Evolutionary Dimensions of Ecosystem Ecology

Ulf Dieckmann
International Institute for Applied Systems Analysis
Laxenburg, Austria
Ecology and Evolution Are Intimately Linked

The Ecological Theater and the Evolutionary Play

G. E. Hutchinson (1967)
Two Common Misperceptions about Evolution

- **Evolution is always slow**
  On the contrary, rapid contemporary evolution is widespread, in particular in response to anthropogenic environmental change.

- **Evolution is always optimizing**
  On the contrary, frequency-dependent selection is ubiquitous, implying that population-level features will rarely get optimized by evolution.
The Need for and Potential of Evolutionary Considerations in Ecosystem Ecology

■ Understanding ecosystem constraints
  With evolution being the architect of ecosystems, many ecosystem features require evolutionary explanations. Example: Evolutionary community assembly.

■ Predicting ecosystem responses
  Whenever rapid evolution cannot be ruled out, understanding past and future ecosystem responses to anthropogenic change and managerial interventions requires evolutionary considerations.
Overview

1. Rapid Evolution
2. Frequency-dependent Selection
3. Adaptive Speciation
4. Evolutionary Suicide
5. Coevolution
6. Evolutionary Timescales
The Overlooked Evolutionary Dimension of Modern Fisheries

- Modern fishing results in such substantial changes of mortality patterns that evolutionary responses of stocks are inevitable.
- Such changes are not as slow as is widely believed: Significant evolution can occur within 10 or 20 years.
- Evolutionary changes are not necessarily beneficial, neither to the stock nor to the exploiting agents.
- Once evolutionary changes have occurred, they may be very difficult to reverse.
- Fishing does not only change the numbers, but also the traits of exploited fish.
North Sea Plaice


+ Loss spawning season
- Gain growing season (30 cm)
- Gain growing season (50 cm)
Northeast Arctic Cod

Northern Cod

Length at 50% maturation probability (cm)

Early warning

Moratorium

3L females maturing at age 5

Which Traits Are at Risk?

- **Age and size at maturation:**
  Reproducing late may not be a viable option.

- **Reproductive effort:**
  Saving for future reproduction may become futile.

- **Growth rate:**
  Staying below mesh size pays.

- **Behavior:**
  Reducing exposure to fishing is selected.
2 Frequency-dependent Selection
Frequency-dependent Selection

- Coping with frequency-dependent selection arguably is the biggest challenge for modern life-history theory.

- Frequency dependence arises whenever selection pressures in a population vary with its phenotypic composition.

- Virtually any ecologically serious consideration of life-history evolution implies frequency-dependent selection. Only carefully crafted (or ecologically unrealistic) models circumvent this complication.
Textbook Coverage: Roughly 1%

The Evolution of Life Histories
Stephen C. Stearns

2 out of 249 pages

Life History Evolution
Derek A. Roff

5 out of 465 pages
If residents are monomorphic or oligomorphic, adaptive dynamics theory offers useful tools; if they are continuously polymorphic, quantitative genetics theory is appropriate.
Envisaging evolution as a hill-climbing process on a static fitness landscape is attractively simple, but essentially wrong for most systems.
Frequency-Dependent Selection

Fitness landscapes change in dependence on a population’s current composition.
Invasion Fitness

Invasion fitness is a function of two variables

$$f(x', x)$$

- Variant trait
- Resident trait: determines environment

Growth rate of $$x'$$ in $$x$$-environment:
- if positive, $$x'$$ can invade into $$x$$
- otherwise not

Pairwise Invasibility Plots (PIPs)

- Invasion of the variant into the resident population possible
- Invasion impossible
- One trait substitution
- Singular phenotype

The canonical equation of adaptive dynamics is given by:

\[
\frac{d}{dt} x_i = \frac{1}{2} \mu_i n_i \sigma_i^2 \frac{\partial}{\partial x_i} f_i (x_i', x) \bigg|_{x_i' = x_i}
\]

where:
- \(\mu_i\) is the mutation probability
- \(n_i\) is the population size
- \(\sigma_i^2\) is the mutation variance-covariance
- \(f_i (x_i', x)\) is the invasion fitness

This equation captures the evolutionary rate in species \(i\) in terms of local selection gradient and invasion fitness. It highlights the direct coupling of ecology and evolution.

A similar result is available in quantitative genetics (Lande 1979).

3 Adaptive Speciation
Adaptive Speciation

- Convergence to fitness minima

Frequency dependence is key: Gold-rush effect

Directional selection
Disruptive selection
Stabilizing selection

Evolutionary Branching

Distribution of phenotypes

Evolutionary branching point

Convergence to disruptive selection

Evolutionary time

Biodiversity Formation

Cyclic pattern of evolutionary branching and selection-driven extinction, endogenously driven by ecological interactions

Distribution of phenotypes

Evolutionary time
Sexual Adaptive Speciation

This mechanism also works when assortative mating is based on a **marker character** and when evolutionary branching is driven by **interspecific interactions**.

Characteristics of Adaptive Speciation

- In adaptive speciation, the speciation process itself is adaptive, enabling a population to resolve a challenge posed by the eco-evolutionary feedback.

- Adaptive speciation is driven by biological interactions, and thus does not require invoking incidental external factors for splitting a population’s gene pool.

- Adaptive speciation can involve both ecological and sexual traits. The origin of variability and the stable coexistence of daughter species is automatically ensured.

- Adaptive speciation can occur in sympatry or parapatry.
Spatial Adaptive Speciation

- Spatial gradients facilitate adaptive speciation
- Gradients of intermediate slope are most speciation-prone

1 / Strength of frequency dependence

4 Evolutionary Suicide
Selection-driven Extinctions

Sexual Evolutionary Suicide

Infinite-allele multilocus genetics

Diallelic multilocus genetics

Evolutionary Suicide through Dispersal Evolution

5 Coevolution
Predator-Prey Coevolution: Traits

- Natural prey mortality
- Predator-induced prey mortality

Predator-Prey Coevolution: Dynamics

Red Queen Dynamics
Mutualistic Coevolution: Traits

Mutualistic Coevolution: Dynamics

Adaptive trait values

Population densities

“Coevolutionary cascade”

Depression 1
Extinction 1
Extinction 4
Reorientation 2
Reorientation 3

6 Evolutionary Timescales
Eco-Genetic Models

- Frequencies of individuals are tracked through time in dependence on five characteristics:
  - Age
  - Size
  - Maturation status
  - Reaction norm position
  - Reaction norm angle

Stock Dynamics

Ecology

Evolution
Modeling Northeast Arctic Cod

Demography
- Linear growth before maturation
- Growth increments negatively correlated with stock biomass
- Growth increments of mature individuals depend on size and gonadosomatic index
- Natural mortality of 0.2
- Density-dependent newborn mortality
- Density-dependent cannibalism on age classes 1 and 2
- Linear maturation reaction norm of constant width
- Fecundity allometrically depends on size

Fishing Mortality
- Historical regime:
  \[ F_{\text{immature}} = 0.05 \quad \text{and} \quad F_{\text{mature}} = 0.2 \]
- Contemporary regime:
  \[ F_{\text{immature}} = 0.4 \quad \text{and} \quad F_{\text{mature}} = 0.3 \]

Estimated size selectivity of fishing gear taken into account
Evolutionary Transient

Heritability = 0.2

Historical Regime

Contemporary Regime

Time (years)

0

100

Age at maturation (years)

0

10

20

30

40

50

60

70

80

90

100

ca. 40 years

Today

Heritability = 0.2
Reverse Evolutionary Transient

Heritability = 0.2

Time (years)

Age at maturation (years)

Contemp. Regime

Historical Regime

Today

c. 250 years
General Conclusions

- Frequency-dependent selection is crucial for understanding ecosystem evolution. Adaptive dynamics theory is geared to account for it, by closely linking evolutionary dynamics and population dynamics.

- Key determinants of biodiversity – including selection responses to environmental change, adaptive speciation, evolutionary suicide, and coevolutionary dynamics – can thus be analyzed.

- Future directions: Ecologically reasonable models of food web evolution are just now emerging (see also WS 5).