Coevolution under constraint, and the special role of mutualism

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Overture: evolution of interaction matrix

Introduce the Δa_{ij} model. Motivations include Kauffman's *Investigations* on non-specifiability of affordances

Figure: evolution of a_{ij} terms in that model.

Major result: accumulation of mutualistic interactions.

That model has problematic discontinuities in a_{ii}, so I introduce an adaptive dynamics counterpart to the model.
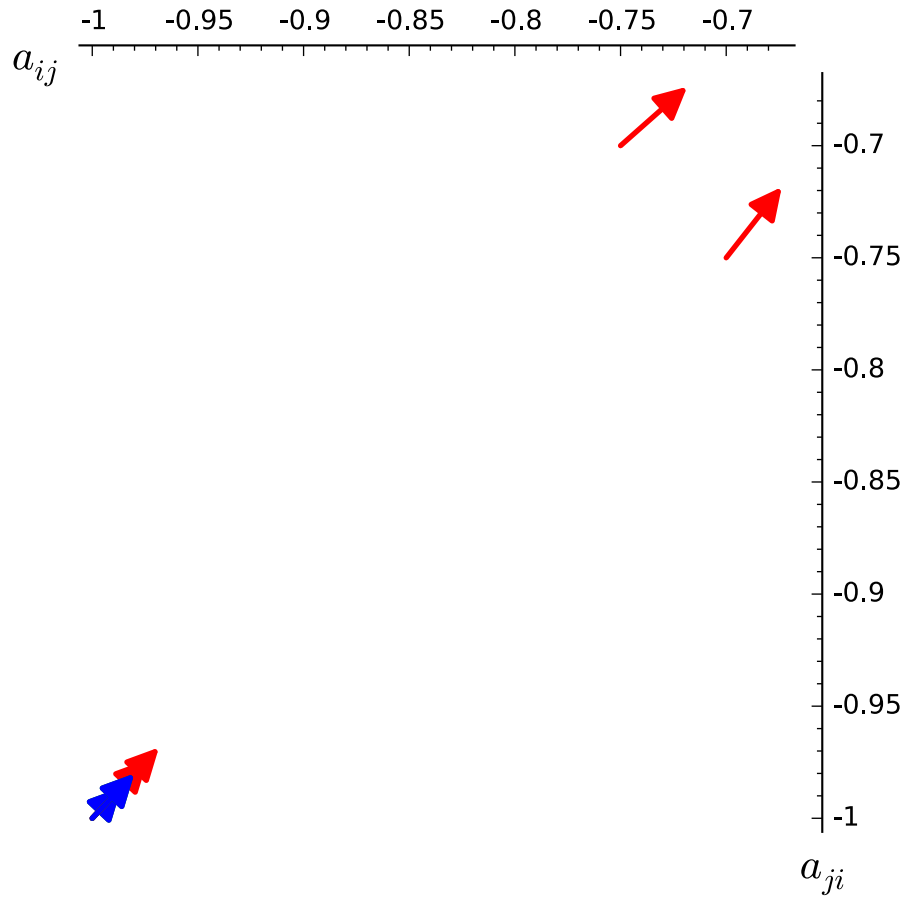
Figure: results in that model.

Something about questions this raises and how it motivates the following theory. Relationship to temptation-to-defect theory of cooperation.

Mention prisoner's dilemma paper.

direct model
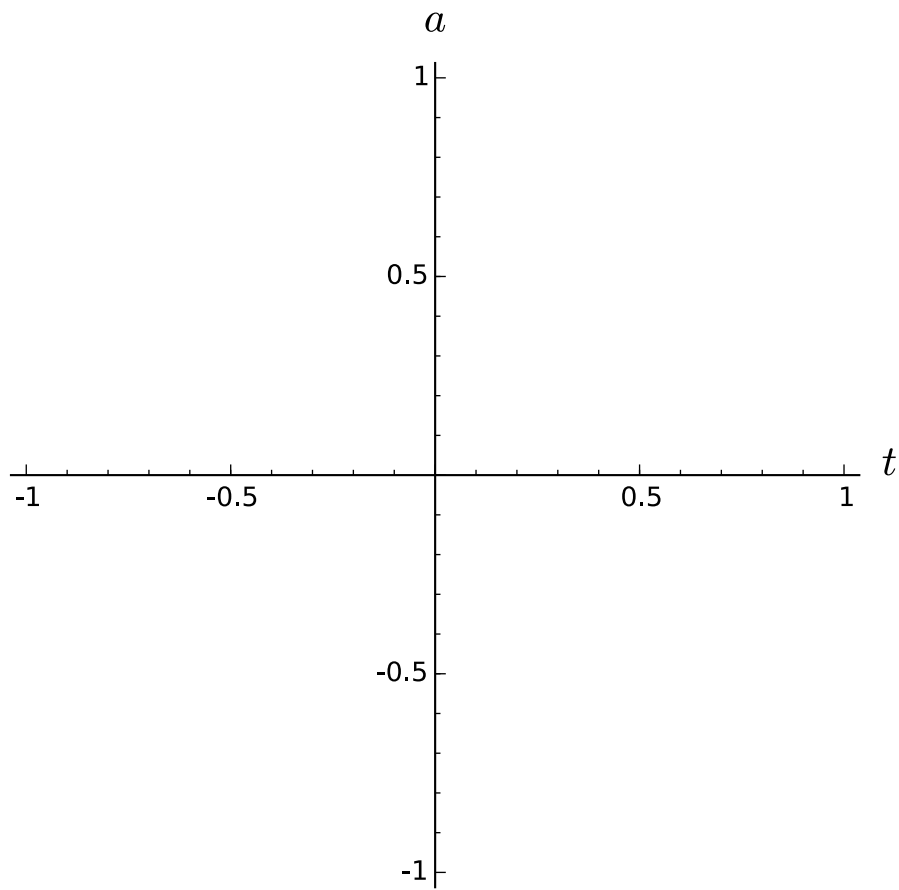
Adaptive dynamics version of byproduct model

- To do: A-vs-a plot of similar model but with an initial branching?

Contrasting example: competition for space

- To do: rewrite, shorten by using Masel's paper

The other classic ecological competition model is the one that gives rise to the traditional distinction between r-selected and K-selected species. We take the simple Verhulst equation for logistic growth in a single population, and suppose that the two parameters r and K are in fact affected by the population's phenotype u:

$$\frac{dX}{dt} = r(u)X\left(1 - \frac{X}{K(u)}\right).$$

If adaptation occurs when the population is at its equilibrium size, the well-known result is that selection acts to increase the carrying capacity K and is indifferent to the per-capita reproduction rate r. If disturbances acts to reduce the population below carrying capacity, on the other hand, then selection tends to increase r.

To recast this result into the terms of this paper, we construct a vector of the population's ecological characteristics:

$$\mathbf{p}(u) = \begin{pmatrix} r(u) \\ K(u) \end{pmatrix}.$$

The selection gradient on $\mathbf{p}$ is

$$S(\mathbf{p}) = \begin{pmatrix} \frac{\partial}{\partial r} \frac{dX}{dt} \\ \frac{\partial}{\partial K} \frac{dX}{dt} \end{pmatrix} = \begin{pmatrix} 1 - \frac{\hat{X}}{K(u)} \\ r(u)\frac{\hat{X}}{K(u)^2} \end{pmatrix} = \begin{pmatrix} 0 \\ r(u)\frac{\hat{X}}{K(u)^2} \end{pmatrix}$$

From this we can see directly that the gradient of selection is entirely in the direction of increasing K, and it follows that selection on u will necessarily be in a direction that increases K, regardless of the impact on r. This is because the first entry of $S(\mathbf{p})$ vanishes when $\hat{X} = K$.

In the r-selection case, we suppose that disturbance acts to reduce population size, so that $\hat{X} < K$. Then

$$S(\mathbf{p}) = \begin{pmatrix} 1 - \frac{\hat{X}}{K(u)} \\ r(u)\frac{\hat{X}}{K(u)^2} \end{pmatrix},$$

so that selection will favor increase in both r and K. If $\hat{X}$ is reduced to near 0, selection will become almost entirely on r.

The Lotka-Volterra terms in this model

The above is actually ambiguous: in order to model adaptation it's necessary to define a multiple-population form of the model, to specify how a resident and rare variant type will interact. The obvious form is

$$\frac{dX_i}{dt} = r(u_i)X_i \left(1 - \frac{\sum_j X_j}{K(u_i)} \right).$$

This model produces the results summarized above. If multiple populations have different $K(u_i)$, the only stable equilibrium will be monomorphic with only the population with largest K persisting. Thus selection increases K without regard to r when it acts on a population at equilibrium.

This model is of course a very simple case of the Lotka-Volterra form, with $r_i = r(u_i)$, and $a_{ij} = -r(u_i)/K(u_i)$. Thus increasing K reduces competition, and increasing r increases competition.

Incentive and impact

It is possible to extend the Verhulst equation to multi-population form differently, however, as we will see, with different results.

For example if

$$\frac{dX_i}{dt} = r(u_i)X_i \left(1 - \sum_j \frac{X_j}{K(u_j)} \right).$$

In the previous form, $K(u_i)$ quantifies what total population size it takes to make population i stop increasing: it's the response of population i to total numbers of all populations. In this form, $K(u_j)$ quantifies how much an individual of population j contributes to suppressing the growth of all populations – to be precise, $K(u_j)$ is the number of type j individuals it would take to stop population growth in the absence of any other population.

In the latter model, all populations come to equilibrium together when $\sum_j X_j/K(u_j) = 1$. There is a continuum of such equilibria. Selection is neutral in this model, and variant types that arise will tend to accumulate in the community at low population sizes. I will refer to these two models as the direct and indirect models, respectively.

The outcome of this model with population at equilibrium is the opposite of the resource competition model above: in that model competition increases as populations use more and more of the resources, and in this model competition decreases as they use more and more of the habitat. To unpack this difference, we want to compare this model to the resource model. In this section we will consider only the equilibrium case with $\hat{X} = K$, which leads to K selection.

In the former of these two models, the quantity $K(u_i)$ describes individuals' sensitivity to crowding while all contribute equally to crowding, while in the latter, $K(u_j)$ describes individuals' contribution to crowding while all are equally

sensitive to it. In a meaningful sense, the former describes **incentive** on individuals due to the environment while the latter describes **impact** on the environment due to individuals. We can study the interplay between the two by making a combined model:

$$\frac{dX_i}{dt} = r(u_i)X_i\left(1 - \sum_j \frac{X_j}{k_s(u_i)k_f(u_j)}\right).$$

where we allow for two carrying-capacity factors, $k_s(u_i)$ describing the sensitivity of population i to crowding and $k_f(u_j)$ describing the "ecological footprint" of population j. One way to interpret this model is as though each individual of type j contributes $1/k_f(u_j)$ "units" to the population, and when the population's total units reaches $k_s(u_i)$, population i is at "carrying capacity". Thus a single population i in isolation will be at carrying capacity when its size is $k_s(u_i)k_f(u_i)$ individuals.

For convenience, let's write $c_s(u_i) = 1/k_s(u_i)$ and $c_f(u_j) = 1/k_f(u_j)$, so that we have $a_{ij} = -r(u_i)c_s(u_i)c_f(u_j)$ (and $r_i = r(u_i)$). The selection gradient on u_i is

$$S(u_i) = r'(u_i)\left(1 - \sum_j c_s(u_i)c_f(u_j)\hat{X}_j\right) - r(u_i)\sum_j c_s'(u_i)c_f(u_j)\hat{X}_j$$

$$= -r(u_i)c_s'(u_i)\sum_j c_f(u_j)\hat{X}_j.$$

This quantity has the sign of $-c_s'(u_i)$ because all its other factors are positive. Thus u_i adapts in the direction that decreases $c_s(u_i)$, which is the direction of increase in $k_s(u_i)$. The actual impact on the habitat is controlled by $k_f(u_i)$, which has no influence on selection.

In general, this model only supports one population at a time at equilibrium. Let us assume a single changing population described by phenotype variable u.

The per-capita impact on the environment, $k_f(u)$, increases if $k_f'(u)$ has the same sign as $k_s'(u)$ and decreases if the derivatives have the opposite sign.

The equilibrium size of the changing population is $k_s(u)k_f(u)$. The change in this size is

$$\frac{d(k_s(u)k_f(u))}{du} = k_s'(u)k_f(u) + k_s(u)k_f'(u).$$

The equilibrium population size increases when that quantity has the same sign as $k_s'(u)$:

$$\frac{k_s'(u)k_f(u) + k_s(u)k_f'(u)}{k_s'(u)} = k_f(u) + \frac{k_s(u)k_f'(u)}{k_s'(u)} > 0$$

$$\frac{k_f'(u)}{k_s'(u)} > -\frac{k_f(u)}{k_s(u)}.$$

This condition is satisfied any time k_f increases along with k_s, any time k_f is unchanging, and additionally when k_f decreases as k_s increases but its rate of change is sufficiently small.

The total impact on the environment is $\hat{X}/k_f(u) = k_s(u)$, which is an increasing quantity. Thus interestingly, even in this more nuanced model, which unhinges environmental footprint from competition to use space, K selection drives increasing impact on the habitat. This is very similar to R^* competition. Yet the Lotka-Volterra competition coefficient, $a_{ii} = -\frac{r(u_i)}{k_s(u_i)k_f(u_i)}$, shrinks toward zero (if r is compliant) while in R^* competition it does the opposite. [TODO: not entirely true. Clarify.]

The direct effect of selection is

$$D_i = \gamma \hat{X}_i \begin{pmatrix} r'(u_i) \\ -(r(u_i)c_s'(u_i) + r'(u_i)c_s(u_i))c_f(u_1) \\ \vdots \\ -(r(u_i)c_s'(u_i) + r'(u_i)c_s(u_i))c_f(u_n) \end{pmatrix} S(u_i).$$

Competition for space vs. resource competition

As above,

$$\mathbf{A}(u) = \begin{pmatrix} r(u) \\ -r(u)/K(u) \end{pmatrix}.$$

For reference, in the one-species, one-resource MacArthur-Levins system,

$$\mathbf{A}(u) = \begin{pmatrix} b(u)c_1(u)w_1 K_1 - b(u)m(u) \\ -b(u)c_1(u)^2 w_1/r_1 \end{pmatrix}.$$

In both cases, the selection gradient on $\mathbf{A}$ is, as always, $\mathbf{S}(\mathbf{A}) = \begin{pmatrix} 1 \\ \hat{X} \end{pmatrix}.$

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Example: Hardin's Tragedy of the Commons

This model turns out to be formally equivalent to the resource competition model with only one species (here called "cattle ranchers").

We understand the tragedy of the commons as an indirect effect of the population on itself: as patient, the adaptive step (deploy more livestock) improves utility, but as agent, that step leads to a degradation in the environment and drags the population's utility down.

It's probably interesting to tease out the direct effects in this model, since we understand the tragedy of the commons as an indirect effect.

But we also need to unpack the difference between using a utility function to define benefit (vs. harm) and using Lotka-Volterra terms to define it. The tragedy of the commons is a question of declining utility, and that may be different from the benefit that's defined by motion up and to the right in the Lotka-Volterra plane: specifically, utility is an absolute quantity while L-V values are marginal. There is no absolute fitness in the coevolutionary analysis I'm using, only differences in fitness relative to a baseline which is always redefined to be zero. (However, the entries of a game theory payoff matrix are closely analogous to L-V interaction terms, and in fact they are indistinguishable from them when the replicator dynamics model is used.)

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

Adaptation of economic actors by learning, under just about any reasonable simple model assumptions (within the rational-choice framework), follows the same gradient as the above evolutionary models. Thus all the geometrical analysis holds, including the three-part research framework.

In this section I demonstrate how the terms of the game's payoff matrix change in just the same way as the Lotka-Volterra interaction terms.

Then make a little sketch of how a social interaction might transition among prisoner's dilemma, snowdrift, stag hunt, and byproduct cooperation structures, seen as a matter of coevolving constrained terms of the payoff matrix.