Invasion as a unifying conceptual tool in ecology and evolution

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ON

THE ORIGIN OF SPECIES

BY MEANS OF NATURAL SELECTION,

OR THE

PRESERVATION OF FAVOURED RACES IN THE STRUGGLE FOR LIFE.

By CHARLES DARWIN, M.A.,

FELLOW OF THE ROYAL, GEOLOGICAL, LINNÆAN, ETC., SOCIETIES;
AUTHOR OF 'JOURNAL OF RESEARCHES DURING H. M. S. BEAGLE'S VOYAGE ROUND THE WORLD.'

LONDON:
JOHN MURRAY, ALBEMARLE STREET.
1859.

Invasion

Invasion is a notion that underpins

- Population Genetics
- Game Theory
- Life History Theory
- Community Ecology

Invasion

Notions of invasion underpin

- Population Genetics
- Game Theory
- Life History Theory
- Community Ecology

Life History Theory

Life History Theory

All organisms grow, reproduce and eventually die

What is the result:

- a growing population?
- extinction?

Need to integrate life-history components

Hal Caswell

Evolutionary Life History Theory

All organisms grow, reproduce and eventually die

Given finite resources, how should an individual invest in growth, reproduction and survival

Kooijman

Since 1960s : Evolutionary Life History Theory

Eric Charnov, Steve Stearns

Life History Theory

Population-level view:

- Net rate of reproduction: $r = b - d$
  - where the rates of reproduction b and mortality d may depend on environmental conditions
- A population invades if (and only if) r is positive

Life History Theory

Individual-level view

- A population increases on average an individual has more than one offspring
- Average lifetime: $1/d$
- Expected lifetime reproductive success or 'Basic Reproduction Ratio' $R_0 = b/d$
- Invasion if (and only if) $R_0 > 1$

Life History Theory

Hypothesis

- Natural Selection maximizes $R_0 = b/d$
- Basic Reproduction Ratio

Most theory is about how individuals might achieve this

Life History Theory

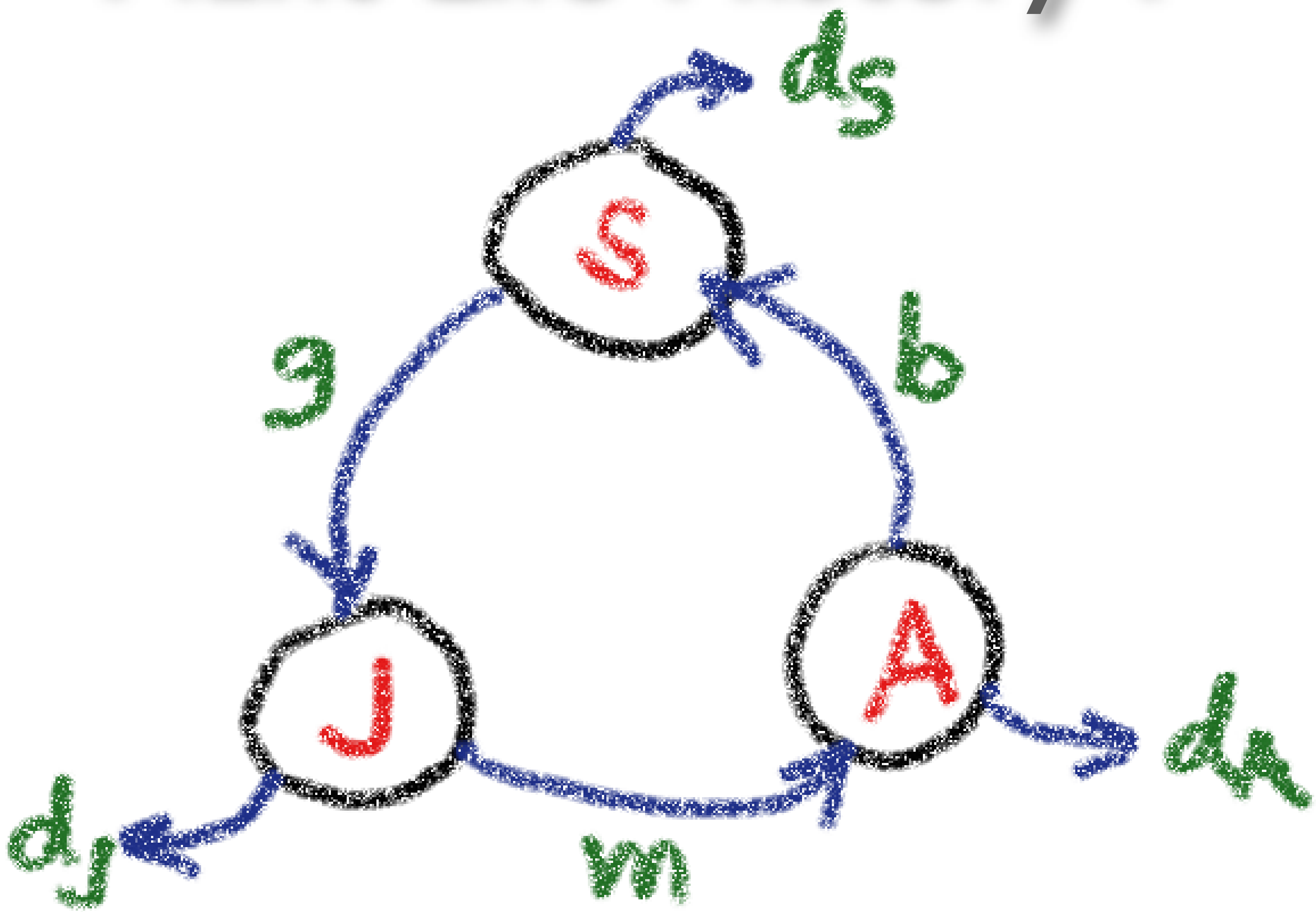
Caricature

- 'Individuals try to maximize their lifetime reproductive success by adopting the optimal allocation of resources into reproduction and survival.'

Plant Life History I

- Continuous time
- Three stages
  - Seeds S
  - Juveniles (non-reproducing) J
  - Adults (reproducing) A

Plant Life History I



Plant Life History I

$$\frac{dS}{dt} = bA - d_S S - gS$$

$$\frac{dJ}{dt} = gS - d_J J - m_J J$$

$$\frac{dA}{dt} = m_J J - d_A A$$

Plant Life History I

$$\frac{d}{dt}\begin{pmatrix} S \\ J \\ A \end{pmatrix} = \begin{pmatrix} -d_S - g & 0 & b \\ g & -d_J - m & 0 \\ 0 & m & -d_A \end{pmatrix}\begin{pmatrix} S \\ J \\ A \end{pmatrix}$$

$$\frac{dX}{dt} = MX$$

Analysis of linear models

$$\frac{dx}{dt} = Mx$$

Linear model

Solution $x(t) = \sum_{i=1}^{n} c_i U_i e^{\lambda_i t}$

U_i i-th eigenvector
λ_i i-th eigenvalue

Dominant eigenvalue λ

Solution converges to $x(t) \propto U e^{\lambda t}$

Population increases if $\lambda > 0$, decreases if $\lambda < 0$

Analysis of linear models

$$MU = \lambda U$$

$$(M - \lambda I)U = \vec{0}$$

I ← identity matrix $\begin{pmatrix} 1 & & 0 \\ & \ddots & \\ 0 & & 1 \end{pmatrix}$

$$|M - \lambda I| = 0$$

characteristic equation

Analysis of linear models

$$|M - \lambda I| = 0$$

$$\begin{vmatrix} -d_S - g - \lambda & 0 & b \\ g & -d_J - m - \lambda & 0 \\ 0 & m & -d_A - \lambda \end{vmatrix} = 0$$

$$-(d_S + g + \lambda)(d_J + m + \lambda)(d_A + \lambda) + bgm = 0$$

complicated cubic equation

but solution gives all three eigenvalues

Analysis of linear models

Out[3]=

$$\Big\{\Big\{\lambda \to \frac{1}{6}\Big(-2\,(g+m+d_A+d_J+d_S) - \big(2\,2^{1/3}\,(g^2 - g\,m + m^2 + d_A^2 + d_J^2 + 2\,g\,d_S - m\,d_S + d_S^2 - d_J\,(g - 2\,m + d_S) - d_A\,(g + m + d_J + d_S))\big)\Big/$$

$$\big(2\,g^3 - 27\,b\,g\,m - 3\,g^2\,m - 3\,g\,m^2 + 2\,m^3 - 3\,g^2\,d_A + 12\,g\,m\,d_A - 3\,m^2\,d_A - 3\,g\,d_A^2 - 3\,m\,d_A^2 + 2\,d_A^3 - 3\,g^2\,d_J - 6\,g\,m\,d_J + 6\,m^2\,d_J + 12\,g\,d_A\,d_J - 6\,m\,d_A\,d_J -$$

$$3\,d_A^2\,d_J - 3\,g\,d_J^2 + 6\,m\,d_J^2 - 3\,d_A\,d_J^2 + 2\,d_J^3 + 6\,g^2\,d_S - 6\,g\,m\,d_S - 3\,m^2\,d_S - 6\,g\,d_A\,d_S + 12\,m\,d_A\,d_S - 3\,d_A^2\,d_S - 6\,g\,d_J\,d_S - 6\,m\,d_J\,d_S + 12\,d_A\,d_J\,d_S -$$

$$3\,d_J^2\,d_S + 6\,g\,d_S^2 - 3\,m\,d_S^2 - 3\,d_A\,d_S^2 - 3\,d_J\,d_S^2 + 2\,d_S^3 + \surd\big(-4\,(g^2 - g\,m + m^2 + d_A^2 + d_J^2 + 2\,g\,d_S - m\,d_S + d_S^2 - d_J\,(g - 2\,m + d_S) - d_A\,(g + m + d_J + d_S))^3 +$$

$$(-2\,g^3 + 27\,b\,g\,m + 3\,g^2\,m + 3\,g\,m^2 - 2\,m^3 - 2\,d_A^3 - 2\,d_J^3 - 6\,g^2\,d_S + 6\,g\,m\,d_S + 3\,m^2\,d_S - 6\,g\,d_S^2 + 3\,m\,d_S^2 - 2\,d_S^3 + 3\,d_J^2\,(g - 2\,m + d_S) + 3\,d_A^2\,(g + m + d_J + d$$

$$3\,d_A\,(g^2 - 4\,g\,m + m^2 + d_J^2 + d_J\,(-4\,g + 2\,m - 4\,d_S) + 2\,(g - 2\,m)\,d_S + d_S^2) + 3\,d_J\,(g^2 + 2\,g\,m - 2\,m^2 + 2\,(g + m)\,d_S + d_S^2))^2\big)\big)^{1/3} -$$

$$2^{2/3}\,\big(2\,g^3 - 27\,b\,g\,m - 3\,g^2\,m - 3\,g\,m^2 + 2\,m^3 - 3\,g^2\,d_A + 12\,g\,m\,d_A - 3\,m^2\,d_A - 3\,g\,d_A^2 - 3\,m\,d_A^2 + 2\,d_A^3 - 3\,g^2\,d_J - 6\,g\,m\,d_J + 6\,m^2\,d_J + 12\,g\,d_A\,d_J - 6\,m\,d_A\,d_J -$$

$$3\,d_A^2\,d_J - 3\,g\,d_J^2 + 6\,m\,d_J^2 - 3\,d_A\,d_J^2 + 2\,d_J^3 + 6\,g^2\,d_S - 6\,g\,m\,d_S - 3\,m^2\,d_S - 6\,g\,d_A\,d_S + 12\,m\,d_A\,d_S - 3\,d_A^2\,d_S - 6\,g\,d_J\,d_S - 6\,m\,d_J\,d_S + 12\,d_A\,d_J\,d_S -$$

$$3\,d_J^2\,d_S + 6\,g\,d_S^2 - 3\,m\,d_S^2 - 3\,d_A\,d_S^2 - 3\,d_J\,d_S^2 + 2\,d_S^3 + \surd\big(-4\,(g^2 - g\,m + m^2 + d_A^2 + d_J^2 + 2\,g\,d_S - m\,d_S + d_S^2 - d_J\,(g - 2\,m + d_S) - d_A\,(g + m + d_J + d_S))^3 +$$

$$(-2\,g^3 + 27\,b\,g\,m + 3\,g^2\,m + 3\,g\,m^2 - 2\,m^3 - 2\,d_A^3 - 2\,d_J^3 - 6\,g^2\,d_S + 6\,g\,m\,d_S + 3\,m^2\,d_S - 6\,g\,d_S^2 + 3\,m\,d_S^2 - 2\,d_S^3 + 3\,d_J^2\,(g - 2\,m + d_S) + 3\,d_A^2\,(g + m + d_J + d$$

$$3\,d_A\,(g^2 - 4\,g\,m + m^2 + d_J^2 + d_J\,(-4\,g + 2\,m - 4\,d_S) + 2\,(g - 2\,m)\,d_S + d_S^2) + 3\,d_J\,(g^2 + 2\,g\,m - 2\,m^2 + 2\,(g + m)\,d_S + d_S^2))^2\big)\big)^{1/3}\Big)\Big\},$$

$$\Big\{\lambda \to \frac{1}{12}\Big(-4\,(g+m+d_A+d_J+d_S) + \big(2\,2^{1/3}\,(1 + i\sqrt{3})\,(g^2 - g\,m + m^2 + d_A^2 + d_J^2 + 2\,g\,d_S - m\,d_S + d_S^2 - d_J\,(g - 2\,m + d_S) - d_A\,(g + m + d_J + d_S))\big)\Big/$$

$$\big(2\,g^3 - 27\,b\,g\,m - 3\,g^2\,m - 3\,g\,m^2 + 2\,m^3 - 3\,g^2\,d_A + 12\,g\,m\,d_A - 3\,m^2\,d_A - 3\,g\,d_A^2 - 3\,m\,d_A^2 + 2\,d_A^3 - 3\,g^2\,d_J - 6\,g\,m\,d_J + 6\,m^2\,d_J + 12\,g\,d_A\,d_J - 6\,m\,d_A\,d_J -$$

$$3\,d_A^2\,d_J - 3\,g\,d_J^2 + 6\,m\,d_J^2 - 3\,d_A\,d_J^2 + 2\,d_J^3 + 6\,g^2\,d_S - 6\,g\,m\,d_S - 3\,m^2\,d_S - 6\,g\,d_A\,d_S + 12\,m\,d_A\,d_S - 3\,d_A^2\,d_S - 6\,g\,d_J\,d_S - 6\,m\,d_J\,d_S + 12\,d_A\,d_J\,d_S -$$

$$3\,d_J^2\,d_S + 6\,g\,d_S^2 - 3\,m\,d_S^2 - 3\,d_A\,d_S^2 - 3\,d_J\,d_S^2 + 2\,d_S^3 + \surd\big(-4\,(g^2 - g\,m + m^2 + d_A^2 + d_J^2 + 2\,g\,d_S - m\,d_S + d_S^2 - d_J\,(g - 2\,m + d_S) - d_A\,(g + m + d_J + d_S))^3 +$$

$$(-2\,g^3 + 27\,b\,g\,m + 3\,g^2\,m + 3\,g\,m^2 - 2\,m^3 - 2\,d_A^3 - 2\,d_J^3 - 6\,g^2\,d_S + 6\,g\,m\,d_S + 3\,m^2\,d_S - 6\,g\,d_S^2 + 3\,m\,d_S^2 - 2\,d_S^3 + 3\,d_J^2\,(g - 2\,m + d_S) + 3\,d_A^2\,(g + m + d_J + d$$

$$3\,d_A\,(g^2 - 4\,g\,m + m^2 + d_J^2 + d_J\,(-4\,g + 2\,m - 4\,d_S) + 2\,(g - 2\,m)\,d_S + d_S^2) + 3\,d_J\,(g^2 + 2\,g\,m - 2\,m^2 + 2\,(g + m)\,d_S + d_S^2))^2\big)\big)^{1/3} +$$

$$2^{2/3}\,(1 - i\sqrt{3})\,\big(2\,g^3 - 27\,b\,g\,m - 3\,g^2\,m - 3\,g\,m^2 + 2\,m^3 - 3\,g^2\,d_A + 12\,g\,m\,d_A - 3\,m^2\,d_A - 3\,g\,d_A^2 - 3\,m\,d_A^2 + 2\,d_A^3 - 3\,g^2\,d_J - 6\,g\,m\,d_J + 6\,m^2\,d_J + 12\,g\,d_A\,d_J -$$

$$6\,m\,d_A\,d_J - 3\,d_A^2\,d_J - 3\,g\,d_J^2 + 6\,m\,d_J^2 - 3\,d_A\,d_J^2 + 2\,d_J^3 + 6\,g^2\,d_S - 6\,g\,m\,d_S - 3\,m^2\,d_S - 6\,g\,d_A\,d_S + 12\,m\,d_A\,d_S - 3\,d_A^2\,d_S - 6\,g\,d_J\,d_S - 6\,m\,d_J\,d_S + 12\,d_A\,d_J\,d_S -$$

$$3\,d_J^2\,d_S + 6\,g\,d_S^2 - 3\,m\,d_S^2 - 3\,d_A\,d_S^2 - 3\,d_J\,d_S^2 + 2\,d_S^3 + \surd\big(-4\,(g^2 - g\,m + m^2 + d_A^2 + d_J^2 + 2\,g\,d_S - m\,d_S + d_S^2 - d_J\,(g - 2\,m + d_S) - d_A\,(g + m + d_J + d_S))^3 +$$

$$(-2\,g^3 + 27\,b\,g\,m + 3\,g^2\,m + 3\,g\,m^2 - 2\,m^3 - 2\,d_A^3 - 2\,d_J^3 - 6\,g^2\,d_S + 6\,g\,m\,d_S + 3\,m^2\,d_S - 6\,g\,d_S^2 + 3\,m\,d_S^2 - 2\,d_S^3 + 3\,d_J^2\,(g - 2\,m + d_S) + 3\,d_A^2\,(g + m + d_J + d$$

$$3\,d_A\,(g^2 - 4\,g\,m + m^2 + d_J^2 + d_J\,(-4\,g + 2\,m - 4\,d_S) + 2\,(g - 2\,m)\,d_S + d_S^2) + 3\,d_J\,(g^2 + 2\,g\,m - 2\,m^2 + 2\,(g + m)\,d_S + d_S^2))^2\big)\big)^{1/3}\Big)\Big\},$$

$$\Big\{\lambda \to \frac{1}{12}\Big(-4\,(g+m+d_A+d_J+d_S) + \big(2\,2^{1/3}\,(1 - i\sqrt{3})\,(g^2 - g\,m + m^2 + d_A^2 + d_J^2 + 2\,g\,d_S - m\,d_S + d_S^2 - d_J\,(g - 2\,m + d_S) - d_A\,(g + m + d_J + d_S))\big)\Big/$$

$$\big(2\,g^3 - 27\,b\,g\,m - 3\,g^2\,m - 3\,g\,m^2 + 2\,m^3 - 3\,g^2\,d_A + 12\,g\,m\,d_A - 3\,m^2\,d_A - 3\,g\,d_A^2 - 3\,m\,d_A^2 + 2\,d_A^3 - 3\,g^2\,d_J - 6\,g\,m\,d_J + 6\,m^2\,d_J + 12\,g\,d_A\,d_J - 6\,m\,d_A\,d_J -$$

$$3\,d_A^2\,d_J - 3\,g\,d_J^2 + 6\,m\,d_J^2 - 3\,d_A\,d_J^2 + 2\,d_J^3 + 6\,g^2\,d_S - 6\,g\,m\,d_S - 3\,m^2\,d_S - 6\,g\,d_A\,d_S + 12\,m\,d_A\,d_S - 3\,d_A^2\,d_S \ldots$$

$$3\,d_J^2\,d_S + 6\,g\,d_S^2 - 3\,m\,d_S^2 - 3\,d_A\,d_S^2 - 3\,d_J\,d_S^2 + 2\,d_S^3 + \surd\big(-4\,(g^2 - g\,m + m^2 + d_A^2 + d_J^2 + 2\,g\,d_S - m\,d_S + d_S^2 - d_J\,(g - 2\,m + d_S) - d_A\,(g + m + d_J + d_S))^3 +$$

$$(-2\,g^3 + 27\,b\,g\,m + 3\,g^2\,m + 3\,g\,m^2 - 2\,m^3 - 2\,d_A^3 - 2\,d_J^3 - 6\,g^2\,d_S + 6\,g\,m\,d_S + 3\,m^2\,d_S - 6\,g\,d_S^2 + 3\,m\,d_S^2 \ldots$$

$$3\,d_A\,(g^2 - 4\,g\,m + m^2 + d_J^2 + d_J\,(-4\,g + 2\,m - 4\,d_S) + 2\,(g - 2\,m)\,d_S + d_S^2) + 3\,d_J\,(g^2 + 2\,g\,m - 2\,m^2 \ldots$$

$$2^{2/3}\,(1 + i\sqrt{3})\,\big(2\,g^3 - 27\,b\,g\,m - 3\,g^2\,m - 3\,g\,m^2 + 2\,m^3 - 3\,g^2\,d_A + 12\,g\,m\,d_A - 3\,m^2\,d_A - 3\,g\,d_A^2 - 3\,m\,d_A^2 + 2\,d_A^3 - 3\,g^2\,d_J - 6\,g\,m\,d_J + 6\,m^2\,d_J + 12\,g\,d_A\,d_J -$$

$$6\,m\,d_A\,d_J - 3\,d_A^2\,d_J - 3\,g\,d_J^2 + 6\,m\,d_J^2 - 3\,d_A\,d_J^2 + 2\,d_J^3 + 6\,g^2\,d_S - 6\,g\,m\,d_S - 3\,m^2\,d_S - 6\,g\,d_A\,d_S + 12\,m\,d_A\,d_S - 3\,d_A^2\,d_S - 6\,g\,d_J\,d_S - 6\,m\,d_J\,d_S + 12\,d_A\,d_J\,d_S -$$

Output generated by *Mathematica*

Analysis of linear models

Often one is not so much interested in the precise rate of invasion, but in whether a population can invade at all.

What is the invasion threshold?

Invasion Threshold

λ solation of $|M - \lambda I| = 0$

Invasion threshold $\lambda = 0$

Given by $|M| = 0$

Invasion threshold

Example: $M = \begin{pmatrix} -d_S - g & 0 & b \\ g & -d_J - m & 0 \\ 0 & m & -d_A \end{pmatrix}$

$|M| = 0$

$-(d_S+g)(d_J+m)\,d_A + bgm = 0$

$$\frac{bgm}{(d_S+g)(d_J+m)\,d_A} = 1$$

$R_0 = 1$ basic reproduction ratio

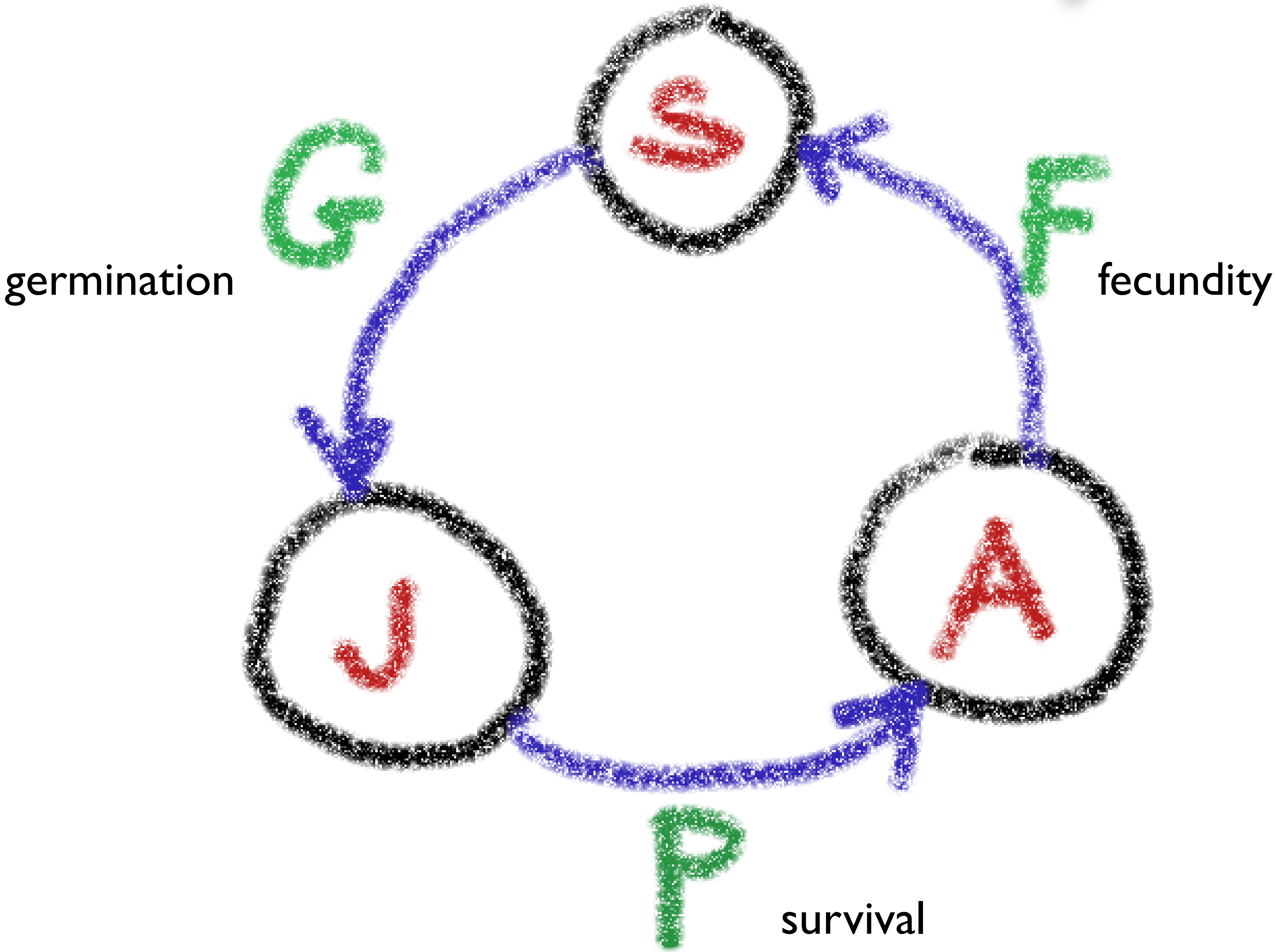
$$b\,\frac{g}{d_S+g}\,\frac{m}{d_J+m} - d_A = 0$$

$r = 0$ per capita growth rate

Plant Life History II

- *Discrete* time
- Three stages
  - Seeds *S*
  - Juveniles (non-reproducing) *J*
  - Adults (reproducing) *A*

Plant Life History II



Plant Life History II

$$S_{t+1} = F A_t$$

$$J_{t+1} = G S_t$$

$$A_{t+1} = P J_t$$

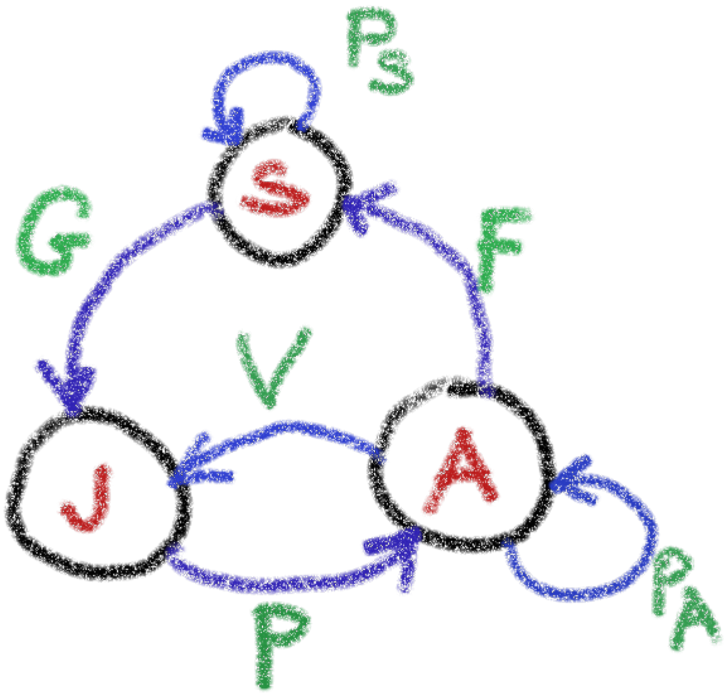
Plant Life History II

$$\begin{pmatrix} S_{t+1} \\ J_{t+1} \\ A_{t+1} \end{pmatrix} = \begin{pmatrix} 0 & 0 & F \\ G & 0 & 0 \\ 0 & P & 0 \end{pmatrix} \begin{pmatrix} S_t \\ J_t \\ A_t \end{pmatrix}$$

$$X_{t+1} = M X_t$$

M: Leslie matrix

Plant Life History II



+Adult survival (perennial plants)
+Seed survival (seed bank)
+Vegetative reproduction

Analysis of linear models

$$X_{t+1} = M X_t$$

Linear model

Solution $$X_t = \sum_{i=1}^{n} c_i U_i \lambda_i^t$$

U_i i-th eigenvector
λ_i i-th eigenvalue

Dominant eigenvalue λ

Solution converges to $X_t \propto U \lambda^t$

Population increases if $|\lambda| > 1$, decreases if $|\lambda| < 1$

Applications

Conservation biology

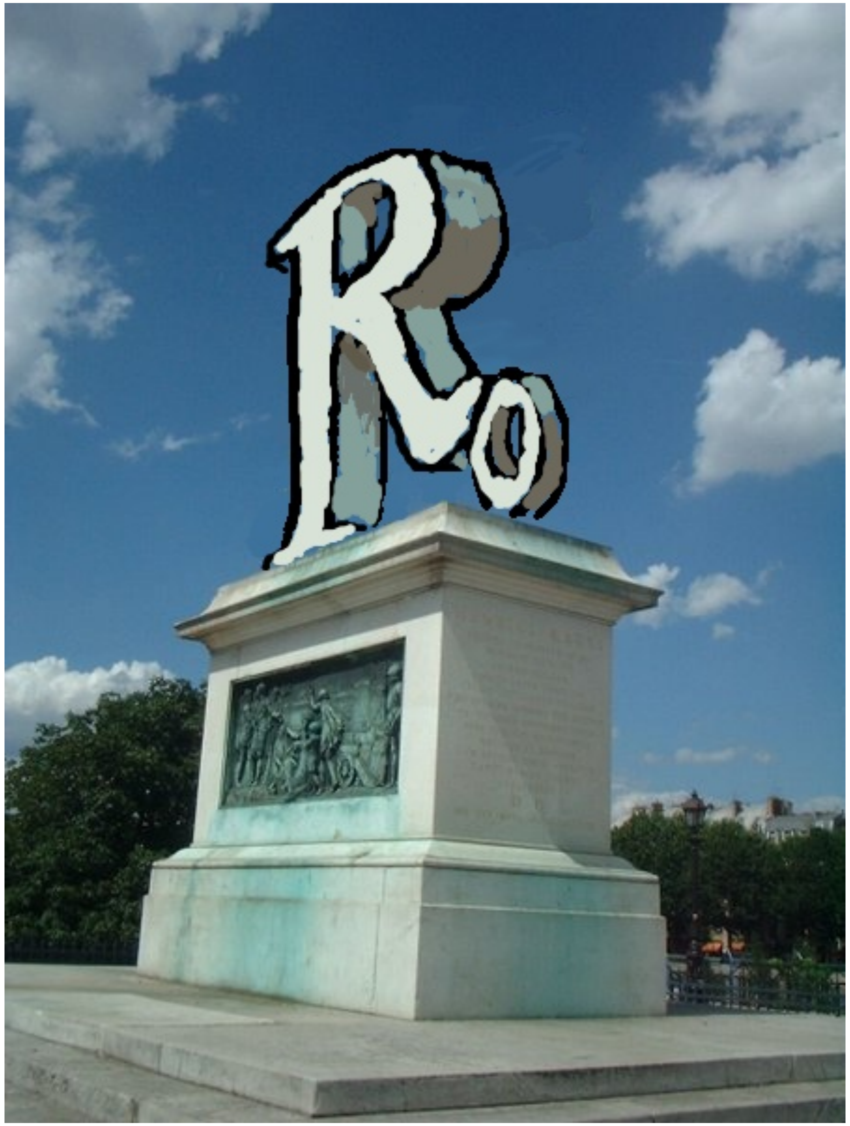
- how can we prevent extinction of menaced populations?

Epidemiology

- how can we prevent invasion of dangerous disease?

References

Caswell, H. (2001). Matrix Population Models. Construction, Analysis, and Interpretation. Sinauer, Sunderland, Mass, 2nd edition edition.


Ro

Measures of increase

Subtle differences

- λ rate of population increase
  - invasion continuous time : $\lambda > 0$
  - invasion discrete time : $\lambda > 1$
- R_0 basic reproduction ratio
  - invasion : $R_0 > 1$
- r net average rate of reproduction
  - invasion : $r > 0$

'typical' individual

population property


Ro
Apologies to Daumier

Life History Theory

Generally

- environment is usually taken to be constant
- whereas in reality demographic rates are likely to be density dependent:

$$b = b(x, y, \ldots),\; d = d(x, y, \ldots)$$

Need to incorporate feedback

Life History Theory

Invasion in a dynamically changing environment

Realm of …

Community Ecology

(Ecosystem Dynamics)

Invasion

Evolution and Ecology

- Population Genetics
- Game Theory
- Life History Theory
- Community Ecology

Ecosystem Dynamics

Species are fixed entities

But there are potentially many of them

Which of these can coexist?

How does it depend on their ecology?

How does it depend on external parameters?

Ecosystem Dynamics

Without ecological feedback

- only one species will dominate!
- species with the highest net rate of reproduction (r)

So how do we explain biodiversity?

Coexistence

Every species needs resources

- nutrients, light, space…
- species compete for these resources

Mathematical result:

- Number of species ≤ Number of resources
- if populations in ecological equilibrium

  (MacArthur in the 60s, Tilman 90s)

Coexistence

Nobody really knows how many different physical and chemical resources there are

But 100000000 different resources?

Nonequilibrium Coexistence

Many if not most ecosystems are

- not in equilibrium
- but fluctuate

Fluctuating systems allow more species

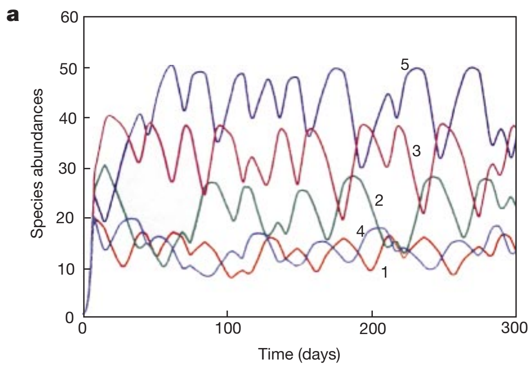
Armstrong & McGehee 1980s, Weissing & Huisman

Attractors

Every combination of species is represented by a dynamical system

Every dynamical system has its attractor(s)

- equilibrium/periodic orbit/chaos



Hofbauer & Sigmund, Rinaldi

Permanence

In a permanent ecosystem no species will go extinct

Every participating species will invade when rare

(ignoring 'Humpty Dumpty' effects)

Therefore to work out which species coexist we have to calculate their invasion exponent

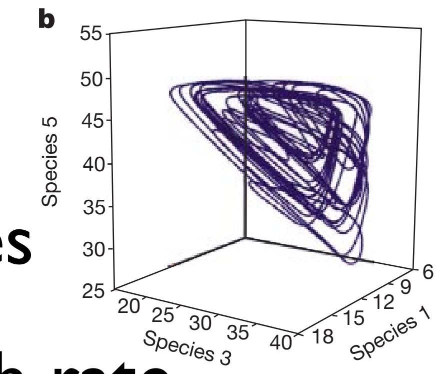
Hofbauer & Sigmund, Rand

Invasion exponent

If a species' invasion exponent is positive it will invade the ecosystem

Invasion exponents can (in principle) be derived from the dynamical system

- work out attractor without species
- calculate long-term average growth rate



Invasion exponent

We can calculate invasion exponent λ of species i

- by considering the attractor of the $n - 1$ species system $(x_j(t))$
- $r_i(t) = f(\dots, x_j(t), \dots) = f(E(t))$
- then

$$\lambda = \lim_{T \to \infty} \frac{1}{T} \int_0^T r_i(t)dt$$

Ecosystem Dynamics

Caricature

- ‘Species dynamics depends on other species directly or indirectly
- Biodiversity is given by how many species from a given species pool can invade the community
- If no new species can invade, the community is saturated’

Jonathan (Joan) Roughgarden, Stuart Pimm

Ecosystem Dynamics

References

- Jonathan (now Joan) Roughgarden
  - *Theory of Population Genetics and Evolutionary Ecology: An Introduction* (1979)
- Josef Hofbauer & Karl Sigmund
  - *The Theory of Evolution and Dynamical Systems* (1988)

Invasion

Evolution and Ecology

- Population Genetics
- Game Theory
- Life History Theory
- Community Ecology