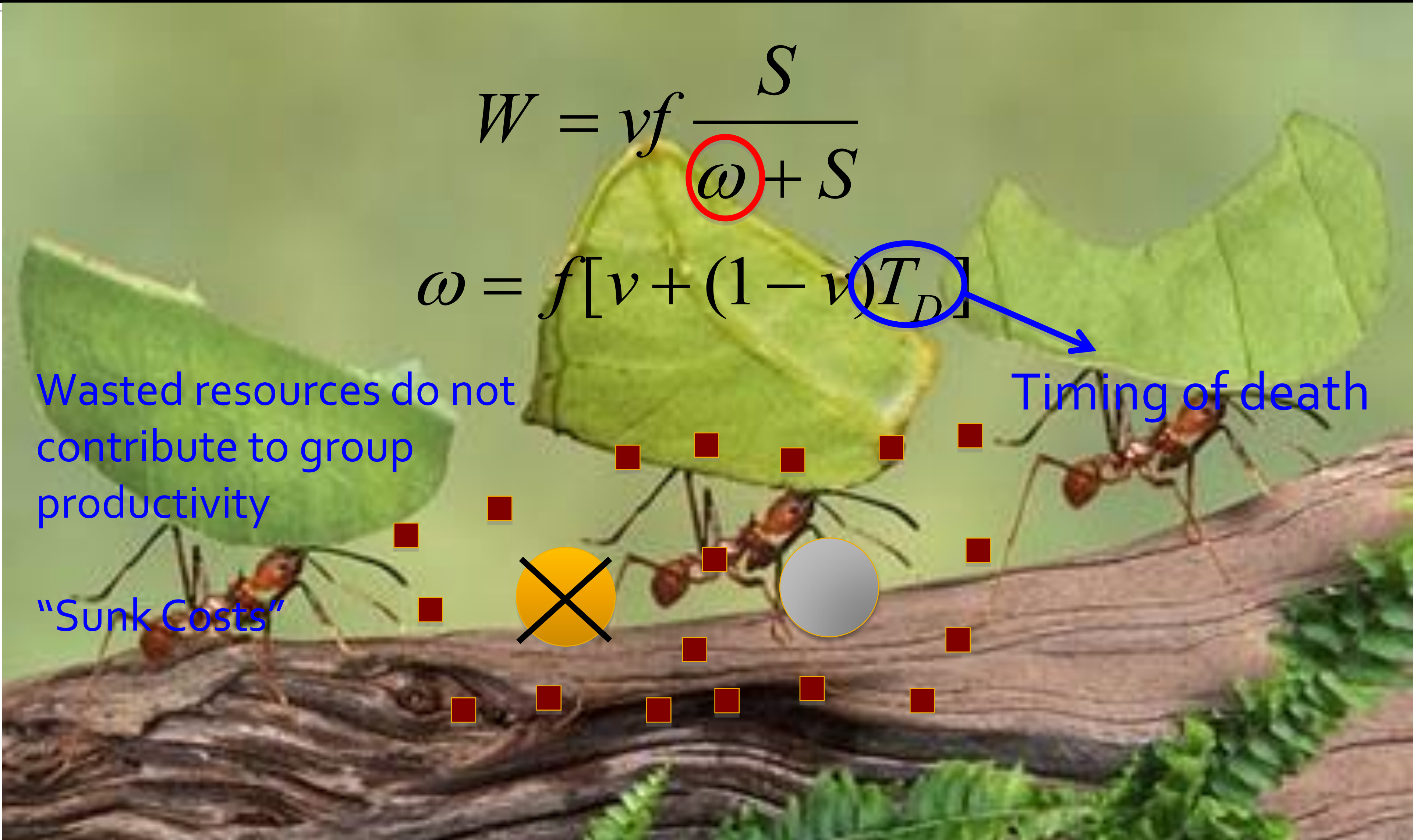


Wasted resources do not contribute to group productivity

"Sunk Costs"

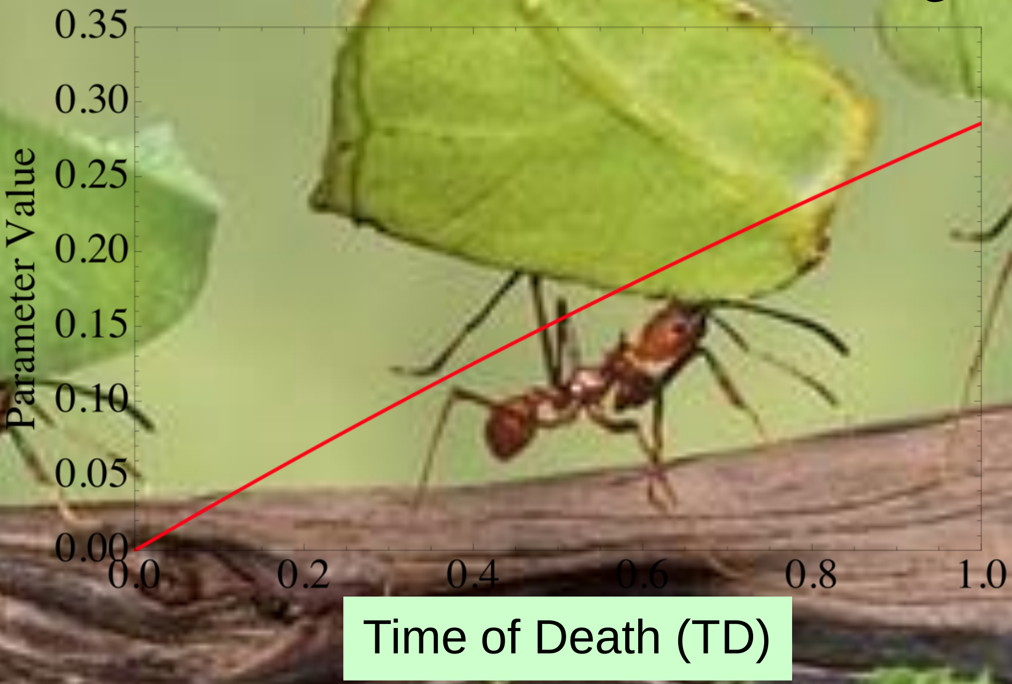
Timing of death

Timing of Death

Survival Altruism

$$(1 - a + e)br - c(1 - ar + er) > 0$$

$$e = T_D\left[stuff\right]$$



Timing of Death

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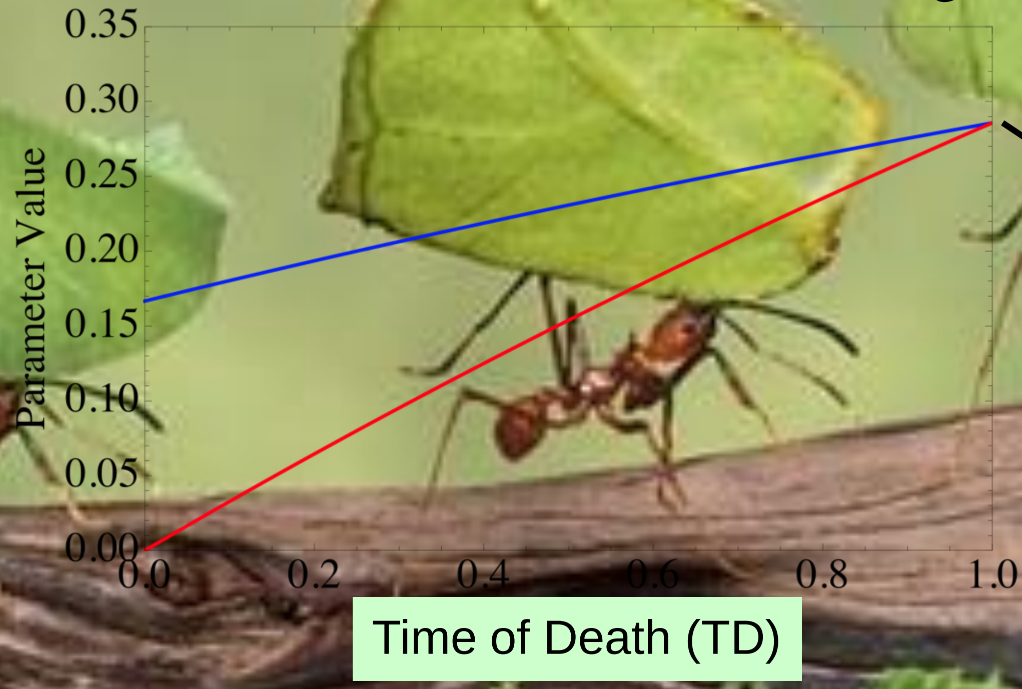
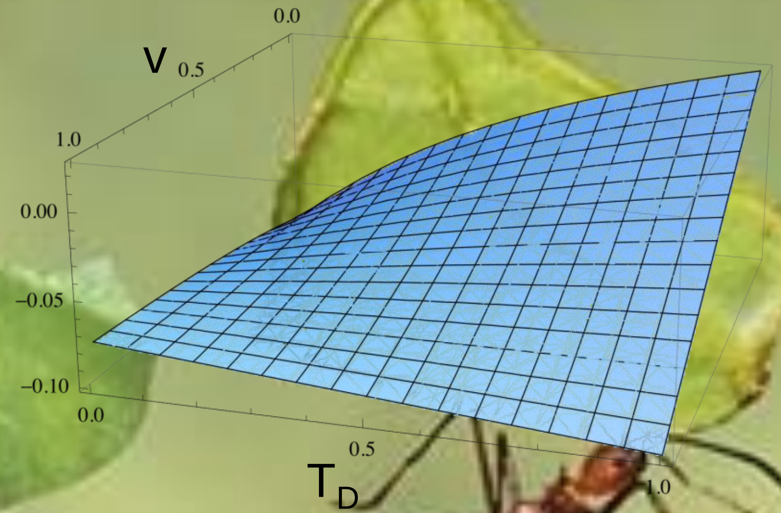


$$br - c > 0 \; !$$

Timing of Death

Altruistic suicide (e.g., Apoptosis)

Selection for dying earlier

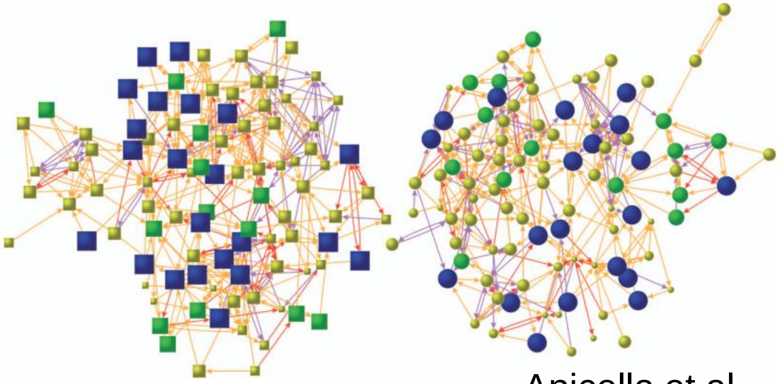


Can increased death rate evolve?

NO.

Resource Sharing

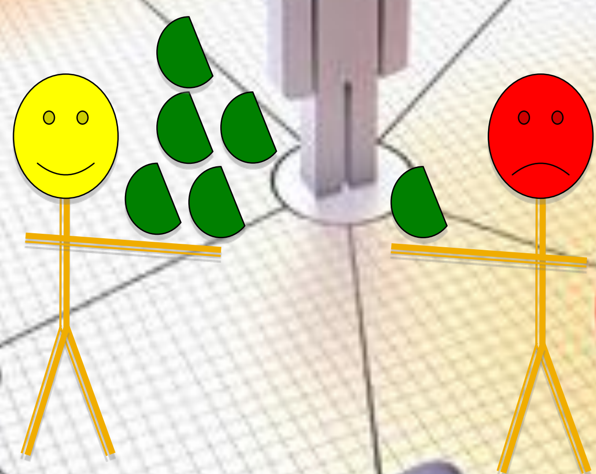
Resource Sharing: Donating resources (acquired independently) to others



Apicella et al (2012)

Problem

- In order for cooperation to evolve, the benefit to the recipient must be greater than the cost to the donor: B > C
- But resource sharing is a zero-sum game: B = C (right?)



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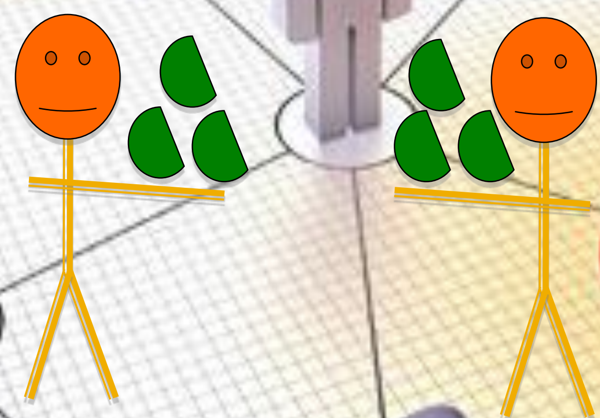

What Are Fitness Benefit of Sharing?

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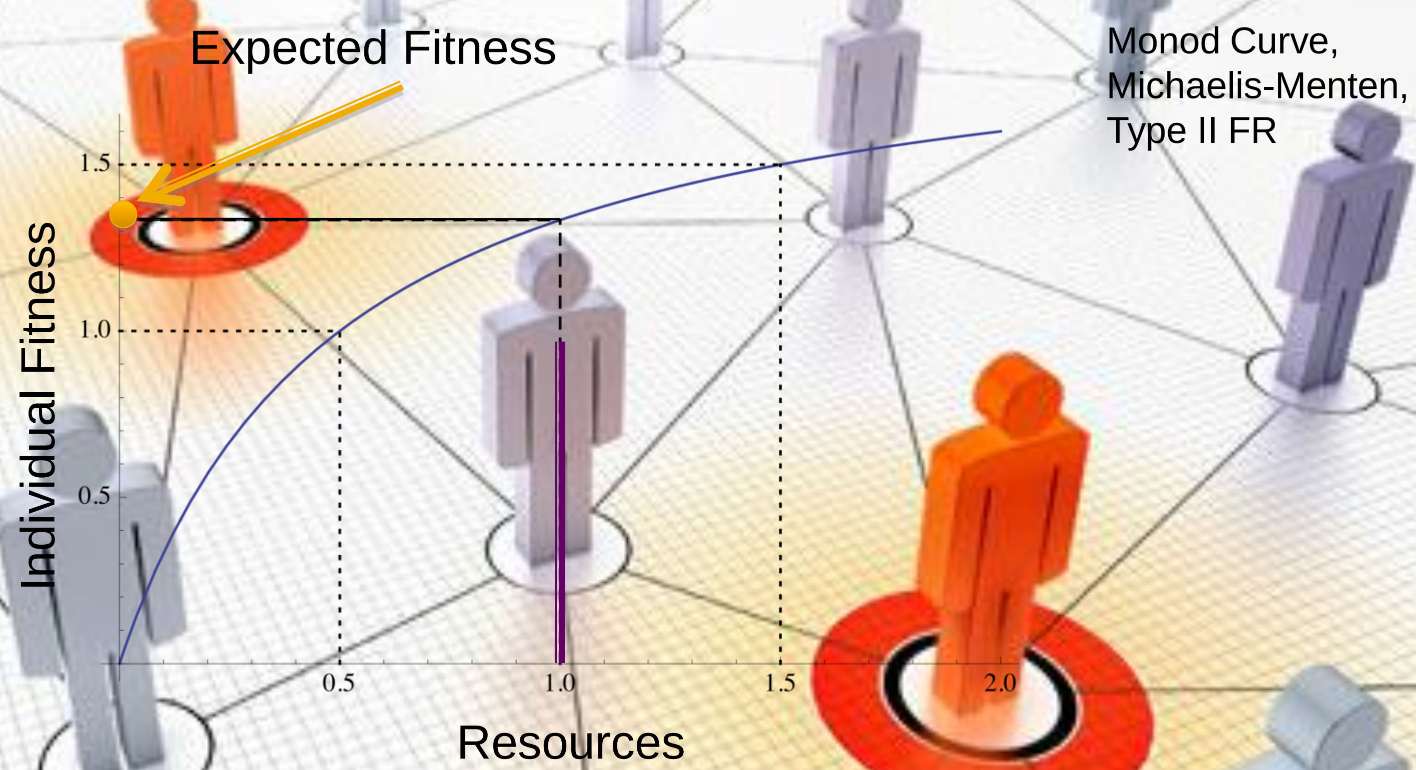
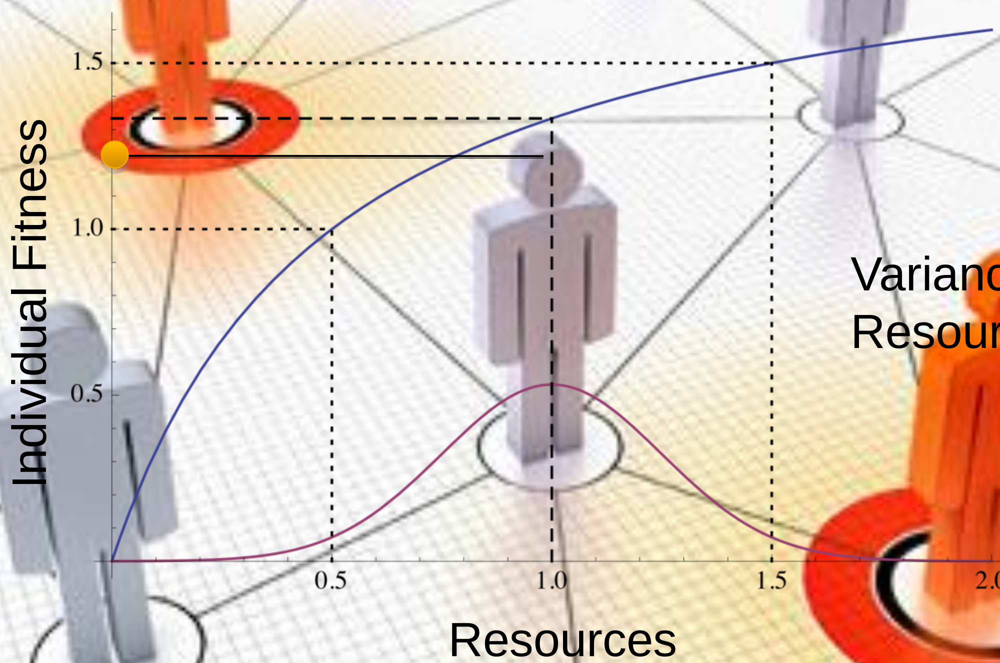


What Are Fitness Benefit of Sharing?

$$W \approx \mu \frac{f}{(k_S + \mu)} - \mathrm{var} \frac{f}{(k_S + \mu)^3}$$



Monod Curve,
Michaelis-Menten,
Type II FR

Variance in Resources ↓

Expected Fitness ↑

Fitness Benefit of Sharing

- Sharing increases an individual's expected fitness by reducing her resource variance.
- Provides a basis for understanding the forces leading to EGALITARIAN hunter-gatherer societies.

Conclusions and Implications for Evolutionary Transitions

- Ecology is not simply an external constraint on cooperation, it is fundamental
- We must pay attention to the *currency of cooperation*
- Eco-evolutionary feedback can lead to extreme altruism
- Eco-evolutionary feedback may be important in the evolution of apoptosis
- Selection to reduce resource variance promotes resource sharing and egalitarianism

Acknowledgments

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