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Physics of evolution: selection without fitness

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Abstract

Traditionally evolution is seen as a process where from a pool of possible variations of a population (e.g. biological species or industrial goods) a few variations get selected which survive and proliferate, whereas the others vanish. Survival probability is typically associated with the 'fitness' of a particular variation. In this paper we argue that the notion of fitness is an *a posteriori* concept, in the sense that one can assign higher fitness to species that survive but one can generally not derive or even measure fitness – or fitness landscapes – *per se*. For this reason we think that in a 'physical' theory of evolution such notions should be avoided. In this spirit, here we propose a random matrix model of evolution where selection mechanisms are encoded in the interaction matrices of species. We are able to recover some key facts of evolution dynamics, such as punctuated equilibrium, i.e. the existence of intrinsic large extinctions events, and, at the same time, periods of dramatic diversification, as known e.g. from fossil records. Further, we comment on two fundamental technical problems of a 'physics of evolution', the non-closedness of its phase space and the problem of co-evolving boundary conditions, apparent in all systems subject to evolution.

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I. INTRODUCTION

The quantitative science of evolution can look back on a series of models dealing with the evolution of biological systems and the dynamics of technological innovation. In this context maybe the most important ones are the models of Kauffman (see e.g. [1]) on biological and Arthur [2] on technological evolution. A traditional way to treat dynamical systems of evolution is to use high dimensional catalytic network equations [3, 4], the Lotka-Volterra equations and the Hypercycle [5] being famous examples. Recently linear versions of these catalytic network equations have been shown to demonstrate the influence of topological aspects of the underlying network topology on the resulting population dynamics [6]. There the existence of highly populated phases have been demonstrated to coincide with the appearance of closed directed feedback loops in the network, the so-called autocatalytic cycles. On the subject of extinction dynamics, which constitutes an important branch in understanding evolution, several specific models have been brought forward lately [7–11].

Of fundamental importance in all of the above models is the notion of *fitness*. Since the times of Darwin fitness is used as a method for selection, which is fundamental to evolution. Fitness of an entity is a function depending on a large number of parameters, describing both the state of the entity and the state of its environment. Due to the high dimensional parameter space one often talks about fitness landscapes. These landscapes may be rather complicated and hard to optimize. As useful as it may be for an intuitive feeling of how selection works, the notion of fitness is clearly an *a posteriori* concept. An entity is fit if it had survived and proliferated well, and unfit if it went extinct. The same is true for the concept of *ecological niches*. Space that never got occupied by entities will not count as a niche. These concepts could be seen as ambiguous, and anthropomorphic. Fitness and niches can not be measured in reality in much the same way as utility functions can usually not be measured in economics.

If there exists something like a physics of evolution it would be necessary to phrase models without using anthropomorphic concepts and, at the same time, provide a framework abstract enough to capture the universality behind e.g. technological and biological evolution in a unified way. This universality manifests itself in the fields of biological evolution, industrial innovation, socio-dynamics, economy, finance, opinion formation, ecological dynamics, e.g. food-webs, and history. In the following we would like to avoid these notions

with itself or other existing things.

It is clear that such a process is far from being of Newtonian nature as usually dealt with in physics. The most obvious problem arises from the innovations happening in the course of the dynamics: the phase space of the system is not closed. Whenever a satisfactory set of variables is found that describes the history of the system well, at some point this set of variables becomes insufficient to describe states of the system in the future. For example, before television was invented history of mankind can be understood without television, whereas it gets increasingly impossible to understand the history of man after the invention without taking the secondary effects of television on society into account. The second major problem is that of co-evolving boundary conditions, which all evolution systems share. As the system evolves (new things come into being) the boundary conditions (interaction possibilities with others) constantly change. This makes such systems extremely hard to phrase in terms of differential equations. Since it is impossible to forecast the invention of entities and new variables associated with them, it seems reasonable, as a starting point, to model their respective interactions based on random interactions.

As stated above new things usually come into existence through a process of (re-) combination or substitution of already existing things. Examples range from sexual reproduction to the assembly of an ipod from its components. Thus models for evolutionary systems minimally require two components: *entities* (things, species, products, individuals, etc.) and *rules* how these entities can be used in combination with each other to produce new things (combination and substitution). For example there is a rule that the combination of hydrogen and oxygen can form water, or there is a rule that a male and female chicken can become parents of baby chicken. However there is no rule that a fish and a dog can be the parents of a chicken, nor is it possible to combine two blocks of U 235 into one big block of uranium. The set of all combination/substitution rules we keep in a 'rule table' denoted as α in the following.

Suppose we characterize the relative frequency of entity i by $x_i \geq 0$ and denote the rule whether entity i can be produced from entities j and k by α_{ijk} . If no such production rule exists, then $\alpha_{ijk} = 0$ and else $\alpha_{ijk} > 0$, when such a rule exists. α_{ijk} represents the rate with which j and k can produce i . For simplicity one can view α as Boolean, i.e. $\alpha \in \{0, 1\}$. If $\alpha_{ijk} > 0$ we call (j, k) a *creative pair* producing (or 'pointing' to) i . The dynamics of the

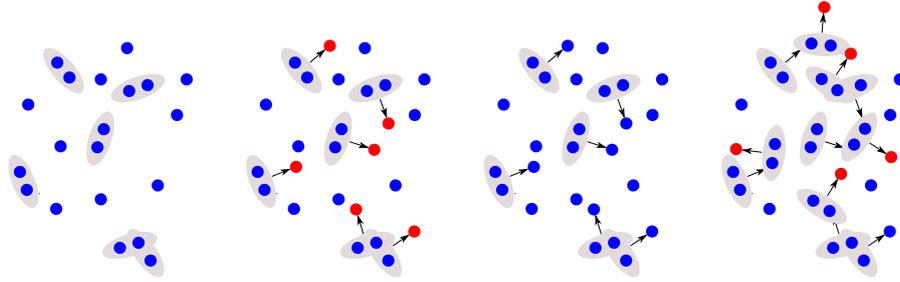


FIG. 2: From left to right: within some initial set of entities (blue dots) there exist several creative pairs, indicated by gray ovals. In the next timestep these pairs produce new entities (red dots). The new entities become part of the environment (red dots turn blue). With the new entities new productive pairs can be formed to again produce new entities.

relative frequencies of the entities can be expressed by a network equation of the type

$$\dot{x}_i = \sum_{j,k} \alpha_{ijk} x_j x_k - x_i \Phi \quad , \quad \Phi = \sum_{i,j,k} \alpha_{ijk} x_j x_k \quad . \quad (1)$$

The quadratic term suggests that i forms proportional to the abundance of j and k weighted by the rate α_{ijk} . The Φ term assures that the abundance of entities is proportional to the relative frequencies x_i , with $\sum x_i = 1$.

Let us assume that the dimension of the system, denoted as d , i.e. the number of all possible entities i , is extremely large, but finite. If we know all i and α_{ijk} we could specify an initial condition $x(t=0)$ and solve the differential equation (1). However, neither d nor α is known in general. So how can one proceed? In previous work [14, 15] we suggested the following combinatorial approach. Suppose we knew the number of productive pairs $N^+ = \sum_{i,j,k} \theta(\alpha_{ijk})$ (where $\theta(x) = 1$ for $x > 0$ and $\theta(x) = 0$ otherwise) in the system and define the creative pair density $r^+ = N^+/d$, which is the average number of productive pairs leading to one specific product. Suppose further that the topology of the productive catalytic network is random (maximum ignorance), then one can use combinatorial arguments to map the catalytic network equation (1) onto the recurrence relation, [14]

$$\begin{aligned} a_{t+1} &= a_t + \Delta a_t \\ \Delta a_{t+1} &= r^+ (1 - a_{t+1}) (a_{t+1}^2 - a_t^2) \quad , \end{aligned} \quad (2)$$

where $a_t \equiv \sum_i \theta(x_i(t))/d$ is the relative diversity of the system at time t , i.e. the fraction of possible entities with non-zero abundance. Here the initial condition is a_0 and $a_{-1} = 0$

by definition; the rule density is r^+ . For a schematic iterative view of a dynamical increase of diversity see Fig. 2. It is remarkable that this equation does not explicitly depend on d any more and therefore is valid for arbitrarily large d . The increment Δa in Eq. (2) can be understood. $r^+ a_t^2$ is proportional to the number of productive pairs in a_t . However, we have to subtract the productive pairs that have already been considered in the last time-step so that at time t only $r^+(a_t^2 - a_{t-1}^2)$ new pairs have to be taken into account. Of these pairs only a fraction $(1 - a_t)$ can be expected to produce something that does not already exist. The resulting update equation Eq. (2) can be solved asymptotically by analytical means [14] and shows that the system has a phase transition in the final diversity a_∞ . If $r^+ > r_{crit}^+$, with a critical value $r_{crit}^+ \sim 2$, then there exists a critical value $a_{crit}(r^+)$ where there occurs a discontinuous jump in the final diversity from low to high final diversity. The transition is equivalent to the van der Waal's gas phase transition. This phase transition is shown in Fig. (3) where the final diversity a_∞ is plotted over the initial diversity a_0 and the creative pair density r^+ . We have analyzed the stability of the fully populated state under external suppression of entities (initial defects) which also leads to scale-invariant update equations for the propagation of secondary defects. Here also a transition from almost linear behavior with respect to the initial defects to a break-down of the complete system can be demonstrated, [15].

II. AN EVOLUTION MODEL WITHOUT FITNESS

The above creative catalytic network dynamics does not yet constitute a model for evolution. The selection mechanism as an intrinsic part of an evolution system is missing. The task is how to introduce selection without changing the set-up and without reference to anthropomorphic *a posteriori* concepts like fitness, niches, selection pressure, etc.

A straight forward way to achieve this, is to include suppressive pairs (j, k) with $\alpha_{ijk} < 0$ such that the (j, k) suppresses the existence of i . Rule table α_{ijk} now encodes creation and suppression, r^+ remains the density of productive rules, and the density of suppressor rules, denoted by r^- , is defined analogously as $r^- = N^-/d$, with $N^- = \sum_{i,j,k} \theta(-\alpha_{ijk})$. A schematic view of the model is presented in Fig. 4.

The influence of suppressors on the final diversity of the system can be estimated analytically. For instance, if a_∞ is the final diversity for the case without suppressors, then the

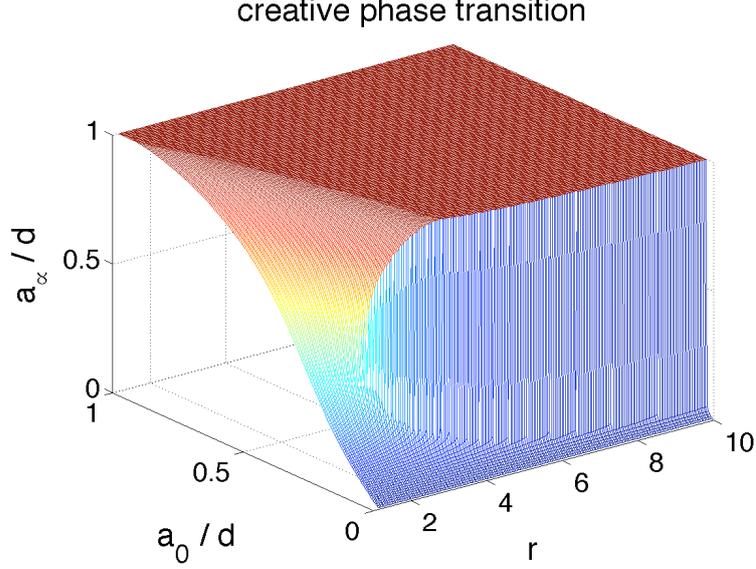


FIG. 3: Final diversity a_∞ plotted over the initial diversity a_0 and the creative pair density r^+ displaying a van der Waals like phase transition from low to high final diversity.

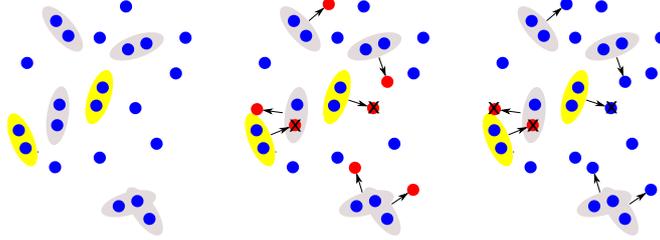


FIG. 4: Left: Within some initial population of entities (blue dots) we find creative pairs (gray ovals) as well as destructive pairs (yellow ovals). In the next timestep creative pairs produce new elements (red dots), suppressive pairs annihilate existing elements (crossed red dots). The resulting population with its potentially new pairs serve as a new initial population for the next timestep.

asymptotic diversity of a system with a suppressor density of r^- can be derived on the basis of combinatorial arguments to be γa_∞ , where

$$\gamma = \frac{\sqrt{1 + 4r^- a_\infty^2} - 1}{2r^- a_\infty^2} \leq 1 \quad . \quad (3)$$

This result has been shown to coincide reasonable well with simulations. Unfortunately it turns out that the diversity dynamics with suppressors is rather resistant to a more detailed analytical analysis and a numerical version of the model has to be implemented on the basis

of the parameters r^+ , r^- and a_0 to learn more about the details of the dynamics of such systems.

A. Implementation of the model

We have implemented the most simple version of the above model. We consider only binary states $x_i \in \{0, 1\}$, an element is present or absent, and a rule table with entries $\alpha_{ijk} \in \{-1, 0, 1\}$. First we sample r^+d random triples (i, j, k) and assign them a value $\alpha_{ijk} = 1$. On the set of remaining triples we do the same for r_- and assign $\alpha_{ijk} = -1$. All remaining entries in α are zero. Next we randomly sample an initial condition such that exactly a_0d components in the initial species vector $x(t = 0)$ are one; all others are zero. The elements $x_i(t)$ are updated to time $t + 1$ in a random sequential order. For each node i we count the number n^+ and n^- of productive and suppressive pairs pointing to node i , respectively. If $n^+ + n^- > 0$ the node will be set to 1 with a probability $p_1 = n^+ / (n^+ + \mu n^-)$, and to 0 with probability $p_0 = 1 - p_1$. Here μ is a parameter that specifies the relative strength of suppressive pairs over creative pairs. For example, if $\mu = 1$ and $n^+ = n^-$ then the chance for an entity i to be created or deleted is 0.5. If neither a creative pair nor a destructive pair is pointing at node i , i.e. $n^+ + n^- = 0$ then i does not get actively suppressed but also not actively produced. In this case i will continue to exist in the next time step with a probability λ (sustain rate), in other words, entities that are not actively produced decay with a rate $1 - \lambda$. At this point we can decide to protect the initial condition $x(0)$ or the initial diversity a_0 , i.e. once the diversity $a(t)$ has dropped down to the level of a_0 no further entity can be eliminated in the update. However, we found that both types of enforcing a minimum diversity lead to very similar characteristics of the dynamics. This protection of entities models e.g. sources of renewable goods which are neither subject to selection nor to decay.

The dynamics of species in vector $x(t)$ can be seen as a point in phase space. Two consecutive points in time have shifted by an 'angle' $\delta(t)$

$$\cos \delta(t) = \frac{\vec{x}(t) \cdot \vec{x}(t-1)}{|\vec{x}(t)| |\vec{x}(t-1)|} \quad , \quad (4)$$

which can be regarded as a potential measure for the relative change of the population of entities and thus for the size of creative/destructive effects within this timestep.

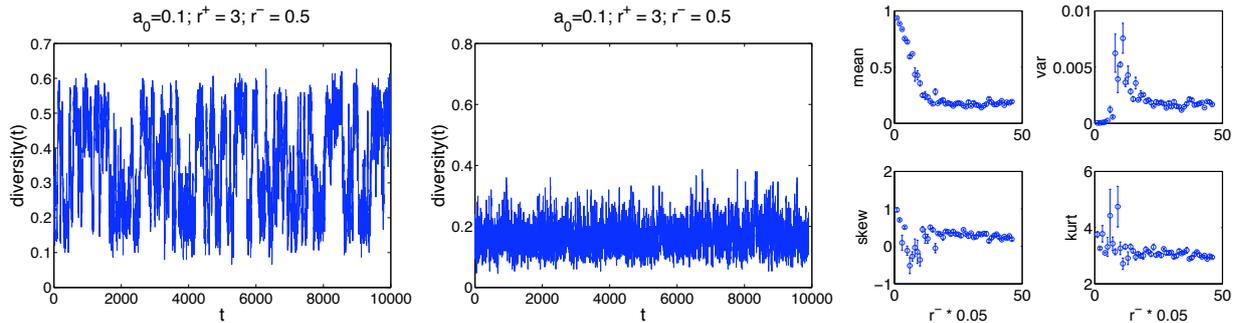


FIG. 5: Two different runs with the same parameters for two different random seeds of the rule table α . One exhibits meta-bi-stable dynamics (left) the other low-diversity dynamics (center). In both cases the suppression factor is $\mu = 1.5$ and the sustain rate $\lambda = 0.08$. The initial condition $x(0)$ was protected. Statistics for the moments of the diversity dynamics for $r^+ = 3$ and $a_0 = 0.1$ fixed is shown based on 25 runs with different random topologies per r^- (right).

B. Results

Most importantly our simple model is capable to produce meta-bi-stable dynamics, or punctuated equilibrium as called in biology. In Fig. 5 two runs for identical parameter settings (left and center) are shown. The two runs with identical dynamical parameters show meta-bi-stable dynamics in the one case and sub-critical dynamics in the other. The only difference appears in the random realization of the rule table α . The role of the parameters μ (relative suppressor strength) and λ (sustain rate) are found to have only a minor influence on the qualitative behavior of the dynamics. In the right image of Fig. 5 the first moments of the diversity timeseries are shown as a function of r^- , for all other parameters fixed. We see that the mean diversity decreases with increasing r^- just as we may expect from Eq. (3), while the variance is below a critical r^-_{crit} where the variance has a peak and then decays for $r^- > r^-_{crit}$. The simulation data we have analyzed indicates that this behavior is widely independent of the system size d , which was typically between 100 and 1000. We compared the characteristics of the diversity dynamics with direct numerical solutions of the catalytic-network equation Eq. (1) and found qualitatively comparable behavior on small systems. In case the time-evolution of the system-diversity is meta-bi-stable, the system seems to be critical. In Fig. (6) the clearly non-Gaussian angular velocity distribution of δ is shown.

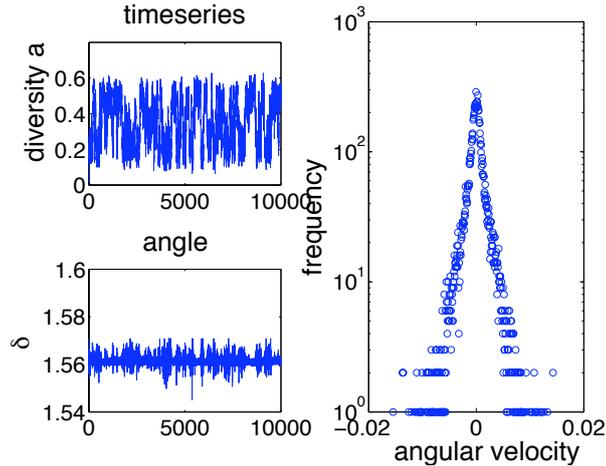


FIG. 6: Diversity (left upper panel) and angular velocity (left lower panel) over time in a particular run displaying meta-bi-stable dynamics. The angular velocity distribution is shown in the right plot.

III. DISCUSSION

We have proposed a simple model of evolution that is based on a set of three relevant parameters r^+ , r^- and a_0 . No anthropomorphic *a posteriori* concepts like fitness or ecological niches are necessary in the model, yet it is capable of explaining punctuated equilibrium in diversity timeseries, which is the most striking feature in experimental data, such as e.g. fossil records. The creative processes are modeled as a consequence of constructive interactions between pairs of entities while selection happens implicitly through suppressors, i.e. the existence of certain elements prevents (suppresses) the existence of others. *A posteriori* it becomes of course possible to interpret fitness and niches in terms of the interaction topology. However, the model indicates that fitness is maybe more a property of the collective state of a system than a property of the individual entities. When the state of the system is such that suppression is minimized and creativity maximized the whole system thrives while in case too many suppressors are supported the whole system breaks down in a 'creative gale of destruction' [16].

Most remarkably, already the simple model we have implemented displays meta-bi-stable dynamics – which is exactly what we would expect to find – for a wide range of r^- , i.e. for $r^+ > r_{crit}^+$, $a_0 > a_{crit}(r^+)$. One may conclude from this that there is a non-vanishing probability to sample evolutionary systems with meta-bi-stable evolution by pure chance.

The behavior of mean and variance indicate that when the system is prepared critically ($a_0 > a_{crit}$) then for small r^- the system will behave supra-critical and approaches a plateau where it stays and the variance is small. When r^- increases we find an onset of meta-bistable evolution. The probability for this behavior seems to be maximal at the critical value of r^- where the variance is maximal. For larger r^- the decreasing variance indicates both a decreasing probability to find meta-bi-stable dynamics and a decreasing amplitude of the high-diversity plateau. The meta-bi-stable scenarios seem to be critical as indicated by the non-Gaussian distribution of the angular speed δ of Eq. (4).

Finally, since the parameters a_0 , r^+ , and r^- are insufficient to fully determine whether the dynamics resulting from some random topology α of the catalytic network will be meta-bi-stable, sub-critical, or supra-critical, this set of parameters is incomplete. The occurrence of meta-bi-stability or punctuated equilibrium has to be associated with topological properties of the catalytic network α . These properties, such as auto-catalytic cycles, have a non vanishing chance to be randomly sampled. It will be a fascinating task to relate the statistics of occurrence of such topological structures with the observation of punctuated equilibrium.

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