

1. Connection: Quasispecies ↔ Replicator ↔ Lotka-Volterra:

1-A. Quasispecies Equation¹

i → denotes a sequence

f_i → denotes the fitness of sequence i

x_i → is the fraction of sequence i in the population of N sequences that constitutes the quasispecies

$$\sum_{i=1}^N x_i = 1 \quad (1.1)$$

Fitness landscape → $\vec{f} = (f_1, f_2, \dots, f_N)$

Average fitness → $\bar{f} = \sum_{i=1}^N x_i f_i = \vec{x} \cdot \vec{f}$

q_{ij} → probability that the replication of sequence i produce the mutant sequence j , i.e. q_{ij} is the probability of mutation from i to j , therefore:

Mutation Matrix $Q = [q_{ij}]$.

Since q_{ij} are probabilities, each row must sum 1: $\sum_{j=1}^N q_{ij} = 1$.

Quasispecies equation:

$$\dot{x}_i = \sum_{j=1}^N x_j f_j q_{ji} - x_i \bar{f} \quad (1.2)$$

constraint to ensure the normalization (1.1)

can be also written as:

$$\dot{x}_i = x_i f_j q_{ii} + \sum_{j \neq i} x_j f_j q_{ji} - x_i \bar{f} \quad (1.2')$$

where $q_{ii} = 1 - \mu$ (μ : mutation rate);

If $\mu = 1 \Rightarrow q_{ii} = 0$ and $q_{ij} = 1 \forall i \neq j$, then:

$$\text{Replicator Dynamics: } \dot{x}_i = x_i (f_i - \bar{f}) \quad i = 1, \dots, N \quad (1.3)$$

1-B. Game Theory: Fitness of a Strategy

f_i → fitness of strategy i (when confronted with the other strategies):

$$f_i = \sum_{j=1}^N p_{ij} x_j \quad \text{or} \quad \vec{f} = P\vec{x} \quad (1.4)$$

¹ See: M. A. Nowak, *Evolutionary Dynamics: Exploring the Equations of Life*, Harvard University Press, 2006.

where p_{ij} is the payoff that gets the strategy i when confronted with the strategy j and

P is the Payoff Matrix

$$P = [p_{ij}].$$

Then,

$$\dot{x}_i = x_i \left(\sum_{j=1}^N p_{ji} x_j - \bar{f} \right) \quad \text{or} \quad \dot{\bar{x}} = (P - \bar{f}) \bar{x} \quad (1.5)$$

And eq. (5) can be mapped into the (ecological) generalized Lotka-Volterra model²:

1-C. Generalized Lotka-Volterra Model

$$\dot{y}_i = y_i \left(r_i + \sum_{j=1}^N b_{ji} y_j \right) \quad i=1, \dots, N-1, \quad (1.6)$$

$$r_i = p_{iN} - p_{NN}$$

$$b_{ij} = p_{ij} - p_{Nj}$$

2. Transition from Quasispecies Phase ↔ Drift Phase

Let's consider the following simplification: the sequence 1 is the master sequence and all the other background sequences are "averaged" into another single sequence 2. Transitions from the background to the master are highly improbable so there are neglected. Hence we get the pair of equations:

$$\dot{x}_1 = x_1 (f_1 (1 - \mu) - \bar{f}) \quad (2-1a)$$

$$\dot{x}_2 = x_2 (f_2 - \bar{f}) + f_1 \mu x_1 \quad (2-1b)$$

Since $x_2 = 1 - x_1$ it is enough to analyze just the equation for the master sequence. Its fixed points are:

$$x_1^* = 0 \quad (2-2a)$$

$$x_1^* = 1 - \frac{\mu f_1}{f_1 - f_2} \quad (2-2b)$$

From the second fixed point we can get the critical values of f_1 for which both roots collapse:

² See Hofbauer and Sigmund, *Evolutionary Games and Population Dynamics*, Cambridge University Press 1998

$$f_1^c = \frac{f_2}{1-\mu} \quad (2-3)$$

This equation can be understood intuitively:

The error catastrophe occurs when the effective grow rate of the master sequence becomes equal to the grow rate (fitness) of the background i.e. when

$$f_1(1-\mu) = f_2$$

For a fixed value of f_2 , equation (2-3) correspond to a line of information catastrophe transition separating the Quasispecies phase from the Drift phase in the phase diagram below:

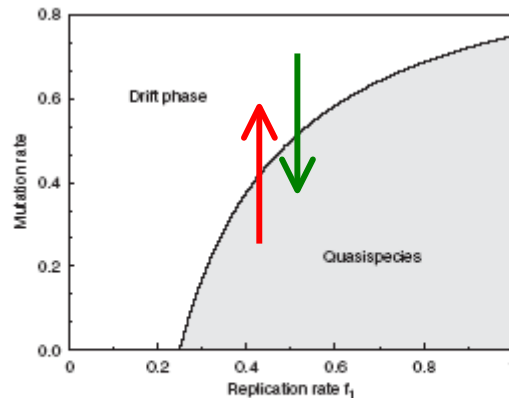


Fig. 1. Interpreting the changes in the RNA population structure observed in the patient sample. As the master sequence reduces its replication rate (due to its identification by the immune system) a rapid decay is observed once a replication threshold f_1^c is crossed.

(Picture from R.V. Sole et al. / Journal of Theoretical Biology 240 (2006) 353–359)

The red arrow indicates a possible way to transition from the Quasispecies to the Drift phase by **enhancing mutations with a mutagenic agent**. Conversely, the green arrow correspond to the inverse transition **by adding polymerase that corrects mistakes during replication**.

3. Transition from Clear ↔ Turbid water in lakes

3-A. A Minimal Model

A minimal model of an ecosystem model (MEM) showing hysteresis describes the change over time of some property s that characterizes the state of the ecosystem (for example water turbidity in a lake) by:

$$ds/dt = a - bs + rf(s), \quad (3.1)$$

where the parameter a represents an environmental factor that promotes s (for instance nutrients loading **rate**), b represents the rate at which s decays in the system (nutrient removal rate), r is the rate at which s recovers (internal nutrient recycling) and f is a Hill function:

$$f(x) = \frac{x^q}{x^q + h^q}.$$

At equilibrium (3.1) reduces to:

$$a - bs + r s^q / (s^q + h^q) = 0. \quad (3.2)$$

or, equivalently:

$$-bs^{q+1} + (a + r) s^q - b h^q s + a h^q = 0. \quad (3.2')$$

Dividing by b we get:

$$-s^{q+1} + (a/b + r/b) s^q - h^q s + (ah^q)/b = 0. \quad (3.2'')$$

If $r = 0$ (no recycling), then a single equilibrium state:

$$s = a/b$$

The value of q doesn't have a qualitative effect: for any q it is easy to prove that the polynomial (3.2'') **has at most 3 real roots**. Taking the second derivative of this polynomial $P_{MEM}(s) = -s^{q+1} + (a/b + r/b) s^q - h^q s + (ah^q)/b$ one gets:

$$P_{MEM}'' = -(q+1)q s^{q-1} + q(q-1)(a/b + r/b) s^{q-2},$$

and equating it to zero we get that the concavity changes sign for s given by:

$$s^* = \frac{(q-1)(a/b + r/b)}{q+1} \quad \text{and} \quad s^* = 0 \quad (3.3)$$

i.e.

only one change of sign for positive values of s and therefore, at most there are 3 real roots for $s \geq 0$. Figure 2 is a plot of P_{MEM} for different values of q and $a/b=0.15$, $r/b=1.7$ and $h=1$.

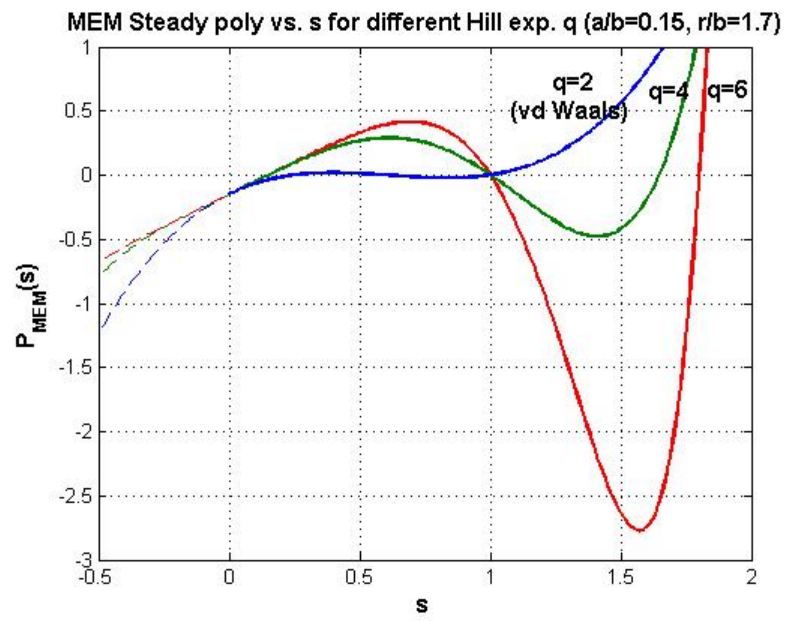


Fig.2

3-B. Parallelism between the clear-turbid transition and the liquid-gas transition

Let's analyze the parallelism between the transition liquid-gas (L-G) and clear to turbid water (C-T) or "without algae"- "with algae".

Let's work with non dimensional variables: $x = s/h$, $b = bh/a$ and $r = r/a$.

In the C-T transition, the 'conditions' of figs. 2 and 3 correspond to a varying parameter (b or r) and the other (r o b) fixed and the 'ecosystem state' specified by the variable x . Thus the curves of these figures would be equivalent to isotherms (the specific volume v varying with P for fixed T) or isobars (v varying with T for fixed P).

The following table summarizes this correspondence:

	L-G	C-T
state of the system specified by	molar volume v	turbidity x
control parameters	P and T	b and r
polynomial P_3 of degree 3 for the state variable	Eq. of State $P_3(v)=0$	Evolution Eq. $P_3(x)=dx/dt$
curves iso-parameter	isotherms, isobars	iso- b , iso- r
metastability	Yes	Yes
hysteresis	Yes ³	Yes
critical slowing down (when the 3 roots of P_3 collapse in one)	Yes	Yes?
Loop or "S" of the isoparam curves	By energetic arguments is replaced by an horizontal line ⁴	?
Kinetics of the transition	Nucleation or Spinodal Decomposition	?

(Al tener para C-T una ecuación dinámica para x y no una ecuación de estado, entonces pueden poner las flechitas indicando hacia donde se mueve el sistema según el punto en el plano conditions-ecosystem_state en que se encuentre.

Esto es, la "S" divide al eje de las x en 4 regiones delimitadas por las 3 raíces con signos + - + -. Por lo tanto los tramos de la S que aparecen llenos son estables y el dashed es inestable.

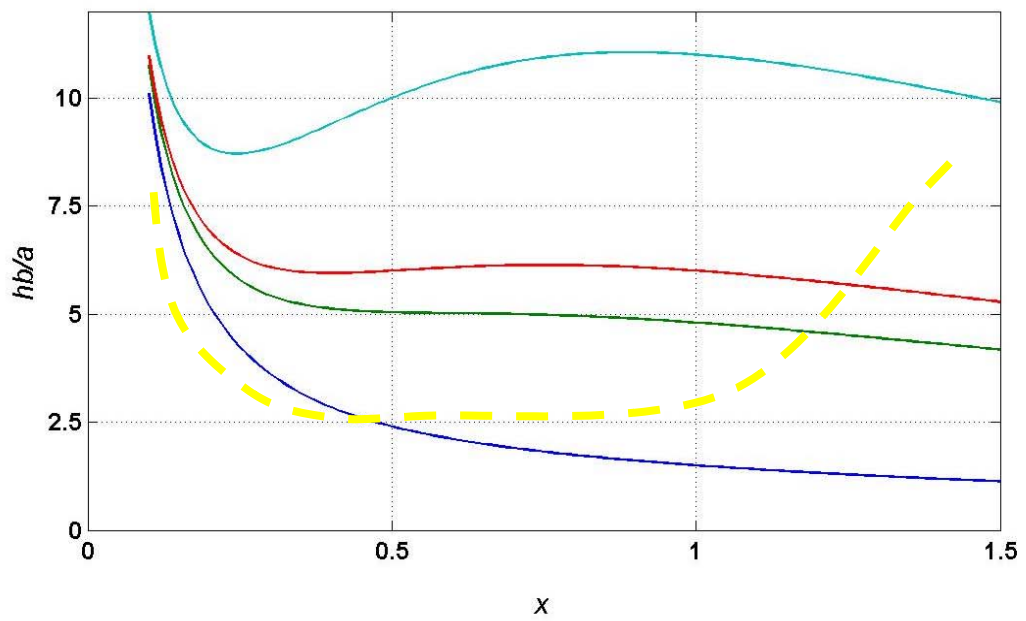
Para L-G dado un punto sobre el tramo recto de una isoterma, lo que determina para donde se mueve es el signo de dQ/dt (Q calor entregado), si $dQ/dt > 0$ (< 0) se mueve hacia la derecha i.e hacia el gas (líquido).

Quizá, siguiendo la analogía hasta sus últimas consecuencias, una ecuación dinámica para L-G sería algo así: dv/dt proporcional $dQ/dt * P_3(v)$

³ With the required provisions (very slow changes, no impurities, no waves or mechanical perturbations).

⁴ Maxwell's construction.

MINIMAL ECO Model iso-r curves (isotherms), $r/a = 1, 7, 10$ & 20



MINIMAL ECO Model iso-b curves (isobars) $b/a = 3, 5, 7$ & 10

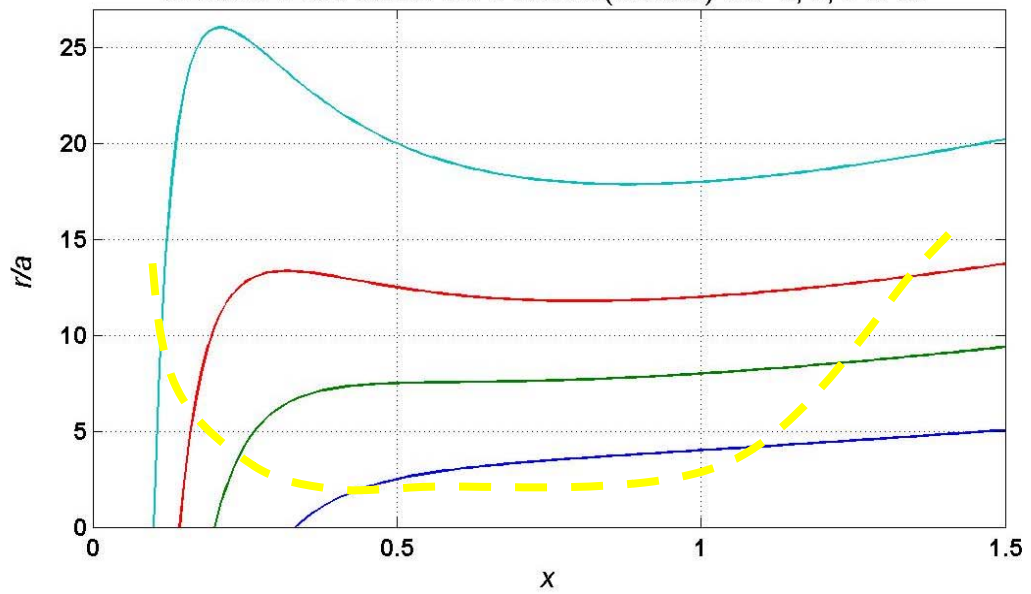


Figure 3 & 4

The co-existence curve (yellow dashed) is inverted i.e. delimits a region for high values of r/a and b/a !

3-C. Photoinhibition

The transition clear to turbid water (C-T) or "without algae"- "with algae" can be connected with the phenomenon of photoinhibition.

Photoinhibition

From Wikipedia, the free encyclopedia

Photoinhibition is a reduction in a plant's (or other photosynthetic organism's) capacity for [photosynthesis](#) caused by exposure to strong light (above the saturation point). Photoinhibition is not caused by high light per se, but rather absorption of too much light energy compared with the photosynthetic capacity, i.e. any excess energy that the photosystem cannot handle is damaging.

Photoinhibition is often reversible, i.e. dynamic photoinhibition, and does in that case not inflict permanent damage to the photosystem. However, severe photoinhibition over a long time may cause highly reactive free oxygen radicals to form, which degrade photosynthetic components, i.e. chronic photoinhibition or photodamage. Plants and algae have several mechanisms to protect against photoinhibition, e.g. through the [xanthophyll cycle](#).

References

- Hall, D. O. & K. K. Rao, 1999, Photosynthesis. – Cambridge Univ. Press, Cambridge.

A simple model for photoinhibition, let's call the *full* version, is:

$$\frac{dg}{dt} = -fg + r \frac{I_0 e^{-kgz}}{I_0 e^{-kgz} + J + \frac{(I_0 e^{-kgz})^2}{K_{inh}}} g \frac{P-g}{P-g+h} \quad (3.4)$$

In the *simplified* version the nutrients factor (encircled in orange in equation (3.4)) is removed. In fact, this factor is almost always close to 1 and, at first sight, doesn't have a relevant effect (see upper panel in the figure below, where the curves with and without this term are filled and dashed respectively).

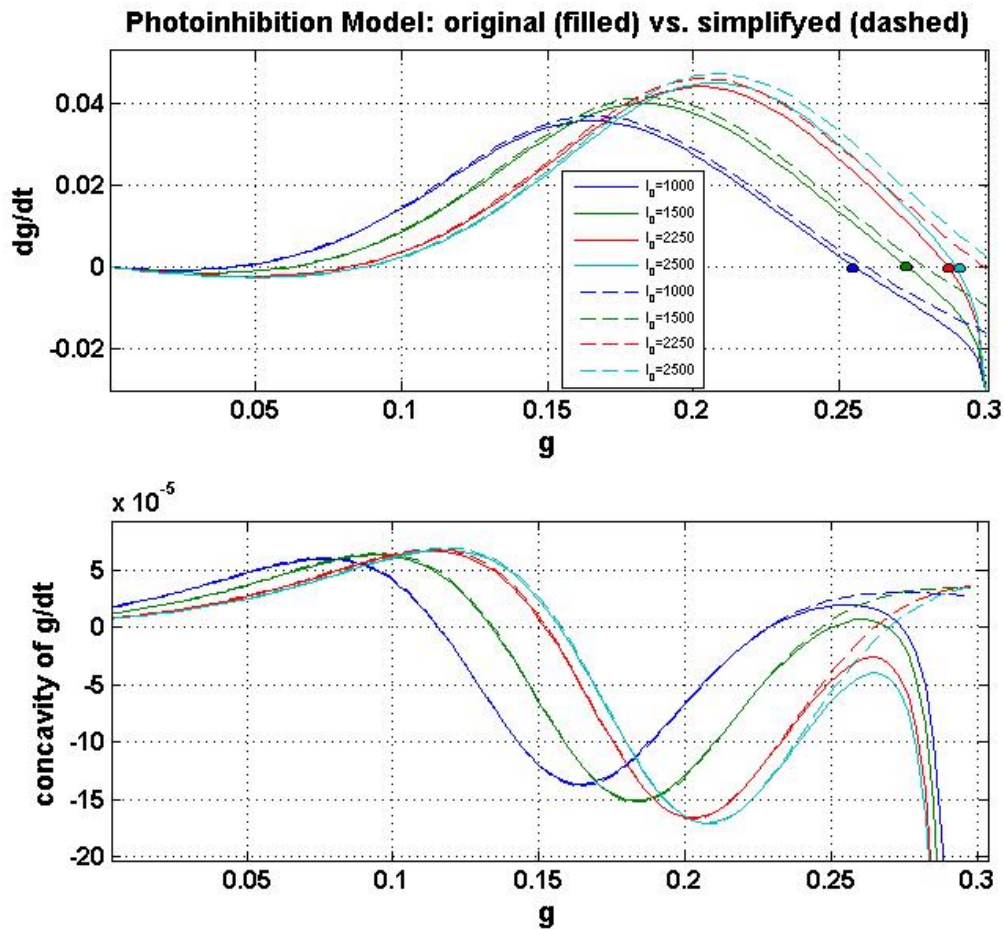


Figure 5

However, Huisman notes that for sufficiently high irradiation (around $2000 \mu \text{ mol photons m}^{-2} \text{ s}^{-1}$) the stable non-null fixed point disappears (see Fig. 3-(A)). In other words, for sufficiently high irradiation the 3 roots can collapse into one. This looks like what occurs at a critical point indeed. So I found a subtle difference between the full and the simplified version: the way dg/dt becomes 0. If we look at the upper panel we see that for $I_0 = 1000$ and $1500 \mu \text{ mol photons m}^{-2} \text{ s}^{-1}$ (blue and green) the curves intersect with the horizontal axis with positive concavity, while for $I_0 = 2250$ and 2500 the concavity is negative, indicating that the rightist root is an artifact. The lower panel is a plot of the concavity that shows that its sign at stable points, marked in the upper panel by thick dots, is positive for $I_0 = 1000$ and 1500 (blue and green dots) and negative for $I_0 = 2250$ and 2500 .

So it seems, after all, that the model can accommodate a critical point for $I_0 \approx 2000 \mu \text{ mol photons m}^{-2} \text{ s}^{-1}$!!!

I think that it would be interesting to look for signatures of criticality. For instance, to measure spatial properties trying to find power laws or temporal correlations to detect critical slowing down.

Of course, the simplified version can be used as a first and guiding approach, but I think that the full version opens the possibility to explore the existence of these interesting properties.