The Interaction Between Evolution and Ecology

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Who am I

Minus van Baalen

- Researcher at the CNRS
- Ex-head of UMR 7625 « Ecologie et Evolution »
- Dutch
- Thesis Evolutionary Biology 1994
- Theoretician
Minus van Baalen

Research Interests

Ecology and evolution

When mutant individuals with a changed trait are successful, they will increase in numbers and thus start affecting population dynamics, resource availability, the prevalence of parasites, the intensity of interspecific competition, community structure, and so on. Together, these effects will cause a feedback because ecological parameters will, in general, affect the traits that are favoured. More on this can be found in the introduction to my thesis.

Interacting populations

Such eco-evolutionary feedback loops will be particularly intense in systems with interacting populations: adaptation and counteradaptation often have population dynamical consequences. A good example is the evolution of virulence. If avirulent parasites are common, host density increases and, with it, the force of infection. But so does the intensity of within-host competition, which favours more virulent parasites. Ecological effects will modify or sometimes even revert selection pressure on virulence.

Space

How spatial dynamics affect evolution (and vice versa) is still poorly understood. When a mutant invades a ‘viscous’ system it typically does so in the form of an expanding cluster of relatives. Ultimately it is therefore the characteristics of these clusters that determine whether the invasion will be successful. On other words, the unit of selection in a viscous systems is a cluster of WL
Research Interests

- Ecology and evolution
- Interacting populations
- Space
- Dangerous Liaisons
- Communication
- Kin selection, coloniality and disease
- Immune functioning and virulence
Ecology + Evolution =

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

} Adaptive Dynamics
Invasion as a unifying conceptual tool
Eco-Evolutionary Feedback

Ecology (environment)

determines

Evolution

modifies
Evolution
History

Before 1800

- various theories of evolution
- species evolve

Lamarck, Erasmus Darwin

After 1800

- mechanism: natural selection

Charles Darwin, Alfred R. Wallace
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, Linnean, etc., Societies;
Author of "Journal of Researches During H. M. S. Beagle's Voyage Round the World."

London:
John Murray, Albemarle Street.
1859.
Reproduction generates variation

Individuals compete

Traits affect individuals’ differential survival

= ‘Evolution by Natural Selection’
Rediscovery of Mendel

Early 1900s

- rediscovery of Mendel’s work
- phenotypes change because genotypes change
- genes remain the same
  - no evolutionary change ?!
Genes are not fixed

- rare mutations modify genes

‘Neo-Darwinian Synthesis’

- fixation of mutations

Hugo de Vries

Ronald A. Fischer
Invasion as a unifying conceptual tool in ecology and evolution

Minus van Baalen (CNRS, UMR 7625 EcoEvo, Paris)
Invasion is a notion that underpins

- Population Genetics
- Game Theory
- Life History Theory
- Community Ecology
Notions of invasion underpin

- Population Genetics
- Game Theory
- Life History Theory
- Community Ecology
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
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
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) $R_0 > 1$
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
\[
\frac{dS}{d\tau} = bA - d_gS - gS \\
\frac{dJ}{d\tau} = gS - d_sJ - m_yJ \\
\frac{dA}{d\tau} = m_yJ - d_wA
\]
Plant Life History I

\[
\frac{d}{dt} \begin{pmatrix} S \\ J \\ A \end{pmatrix} = \begin{pmatrix} -d_s - g & 0 & b \\ g & -d_j - m & 0 \\ 0 & m & -d_A \end{pmatrix} \begin{pmatrix} S \\ J \\ A \end{pmatrix}
\]

\[
\frac{dX}{d\mathcal{E}} = M X
\]
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

\( \lambda_i \) i-th eigenvalue

Dominant eigenvalue \( \lambda \)

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

Population increases if \( \lambda > 0 \), decreases if \( \lambda < 0 \)
Analysis of linear models

\[ MU = \lambda U \]

\[ (M - \lambda I)U = \hat{\sigma} \]

\[ |M - \lambda I| = 0 \]

characteristic equation
Analysis of linear models

\[ |M - \lambda I| = 0 \]
\[
\begin{vmatrix}
-d_s-g-\lambda & 0 & b \\
-g & -d_j-m-\lambda & 0 \\
0 & m & -d_A-\lambda
\end{vmatrix} = 0
\]

\[-(d_s+g+\lambda)(d_s+m+\lambda)(d_A+\lambda) + bgm = 0\]

Complicated cubic equation, but solution gives all three eigenvalues.
Analysis of linear models

\[
\text{Output generated by Mathematica}
\]
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?
A solution of $|M - \lambda I| = 0$

Invasion threshold $\lambda = 0$

Given by $|M| = 0$
Invasion threshold

Example: \( M = \begin{pmatrix} -d_s - g & 0 & b \\ g & -d_j - m & 0 \\ 0 & m & d_A \end{pmatrix} \)

\[ |M| = 0 \]
\[ -(d_s + g)(d_j + m)d_A + \log bm = 0 \]
\[ \frac{\log bm}{(d_s + g)(d_j + m)d_A} = 1 \quad R_0 = 1 \]
\[ b \frac{g}{d_s + g} \frac{m}{d_j + m} - d_A = 0 \quad r = 0 \]
Plant Life History II

- *Discrete* time
- Three stages
  - Seeds $S$
  - Juveniles (non-reproducing) $J$
  - Adults (reproducing) $A$
Plant Life History II

- **Germination** (G)
- **Survival** (S)
- **Fecundity** (F)
- **J**
- **A**

Diagram shows the cycle of plant life history with arrows connecting the stages.
Plant Life History II

\[ S_{t+1} = FA_t \]
\[ J_{t+1} = GS_t \]
\[ A_{t+1} = PJ_t \]
Plant Life History II

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

\[X_{t+1} = MX_t\]

M: Leslie matrix
Plant Life History II

+Adult survival (perennial plants)
+Seed survival (seed bank)
+Vegetative reproduction
Analysis of linear models

\[ X_{t+1} = MX_t \]

Linear model

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

Dominant eigenvalue \( \lambda \)

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?
Measures of increase

Subtle differences

\( \lambda \) 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
Life History Theory

Generally

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

\[ b = b(x,y,...), \quad d = d(x,y,...) \]

Need to incorporate feedback
Invasion in a *dynamically changing* environment

Realm of …
Original Proposition

- Introduction into Adaptive Dynamics
- Application: Virulence Evolution
- Application: Kin Selection, Cooperation, and Units of Adaptation
Potential Topics

Synthetic Biology, Experimental Evolution
Mechanisms and Evolutionary Outcomes
Invasion Biology & Evolution
Genomics & Information Theory
Community Ecology
(Ecosystem Dynamics)
Invasion

Evolution and Ecology

- Population Genetics
- Game Theory
- Life History Theory
- Community Ecology
Species are fixed entities
But there are potentially many of them
Which of these can coexist?
How does coexistence 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 $\leq$ 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?

– 100000000 is a low estimate of the number of currently existing species
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
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 $\lambda$ of species $i$

- by considering the attractor of the $n - 1$
  species system $(x_j(t))$

- $r_i(t) = f(\ldots , x_j(t), \ldots ) = f(E(t))$

then

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

Josef Hofbauer & Karl Sigmund
Invasion

Evolution and Ecology

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