

Meeting 1 Introduction

Unification of modern Coexistence theory and Price equation
(UNICOP)

2022-09-04

Synthesis of community ecology and evolutionary biology

“Our project addresses a major limitation of current theoretical developments in modern coexistence theory. In particular, the consequences of evolutionary dynamics on the ecological stability of complex communities are still poorly understood.

We argue that further understanding of the interplay between ecological and evolutionary dynamics in complex communities can only be gained by taking a more abstract perspective and working from first principles, rather than trying to add ecology or evolution to specific models.’ ’ - UNICOP proposal

Fundamental theorem of evolution

(Price equation)

$$\Delta \bar{\phi} = \frac{1}{\bar{w}} (\text{cov}(w, \phi) + E(w\delta))$$

Partitions selection and transmission bias

$E(w\delta) = 0$ (no transmission bias)
 $\phi = p$ (measured genotypes)

$E(w\delta) = 0$ (no transmission bias)
 $\phi = g$ (unmeasured genotypes)

Fundamental theorem
of gene selection
(Average excess)

$$\Delta \bar{p} = \frac{\bar{p}a_A}{\bar{w}}$$

Selective change in gene frequencies

Fundamental theorem
of phenotype selection
(Robertson equation)

$$\Delta \bar{z} = \frac{1}{\bar{w}} \text{cov}(w, g)$$

Selective change in traits

$$r_{w, z} = 0$$

$$g = g_{(w)}$$

Fundamental theorem
of selection and heritability
(Breeder's equation)

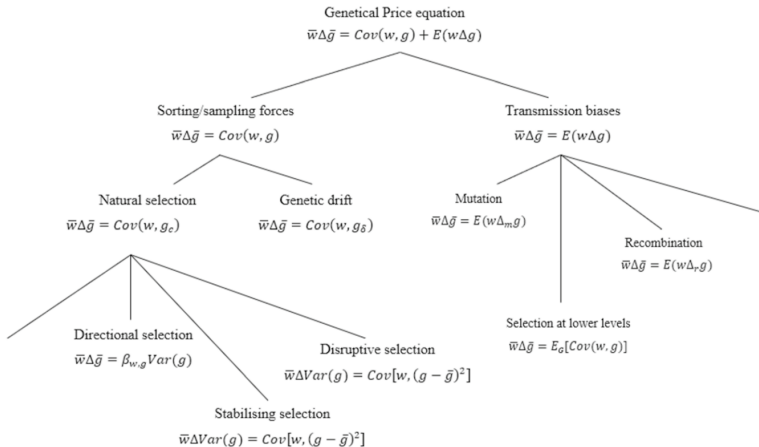
$$\Delta \bar{z} = sh^2$$

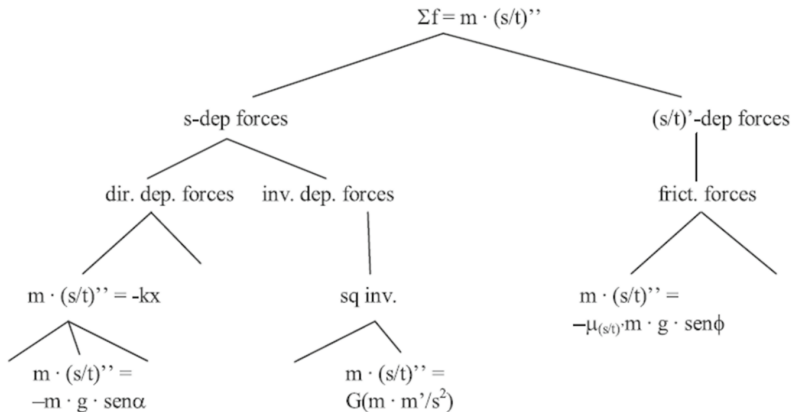
Partitions selection and heritability

Fundamental theorem
of adaptation
(Fisher's fundamental theorem)

$$\Delta \bar{w} = \frac{1}{\bar{w}} \text{var}(g_{(w)})$$

Selective change in fitness





Theoretical framework for modern coexistence theory

$$r_i(t) = g_i(E_i(t), C_i(t)) .$$

Theoretical framework for modern coexistence theory

$$r_i(t) = g_i(E_i(t), C_i(t)).$$

Consider deviations from equilibrium values E_i^* and C_i^* ,

$$g(E_i^*, C_i^*) = 0.$$

Density-independent effects on $r_i(t)$ defined by deviations of $E_i(t)$,

$$\mathcal{E}_i = g(E_i(t), C_i^*).$$

Density-dependent effects on $r_i(t)$ defined by deviations of $C_i(t)$,

$$\mathcal{C}_i = g(E_i^*, C_i(t)).$$

Theoretical framework for modern coexistence theory

$r_i(t)$ completely attributed to \mathcal{E}_i , \mathcal{C}_i , and their interaction \mathcal{I}_i ,

$$r_i(t) = \mathcal{E}_i(t) + \mathcal{C}_i(t) + \mathcal{I}_i(t).$$

The full description of invasion growth,

$$\bar{r}_i = r'_i + \Delta\rho_i + \Delta N_i + \Delta I_i + \Delta\kappa_i.$$

- ▶ r'_i Frequency-independent effects
- ▶ $\Delta\rho_i$ Static niche differences (e.g., resource partitioning)
- ▶ ΔN_i Non-linear responses to factors affecting \mathcal{C}
- ▶ ΔI_i The storage effect
- ▶ $\Delta\kappa_i$ Population density and growth covariance

Multiple coexistence models, but limited organisation

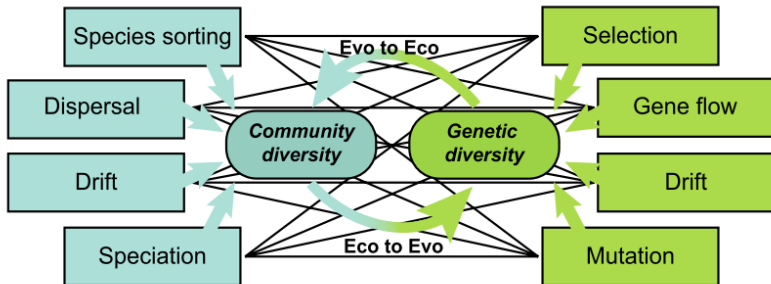
TABLE 1. Models.

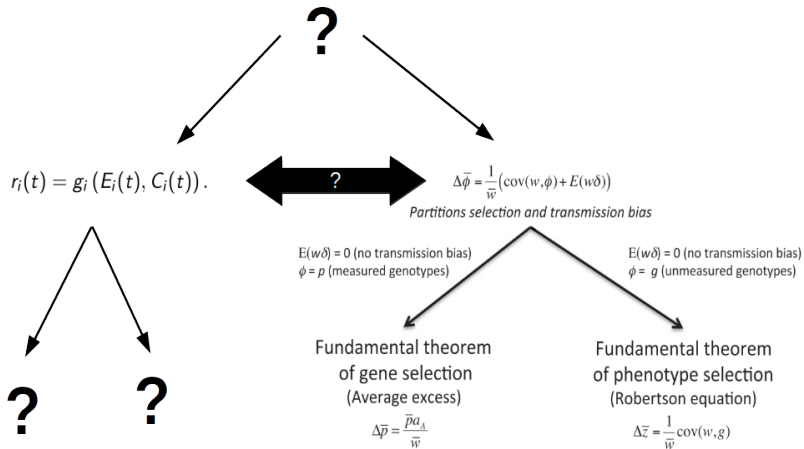
Model	$r_j = g_j(E_j, C_j)$	Meaning of E_j	Meaning of C_j	Other parameters
Lottery model, ratio-scale parameters (Chesson 1994)	$\ln\left\{1 - \delta_j + \frac{E_j}{C_j}\right\}$	per capita births	(demand for space)/(supply of space) $\sum_{k=1}^n E_k N_k / \sum_{k=1}^n \delta_k N_k$	δ_j adult death probability
Lottery model, ln-scale parameters (Chesson 1994)	$\ln\{1 - \delta_j + e^{E_j - C_j}\}$	ln(per capita births)	ln(demand for space/supply of space) $\ln\left[\sum_{k=1}^n e^{E_k} N_k / \sum_{k=1}^n \delta_k N_k\right]$	δ_j adult death probability
Seedbank model (Chesson 1990)	$\ln\left\{\frac{s_j(1 - E_j)}{+ Y_j E_j / C_j}\right\}$	germination probability	total seedling competition $1 + \sum_{k=1}^n \alpha_{jk} E_k N_k$	s_j seed survival probability; α_{jk} competition coefficient
MacArthur consumer–resource model (Li and Chesson 2016)	$E_j(H_j - C_j) - \mu_j$	resource uptake rate	reduction in resource availability due to competition	μ_j maintenance requirement; H_j maximum resource availability

Note: The variables r_j , E_j and C_j , and the function g_j , are defined in *Multispecies coexistence in a variable environment* before Eq. 1.

TABLE 1 Overview of less explored directions (first column), potential hypotheses (second column), and how they can be experimentally tested (third column). Light green rows reflect questions concerning how evolutionary processes and genetic diversity influence community diversity and processes. White row reflects how ecology (here niche overlap between species) can influence evolutionary processes. Dark green rows reflect broader questions about interactions between evolutionary and community processes. This table does not test all possible ideas or interactions, but highlights a few that are interesting

Less explored directions	Hypotheses	How to test?
1. Does genetic drift affect community structure and dynamics?	We expect a stronger impact of genetic drift on community processes, when species on average have small population sizes with additional potential interactions from ecological drift. Genetic drift in just one species might have a strong effect if that species is a foundation or keystone species	Experimentally vary population sizes and genetic diversities of species to estimate effects of genetic drift on community structure via its interaction with each of the four community processes. This would result in, for example, measuring species abundances (species sorting), or extinction probability of species (ecological drift)
2. Does evolution by natural selection interact with ecological drift?	We expect hard selection to initially reduce community size and therefore increase the effect of ecological drift. This may lead to alternative community assembly trajectories linked to ecological drift, even though community sizes may increase again following adaptive evolution	Experimentally vary the level of hard selection in a multi-species community to determine effects on ecological drift by measuring species abundances and the role of stochasticity in population dynamics
3. Does gene flow interact with ecological drift?	We expect moderate gene flow could increase population sizes by overcoming inbreeding and thus reducing ecological drift. High gene flow could depress absolute fitness by swamping local adaptation, causing population declines, reducing community size, and increasing ecological drift	Experimentally vary the level of gene flow in a multi-species community to determine effects on ecological drift by measuring species abundances and the role of stochasticity in population and community dynamics





Some thoughts on starting points

- ▶ Different scales (communities of populations versus populations of entities)
 - ▶ Different entities (population densities, trait values)
 - ▶ Same system (birth, death, growth/fitness)
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The Price equation starts with frequencies (p_i), while population dynamics start with densities (n_i). How can this be reconciled?

The Price equation is recursive, and could potentially accommodate scales of within community (among population) and within population (among individual) change at both levels.

The original plan

- ▶ **APR 2020:** Establish evolutionary and ecological axioms
- ▶ **SEP 2020:** Derive a unified equation (or set of equations) that encompasses all ecological and evolutionary change within a community, and partitions change into terms of ecological and evolutionary components.
- ▶ **JAN 2021:** Explore the consequences of the conceptual unification of modern coexistence theory and evolutionary theory.
- ▶ **MAY 2021:** Disseminate the theoretical work in the form of peer-reviewed journal articles.

Original UNICOP objectives

1. Derive fundamental equations underlying modern coexistence theory and evolution from a minimal sets of axioms of biological processes (e.g., birth, death, reproduction).
2. From the minimal set of axioms underlying modern coexistence theory and evolution, derive an equation(s) that encompasses all ecological and evolutionary change, from which fundamental equations of population and phenotypic change can be re-derived by removing uniquely evolutionary or ecological assumptions, respectively.
3. Investigate the (conceptual, theoretical, and empirical) consequences of a unifying equation of ecology and evolution for modern coexistence theory, and attempt to formally prove one or more general relationships between (co)evolution and species coexistence.
4. Apply new equation(s) and proof(s) to suggest new approaches for modelling eco- evolutionary systems.

