1. Setting the Stage

Models are (families of) mathematical structures together with an interpretation rule.

Theories are either rules for constructing models (in the sciences), or frameworks dealing with many different models of similar type in one go (in mathematics).

Adaptive Dynamics belongs to the latter class.

The reason to go axiomatic is to delineate classes of problems that keep recurring.

The interpretation rules for AD models are in terms of underlying community models.

The interpretation rules for community models can be decomposed in a step to some underlying individual-based stochastic model, and from there to reality.

These considerations serve as guidelines for a proper choice of definitions and axioms.
Adaptive Dynamics aims at making the transition to macro-evolution, but concentrates on only one component of the evolutionary mechanism: the filtering of novel mutations by the ecology.

The modern synthesis has only shown that micro-evolutionary mechanisms and macro-ecolutionary patterns are compatible.

It did not add flesh and blood to the connection.

Adaptive Dynamics aims at making the transition to macro-evolution, but concentrates on only one component of the evolutionary mechanism:

the filtering of novel mutations by the ecology

Credo:

- The fitness of a given type in a given stationary environment can be defined as the (asymptotic, average) exponential growth rate of a (hypothetical) clone of individuals of that type in that environment.
- For mutants the environment is set by the population dynamics of the resident types.

Note that as fitness is measured here on a logarithmic scale, zero is neutral.

Corollaries:

- Fitneses are not given quantities, but depend (1) the traits of the individuals, (2) the environment in which they live.
- The ecological feedback loop sets the fitnesses of all resident types equal to zero.
- Evolutionary progress is largely determined by the signs and sizes of the fitnesses of potential mutants.
2. The Population Dynamical Basis

Evolution proceeds through uphill movements in a fitness landscape that keeps changing so as to keep the fitness of the resident types at exactly zero.

Levels of Abstraction
illustrated by the spaces that play a role in adaptive dynamics theory:

1. the physical space in which the organisms live
2. the state space of their individual-dynamics
3. the state space of their population-dynamics
4. the abstract space of influences which they undergo, (the fluctuations in light, temperature, food, enemies, conspecifics): their 'environment'
5. the ‘trait space’ in which their evolution takes place (= parameter space of their i- and therefore of their p-dynamics): the 'state space' of their adaptive dynamics
6. the parameter spaces of simple families of adaptive dynamics
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\[ s_X(Y) := \rho(E_{\text{attr}}(X), Y) \]

Simplifying assumptions

1. mutation limited evolution \(^1,2)\)
2. good local mixing \(^2\)
3. clonal reproduction \(^2\)
4. largish system sizes,
5. "good" c-attractors
6. interior c-attractors unique \(^3\)
7. smoothness of \( s_X(Y) \) \(^3\)
8. small mutational steps \(^3\)

\(^1\) i.e. separated population dynamical and mutational time scales
\(^2\) can often be relaxed!
\(^3\) only made on some occasions

( often = often.....sometimes ?
  some = some.....most ?)
On the individual-based justification of Adaptive Dynamics

1 Individual-oriented model ("the ecological basis"):
\[ X_i \rightarrow X_i + Y, \ Y = X_i \quad \text{at rate} \quad 1 - \varepsilon \]
\[ X_i \rightarrow X_i + Y, \ Y \in (y, y + dy) \quad \text{at rate} \quad \varepsilon p(y - X)dy \]
\[ X_i \rightarrow , \quad \text{at rate} \quad \sum_j a(X_j, X_i) / [\Omega k(X_i)] \]

2 "classical" deterministic limit: \[ \int_A n(x)dx = \frac{\#[\text{individuals in A}]}{A \Omega} \]
\[ \frac{\partial n(x,t)}{\partial t} = \left( 1 - \varepsilon - \int_{-1}^{1} a(x,y)n(y,t)dy / k(x) \right) n(x,t) + \varepsilon \int_{-1}^{1} p(x-y)n(y,t)dy \]

3 adaptive dynamics: let \( \Omega \rightarrow \infty, \ \Omega \varepsilon \rightarrow 0, \) and rescale time to on average one mutated birth per time unit
\[ X \rightarrow Y, \ Y \in (y, y + dy) \quad \text{at rate} \quad \Omega \Omega(X) \varepsilon p(y - X)dy Q_x(y) [1 - H(s_y(x))] \]
\[ X \rightarrow (X, Y), \ Y \in (y, y + dy) \quad \text{at rate} \quad \Omega \Omega(X) \varepsilon p(y - X)dy Q_x(y) H(s_y(x)) \]

3a canonical equation: subsequently let \( \text{Var} p \rightarrow 0, \) and rescale time to keep the directional movement in view
\[ \frac{dX}{dt} = \frac{1}{2} \alpha \varepsilon \Omega \Omega(X) C \left[ \frac{\partial s_x(Y)}{\partial Y} \right]_{Y=X}^T \text{ with } \alpha = 2 T_f / (T_s \sigma^2) \]
3. Directional Adaptive Dynamics

Adaptive Dynamics: I the monomorphic case

\[ X: \text{trait value of resident} \]

\[ Y: \text{trait value of mutant} \]

Environment

fitness (rate of exponential growth in numbers) of mutant:

\[ s_X(Y) := \rho(E_{attr}(X), Y) \]

* \( Y \) has a positive probability to invade into an \( X \) community if and only if \( s_X(Y) > 0 \).

And after that:

* \( X \) can be ousted by \( Y \) only if \( s_Y(X) \leq 0 \).

Starting from a single individual:

In an ergodic environment:

a population starting from a single individual either goes extinct, with probability \( 1-Q \), or "grows exponentially" at a relative rate \( \rho(E) \).
back to the deterministic theory

Interpretation:

In the community model we linearise around an attractor in the $N_{\text{mut}} = 0$ boundary:

$$
\begin{bmatrix}
N_{\text{mut}}(t+1) \\
N_{\text{res}}(t+1) - \hat{N}_{\text{res}}(t+1)
\end{bmatrix}
\approx
\begin{bmatrix}
A_{\text{mut}} (E_{\text{res}}(t)) & 0 \\
\text{something} & \text{something}
\end{bmatrix}
\begin{bmatrix}
N_{\text{mut}}(t) \\
N_{\text{res}}(t) - \hat{N}_{\text{res}}(t)
\end{bmatrix}
$$

**Example:**

1. $s_{x}(y) > 0$: $y$-mutant can invade in $x$-population
2. $s_{x}(y) < 0$: $y$-mutant disappears from $x$-population

**Graphical representation for 1-dimensional trait spaces:**

Pairwise Invasibility Plots

For univariate (one-dimensional) traits the direction of evolution
Substitution resident by mutant I:

If $s_X(Y) > 0$ and $s_Y(X) < 0$, and nothing untowards happens in the interior of the c-state space, the duration of a substitution is essentially determined by the initial and final exponential phases and therefore by $s_X(Y)$ and $s_Y(X)$.

Example: Gene substitution in Nicholson’s blowflies

![Graphs showing changes in gene frequency and population dynamics](image)

Substitution resident by mutant II:

Let $X$ not be a c-dynamical bifurcation point, nor close to an evolutionarily singular point. Moreover let $\epsilon = |Y-X|$ be sufficiently small.

* Invasion of a "good" c-attractor of $X$ leads to a substitution such that this c-attractor is "inherited" by $Y$, and

$$s_Y(X) = - s_X(Y) \quad \text{up to } O(\epsilon^2).$$

* When an equilibrium point or a limit cycle is invaded, the relative frequency $p$ of $Y$ satisfies

$$\frac{dp}{dt} = s_X(Y) \ p(1-p) \quad \text{up to } O(\epsilon^2),$$

(the classical equation for gene frequency change) [note that $s_X(Y) = O(\epsilon)$], while the convergence of the dynamics of the total population densities occurs $O(1)$. 

![Graph showing gene frequency change](image)
Problems with $E$ determined by an attractor:

For bounded deterministic c-dynamics perturbed by the smallest possible amount of noise convergence to (so-called ep-chain) attractors is guaranteed. However, these attractors do not always give an ergodic $E$.

What is needed is a dense orbit. Moreover, in chaotic attractors there are other, periodic, or orbits, along which one gets different $E$'s and therefore different $\rho$'s: (transversal) Lyapunov spectrum.

The $\rho$ associated with the dense orbit is called natural. This is the only $\rho$ that persists with (a little) noise.
4. Beyond the directional mode: Stepping to Dimorphism

**Dimorphisms I:**

Let $X$ not be a $c$-dynamical bifurcation point.

Moreover let $\varepsilon = |Y - X|$ be sufficiently small, and let $s_X(Y) > 0$ and $s_Y(X) > 0$

$(\Rightarrow X$ is close to an evolutionarily singular point$)$

and let the monomorphic $c$-attractors of $X$ and $Y$ be "good"

Then an invasion of $X$ by $Y$ leads to a

"genetically protected" dimorphism
Dimorphisms II:

In general, $s_X(Y) > 0$ and $s_Y(X) > 0$ does not guarantee that invasion of $X$ by $Y$ leads to coexistence.

Example:
Consider the following recurrences for two mutualistic populations:

$$n' = R_0 2^{+km+(n-1)^{-1}} n \text{ for } 0 \leq n < 1,$$
$$= 0 \text{ for } 1 \leq n,$$

$$m' = R_0 2^{+kn+(m-1)^{-1}} m \text{ for } 0 \leq m < 1,$$
$$= 0 \text{ for } 1 \leq m.$$

These equations may look pretty artificial, but they have all the mathematical properties required of a good population model.

When internal c-attractors are always unique (slightly weaker: when dimorhisms are allways protected):

Mutual invasability: also consider "role reversal" of $x$ and $y$

The purple set supports dimorphisms.
Adaptive Dynamics, II polymorphisms:

In (spatially and/or physiologically structured) locally largish populations characterized by trait values (≡ strategies) \( Y, X, \ldots, X_n \):

\[
\rho(E, Y): \text{ asymptotic average rate of relative increase (≡ dominant Lyapunov exponent) of } Y \text{ population in a given ergodic environment } E
\]

\[
E_{\text{attr}}(C): \text{ the environment "created" by a strategy coalition } C = (X_1, \ldots, X_n)
\]

Implicit presupposition: An \( X_1, \ldots, X_n \) (plus...) community has a unique global attractor (stationary probability measure on \( E \)) with all \( n \) strategies present [or else consider local theory only]

\[
s_C(Y) := \rho(E_{\text{attr}}(C), Y)
\]

Invasion in a dimorphic population:

two residents: \( x_1, x_2 \); one mutant: \( y \)

fitness of mutant = \( s_{x_1,x_2}(y) \)

\[
\rightarrow \text{ or } \leftarrow: \quad \text{successful mutation of } x_1
\]

\[
\downarrow \text{ or } \uparrow: \quad \text{successful mutation of } x_2
\]
classifying the evolutionarily singular points

\[ \frac{\partial^2 s_x(y)}{\partial y^2} |_{y=x=x_0} \]

x_0 uninvadable

\[ \frac{\partial^2 s_x(y)}{\partial x^2} |_{y=x=x_0} \]

monomorphic convergence to x_0

Evolutionary Repellers

\[ \frac{\partial^2 s_x(y)}{\partial y^2} |_{y=x=x_0} \]

dimorphic convergence from x_0

Evolutionary Attractors

\[ \frac{\partial^2 s_x(y)}{\partial x^2} |_{y=x=x_0} \]

monomorphic convergence to x_0

Evolutionary "branching"
One of the main results from AD is the discovery of a near ubiquitous potential mechanism for adaptive speciation.
Dieckmann & Doebeli considered a few ways of achieving assortative mating. What about other ways? In particular, which ones are easiest to realise? (Spatial structure can help!)

1. There are more ways of achieving a split in the types around than thwarting the Mendelian mixer, like using a developmental switch to produce different types, and letting the types so produced evolve by means of modifier genes. Possible switches:
   (a) a single locus with a dominant-recessive allele pair,
   (b) sex (a special case of 1; disadvantage: there are other selective pressures to let the types occur in special ratios).
   (c) some incidental environmental cue.
4. Polymorphisms / More than Two Species

More Species Coevolution:

What are the regularities?

(cf. talk by Vincent Jansen)

We need to put in more ecological constraints,
or else ..........
5. And beyond: Higher Dimensional Traits, Bifurcations

To first order of approximation for small mutational steps:

\[
\frac{dX}{dt} = \frac{1}{2} \alpha \varepsilon \bar{N}(X) \begin{bmatrix} \frac{\partial s_x(Y)}{\partial Y} \end{bmatrix}^T C \begin{bmatrix} \frac{\partial s_x(Y)}{\partial Y} \end{bmatrix} Y = X
\]

where \( \varepsilon \) is the probability of a mutation per birth event, \( C \) is the mutational covariance matrix, and \( \alpha \) depends i.a. on the reproductive variability.

When everybody is born equal & the community attractor is just a point:

\[
\alpha = 2 \frac{T_f}{T_s \sigma^2}
\]

\( T_f \) = average age of giving birth, \( T_s \) = average lifetime
\( \sigma^2 = \text{Var}[\text{lifetime offspring number}] \).

message: the canonical equation is now our main tool

in higher dimensional trait spaces
at higher degrees of polymorফিজm is \( s_x(Y) \) is no longer differentiable
near the lower dimensional singular points:
In the fossil record we probably see mainly the slow tracking of adaptive equilibria, punctuated by phases of fast evolution when the equilibrium structure bifurcates.
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"just so"
more bifurcations

From a model for the evolution of seed sizes

Global constraints on the isoclines:
6. Future

Open problems in AD:

**Internal:**
* hard proofs
* range of applicability of local results
* fully classifying local behaviour
  for higher dimensional trait spaces
* developing a full-fledged bifurcation
  theory (including good computational tools)
* classifying generic properties

**Population dynamical justification:**
* hard proofs of stochastic limit theorems
* elucidating generic behaviour of community models
  on those points relevant for AD

**Genetic considerations:**
* what survives under Mendelian inheritance?
* when do the assumed smoothness
  properties (i.a. similarity of mutational
  and ecological metrics), apply,
  and how to proceed if they don't?

**Applications:**
* analysing specific eco-evolutionary models
* predicting generic macro-evolutionary patterns
* improving the connection with real biology
  and the argumentation style of "real" biologists
7. Afterthoughts 1: Why small mutational steps?

- Internal selection processes
  Officially: selection processes occurring so early in life that they are largely independent of the ecological feedback loop.
  In our case: such that their effect on the fitness landscape is always the same.

- Both functional morphologists and developmental biologists talk in terms of mechanisms that keep working properly through a sequence of small transformational steps.

- Only properly functioning organisms have fitnesses in a relevant range, malfunctioning ones have fitnesses near $-\infty$.

- This leads to a picture of narrow, slightly sloping, ridges, surrounded by a fitness abyss

- The trait spaces considered by morphologists and evo-devo-researchers are, at least in principle, very high dimensional.

| NB | For an n-dimensional trait space the top of a fitness ridge can easily have a dimension $k > 1$ while away from the ridge fitness decreases in an $(n-k)$-dimensional set of directions |

- The slope of the ridges is the domain of ecology, their location is largely ecology independent.

The ratio of the size of the intersection of two spheres with constant radii and the distance of their centers equal to the largest radius, to the size of the smallest sphere rapidly decreases when the number of dimensions increases.

1 dimensional spheres: 2 dimensional spheres: 

To offset this effect one has to let the size of the smaller sphere go to zero.
2 Afterthoughts 2: Beyond Adaptive Dynamics

about trait spaces:

So far the implicit assumption was that the trait space has an ‘ordinary’, i.e., manifoldlike, geometry.

This need not be the case, as the geometry should reflect everything that can be generated by the developmental system.

some further long-term considerations

evolution tinkers (Jacob):

- The properties realised during evolution can often be realised by very different mechanisms.
- The first mechanism that does a sufficient job inherits the earth. → Considering which mechanisms should be easiest to realise has considerable predictive power.
- Evolution does not necessarily solve a problem in the best possible manner.
- Evolution optimises only under very special circumstances, and only very locally.
- In the longer term different mechanisms for solving a problem lead to different mutational covariances and hence to different evolutionary routes.
The real evolutionary state space is not phenotype space but **genotype space**.

The mutational covariances reflect the geometry of genotype space (mutational distances) as well as the genotype to phenotype map. This reflection is only adequate **locally** in genotype space, and therefore **locally** in evolutionary time.

Presently
the detailed nitty-gritty at the molecular level does not help yet in developing a predictive framework for dealing with large-scale evolution.

**The reason is the evolved complexity of the developmental processes and the resulting convolutedness of the genotype to phenotype map.**

There is a need for intermediate abstractions.

**some arguments:**

- There is a discrepancy between the good job done by random models at the level of molecular evolution versus the domination of adaptive processes perceived by ecologists, functional morphologists, and the like.
- This discrepancy nicely fits with the assumption of a great convolutedness of the genotype to genotype map.
- The exceptions to the random model also fit in nicely:
  - Different pieces of the genome evolve at different speeds, which tie in with the function a few translation steps away, but not further.
  - The variance in the number of substitutions is much too high. This presumably reflects repeated selective sweeps.
on adaptive walks in genotype space:

The very high dimension of genotype space

1. makes that every point has very many neighbours

2. makes that by far the most points in any set lie close to the boundary

Addendum: Topics in Adaptive Dynamics s.l. that presently presently have my interest

1. Development of the mathematical framework: Finding canonical forms of the invasion fitness function for higher degrees of polymorphism locally near evolutionarily singular points for higher dimensional trait spaces. Result: Up to quadratic terms the algebraic form derived on the basis of Lotka-Volterra population models is universal, or, equivalently, the monomorphic invasion fitness locally fully determines the polymorphic invasion fitnesses in a manner that does not depend on the underlying ecological model.

2. Ecological justification: Heuristically justifying the AD framework for physiologically structured (PS) population models, and more in particular the derivation of procedures for calculating the various quantities like invasion fitnesses and coefficients of the canonical equation for such models. Results: (a) For PS population models the canonical equation looks exactly the same as for simple ODE population models but for an additional multiplicative factor that relates to details of the resident life history, like the variance of the lifetime offspring production. (b) The result mentioned under 1 applies in full generality for PS population models.

3. Relationship with the Mendelian world (a): Exploring the consequences of male and female life history differences for measures of invasion fitness for polymorphic Mendelian PS populations. I do have interesting closed expressions for single locus genetics but I still have to explore their multi-locus extension, and to see what their consequences are for e.g. life-history evolution and the like.

4. Relationship with the Mendelian world (b): Exploring the influence of the genetic architecture on the choice made by Mendelian populations for the solution of ecologically posed branching problems as defined by AD theory, where the solution may be e.g. speciation, sexual role differences, random assignment of different types based on external cues, or the gradual evolutions of single locus dimorphisms with large phenotypic effect.