

Coevolution under constraint, and the special role of mutualism

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Notes on Meta

Take out Δa model and direct model. Just discuss already-published cases of accumulation of mutualism.

Add some info about natural historical evidence, via Bronstein/Akcay book and Boucher.

Do exposition of basic AD stuff in body of text simple and clear. Leave details to appendix.

Put predation model before competition model - it illustrates direct and indirect very well, while the competition model involves evolution of an exterior quantity R^* .

Distinguishing ToC concept of utility from what's in these models. For most part, probably take ToC out of this ms.

Complete analysis of how constraints cause qualitative results, in competition, predation, mutualism model. Connect it to published discussion of adaptation in these systems.

Analyze competition model in terms of evolution of R^* quantities?

Concise discussion of Masel's paper? Is it necessary?

Selection gradient, etc, in pop gen?

Response to Roughgarden's thing about change in the a matrix?

Mention of change in game matrix, don't actually do the math in this paper. Likewise $S()$ in microeconomics, learning.

The major points:

- Direct effect is biased positive
- 3-part program for study of adaptation and cooperation
- Connection to game theory/altruism literature.

Introduction

To be written.

Use of the four types (quadrants) of Lotka-Volterra interactions to classify ecological relationships

Interest in the causes of mutualism and antagonism

Natural history examples: emergence of mutualism, and loss of mutualism

Evolution of constrained phenotypes; connection to Levins fitness sets

Coevolutionary dynamics, frequency-dependent selection

Related questions about cooperation, incentives, and externalities. Comments on +/+ cooperation vs. standard ideas of cooperation/altruism. Cost of cooperation, emergence of dilemmas and tragedies.

Review of multidimensional adaptive dynamics

[bring (some?) from appendix.]

Cover selection gradient, covariance matrix of mutation distribution.

Sidebar?: selection gradient stuff in pop gen

Coevolution of constrained characters

When relevant characters p are parametrized by fewer u 's

Projection of gradient.

Angle of projected motion is within 90° of the unabridged gradient.

Stasis is when original S is 0 or the curve is perpendicular.

Figure illustrating the gradient before + after, with curve.

Coevolution of interaction terms

GLV model structure, with $r(u)$ and $a(u,u)$.

a_{ij} terms are sort of like p 's, controlled by u 's, but with the influence of the other u as well.

Agent and patient roles.

Gradient of selection is projected through patient roles.

That selection produces “direct effect”.

There is also “indirect effect” of the agent population, also known as frequency-dependent selection (?).

Gradient $S(A)$ is always positive.

Direct effect is within 90° of that positive vector S .

Resulting change in A values is direct effect + indirect effect, therefore biased toward positive but can be negative.

Figure: Evolution of (a_{ij}, a_{ji}) pair on the plane of Lotka-Volterra interactions.

Figure: The vector $A_i = (r_i, a_{i1}, \dots, a_{in})$ moves in an $n + 1$ -dimensional space (in the illustration $n = 1$ or 2).

Figure: Gradient of selection on A_i in one dimension is in direction closest to abstract gradient of selection S .

Figure: Each population j changes due to selection on a_j terms. It causes change in a_{ij} , which is the source of the indirect effects on A_i .

Figure: The direction of the direct effect is always in the half-space within 90° of the abstract selection gradient S . S is always positive, which implies that the direct effect vector D is largely positive. The resultant direction of actual change in A_i is the sum $\mathbf{D}_i + \mathbf{I}_i$. The positive bias in \mathbf{D}_i may produce a positive bias in the motion of A_i .

Figure: direct and indirect effects on the pair (a_{ij}, a_{ji}) .

Claims and questions about evolution of interactions

The above argument establishes that if direct effects and indirect effects were IID random variables, interaction terms would drift upwards.

They may not, though.

- The “default”, or *ceteris paribus*, outcome is the direction of unconstrained selection: positive drift, toward the mutualistic quadrant. When interactions do not move in that direction, there are two categories of constraints interfering with positive drift:
- Populations may not be able to increase the value of all their interactions due to tradeoffs in the different interaction terms affecting the population as patient. That is, the shape of the “fitness set” of the interactions affecting the population.

- Gains in the value of interactions may be lost due to negative indirect effects of agents' adaptation on patients. This can imply a zero-sum situation in which one population's gain is another's loss, or a Hardin-like tragedy ("race to the bottom", or social trap), in which a population's direct gain is indirectly its own loss.

earlier paper proposed to focus away from presumed costly cooperation.

I propose the above three-part structure as an alternative framework for researching the evolution of cooperation, focusing on **factors that interfere with the emergence of cooperation** in addition to studying means for mitigating tragic situations in which cooperation is hard.

This research may help us to explain both mutualistic and antagonistic situations in nature and society, and may also help illuminate opportunities to transform antagonistic situations or social traps to opportunities for mutual benefit.

Example: Predator-prey model

Along with competition, predation is the other big failure to mutualize. [or parasitism/disease?]

Predation interactions are in the $+/-$ quadrants.

I imagine predator and prey will have benefits from direct effects, detriment from indirect effects on each other, some balance of the two.

Model is a foodweb graph with simple density-dependent competition on the autotroph level.

Predation is a function $f(u_i, u_j)$, on both a_{ij} and a_{ji} terms, because it's number of predation events.

r is 1 for autotrophs, -1 otherwise.

We consider scalar u for each population.

Selection pressures on predators and prey

Selection is only in a terms, via $f(u,u)$

Gradient is made up of $\partial f / \partial u$ terms.

I will use the functional form $f(u_i, u_j) = 2 + \alpha \cos(u_i - u_j)$, with some $\alpha \in (0, 1)$.

Antisymmetry allows use of a single f

Thus the direction of selection on u_i depends on a weighted sum of influences of its prey and/or predators

Example: one prey, one predator

When there is only population 1 eating population 0

Simple S vector, -1, +k

Selection is stronger on the prey, so it escapes.

This example perhaps follows the “life-dinner hypothesis”, in which selection acts more strongly on prey because they have more to lose from each interaction (Dawkins and Krebs 1979).

Using the cosine form, equilibrium is at $u_0 - u_1 = (2n + 1)\pi$, where predation is least.

Figure: prey u escaping from predator u

Another example here?

Direct and indirect effects in the 2-species example

Write the A vector

The direct effect is increase in the predation interaction that affects you, with a factor of k^2 for the predator.

The indirect effect is harm to the interaction that affects you, due to the other's incentive, with a factor of k on both.

The resultant change is one mitigated by the other. The k factors make it so the prey prevails.

The 1:-k ratio between the pair is preserved.

The expression for change in (a,a) pair is nice and clean.

Direct and indirect effects in the general case

In general community structure, here is $S(u)$ - move away from predators and toward prey, with weighting by \hat{X} and k.

Motion of each (a,a) pair is a natural quantity

Weakening the constraint

Can I analyze the role of the constraint that prevents $S(A)$ from happening?

Do a model where variation can violate the constraint, Show it introduces up-and-right drift

Example: Resource competition

Here we analyze the classic MacArthur-Levins formulation of n species competing for use of n resources.

ML equations.

It's an LV system.

Function forms of a and r terms.

It's constrained to competition only - we will relate that constraint to the direct and indirect effects.

Evolution of ecological parameters

Logistic equation with $r(u)$, $K(u)$

Given rare mutations, popdyn equilibrium, selection purely increases K , if population is lower it increases r .

We write an vector $p=(r,K)$.

The former result is in the selection gradient.

We impose smaller \hat{X} to get the r -selection result from the selection gradient as $\hat{X} \rightarrow 0$.

The Lotka-Volterra terms in this model

To do adaptation we really need a resident-mutant form of the eqn - doing it the most obvious way gives the above results.

The r and A are simple functions of r and K

Incentive and impact

We can write the multitype form differently though, and get different outcomes.

If we make K go with the agent rather than the patient in the interaction

Selection is neutral on K and r , drifts.

Why does the former Verhulst model decrease competition while the resource one increases it?

In the former V model, K is connected to incentive, while in the latter it's impact, which is ignored by natural selection.

Here's a combined model that has both - k_s for incentive (other's impact on self), k_f for impact (self's impact on the other).

Do a change of variables, write the selection gradient.

Incentive is to increase k_s , ignores k_f .

Introduce u , monomorphic population.

k_f changes as a side effect of u changing via selection on k_s

population size increases unless change in k_f is *sufficiently* anticorrelated with k_s .

The total impact on the environment increases no matter what, due to some oddity of the population size self-regulation.

Yet the a term moves away from competition? Or does it?

The direct effect of selection is something (so what?)

Competition for space vs. resource competition

Form of the A vector in each model.

Then what?

Externalities and the threat of “cheating” in evolution of mutualisms

Transitions between mutualism and parasitism

[To come. Roughgarden symbiosis model.]

Example: statistical mechanics of interactions.

Model of n species where the angle on the (a,a) plane is chosen uniformly.

There is a trend up and right.

Example: Hardin's Tragedy of the Commons

simple ToC model is same as the MacLev model

ToC is understood to be an indirect effect.

Direct effects are interesting in the model too.

But ToC uses a different definition of utility/benefit/detriment than we are using here, with more or less competition.

Game theory payoff terms are somewhere in between.

[This and the game theory section below might be better to leave for a future paper]

Example: adaptive change in a game theory payoff matrix

[selection gradient in rational action models.]

[game theory payoff matrix entries behave just like L-V matrix entries under certain assumptions about changing game.]

[transition from one game structure to another, like shift in interaction types.]

Discussion

Appendices

Adaptive change in constrained characters

dynamics of phenotypic character vector p via invasion fitness, Metz, Ma

Notation, p a column vector, $\partial_1 \mathcal{I}(p)$ a row, etc.

Change in p follows the selection gradient $S(p)$.

[Discuss how the rare mutant is the patient and the resident is the agent]

[Consider discussing how this is in population genetics as well.]

Per Levins, motion to the boundary leads to lower-dimensional dynamics, motivating $p(u)$.

Above analysis applies to $S(u)$.

dp/dt comes from the chain rule.

Derivation of constrained selection gradient $S_c(p)$.

Covariance matrix imposed by the constraint $\partial p / \partial u$.

Lemma: the angle between $S(p)$ and $S_c(p)$ is no more than 90° .

Corollary: S_c is within the half-space defined by S .

On a curve, the half-space generally defines one of the two available directions.

Direct and indirect effect of adaptation on interaction terms

a values are similar to $p(u)$ but parametrized by two u values at a time, so there are extra complexities.

$S(u)$ in a GLV model

du_i/dt in GLV

Chain rule to write motion of r and a

$S(u_i)$ cares only about places where u_i is *patient*, not agent.

Define patient and agent.

Construct vector A of GLV quantities that drive motion of u_i

Write du_i/dt in terms of that vector - it looks like the case with p .

Define $S(A)$

$S(u)$ in terms of $S(A)$ is just like the $S(p)$ case.

But the motion of A is not like the motion of p , because agent roles also affect it.

Split motion of A into *direct effect* of patients responding to selection p -like, and *indirect effect* of agents altering course of interactions with externalities.

Figure: selection and indirect effect on a - a plane

Direct effect is within 90° of $S(A)$

- Given n populations, there are n intrinsic growth terms r_i and n^2 interaction terms a_{ij} .
- We arrange those values into n “interaction phenotypes” \mathbf{A}_i .
- For each \mathbf{A}_i there is a selection gradient $\mathbf{S}(\mathbf{A}_i)$, which is the direction of greatest increase in the invasion fitness of population i , when we vary population i as a rare invading population with all resident populations’ phenotypes held fixed (including population i), that is, as the first argument to $k(\mathbf{u}_i)$ and $a(\mathbf{u}_i, \mathbf{u}_j)$, the patient.
- Adaptive change in the i th population must be in a direction that would move \mathbf{A}_i within 90° of its selection gradient $\mathbf{S}(\mathbf{A}_i)$, considering i as an invader with all resident populations held fixed.
- The direction of change in \mathbf{A}_i due to that change in the i th population is the “direct effect” of selection on \mathbf{A}_i , \mathbf{D}_i .
- The direction of change in \mathbf{A}_i due to changes in all the resident populations, considered as agents, i.e. as the second argument to $a(\mathbf{u}_i, \mathbf{u}_j)$, is the “indirect effect” of selection on \mathbf{A}_i , \mathbf{I}_i . Note that this includes an indirect effect of population i on itself.

Upward bias in direct effects

$R()$ and $a()$ can have any form

But these results imply an upward bias.

$S(A)$ is always 1,X

That's all positive.

Therefore the direct effect can't be all negative, and is within 90 degrees of that positive vector. Ceteris paribus argument about rise.

Can we assume indirect effect to be unbiased? There's an argument to be made.

Sometimes a values increase and sometimes don't. Framework for examining when they do and do not increase:

- The all-positive entries of the interaction selection gradient can be interpreted in terms of the meaning of a specific model's parameters, describing what selection "would like to do" if all degrees of freedom were available.
- Constraints on actually available variation in r and a terms cause the direct effect to point in a different direction from the interaction selection gradient. This can be interpreted in terms of tradeoffs and constraints imposed by the functional form of r and a , as functions of the model's parameters. Unpacking these constraints can shed light on how model assumptions constrain the evolution of interactions.
- The indirect effects of each population's adaptation on other populations, and on itself, can change the resulting dynamics of interactions from what they would be due to direct effects alone. These effects can be interpreted in terms of interplays or tensions between evolutionary "self-interest" and impacts of ones change on others.

Use of these three parts to study how changes in interactions depend on assumptions.

In this paper I explore these themes in various familiar models.

Direct and indirect effects in the Lotka-Volterra plane

Motion of pairs on a-a plane.

Definition of direct and indirect effect on a single a_{ij} value

And on a pair.

Equation for motion of pair

Reveals nothing in particular about upward bias, but it's there because they're entries in the A vectors.

motion of (a,a) in terms of partials of $a()$ instead

Direct effects of constraints on interactions

The direct effect is $S(A)$ constrained to available-variation curve

“effect of constraint” $C_i = D_i - S(A)$

$$dA/dt = S(A) + C_i + I_i$$

Rewrite of D_i

Leading to the form of C_i

When you have constraint but not indirect effect, it's **density-dependent selection**, while indirect effect is **frequency-dependent selection**.

Indirect effects of externalities on interactions

[nothing here yet]

Structure of direct and indirect effects in monomorphic models

Direct effect

Direct effect is the motion without frequency dependence.

Consequence: in monomorphic model, density-dependent selection can reduce r or a but not both [and should be a polymorphic thing where at least one term increases?]

Sign condition for selection on r and a to be in conflict.

If not in conflict (and no zeros) then both increase.

If in conflict then one increases, other decreases.

Condition for increase in r

Condition for increase in a

Those give 3 cases, one increases, the other does, or both do.

There is no case in which both r and a decrease due to direct effects of selection.

Externalities

Externalities aka indirect effects act on a but not on r .

Indirect effect in monomorphic model

I.e. on a term uses $\partial_a a$ to relate effect to $S(u)$.

Combine it with D to write full effect of adaptation on a
Condition for decrease in a, i.e. sort of “tragedy of commons”
 $\partial_2 a$ has to be opposite in sign from ∂_1 , and sufficiently large.

Details of resource competition model

[this stuff is in the main body currently]

Details of predator-prey model

Details of mutualism model

Details of “statistical mechanics” model

How to choose $a()$ functions or phenotype vectors to get random angles
 $\partial_1, \text{partial}_2$.

Do community assembly to get some coexisting species.

Then watch what adaptation does.

Example plots on lv plane.

Also statistics on many runs?

Adaptive change in game theory payoff matrix

Details of game theory models

Bibliography

Dawkins, R., and J. R. Krebs. 1979. “Arms Races Between and Within Species.”
Proceedings of the Royal Society of London. Series B, Biological Sciences 205
(1161): 489–511.