



# The evolutive role of symbiosis and the external environment: a mathematical model

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## Abstract

By recourse to an evolutive mathematical model recently introduced in the literature we investigate major macro-aspects of an ecosystem's evolution, such as symbiosis and the influence of (variable) environmental effects. © 1999 Elsevier Science B.V. All rights reserved.

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## 1. Introduction

The last years have witnessed great activity in the study of physical models that mimic biological evolution processes. As a consequence, much light has been shed on diverse features of the rich Darwinian landscape. Of course, intriguing questions still require elucidation. One aspect of the Darwinian outlook that is of obvious importance refers to the role played by the external environment in the dynamics of the adaptive process [1–7]. Current theories rank this role in diverse fashion, from considering it to be a fundamental dynamical factor to regarding it as being an insignificant one.

The relevant problem is, of course, that of explaining the observed patterns (fossil records) of biological evolutive activity, related to the extinction events. Gould [8] has conjectured that biological evolution takes place in terms of intermittent bursts

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of activity separating relatively long periods of quiescence, rather than in a gradual fashion. Such an intermittent pattern has been indeed observed by Raup et al. [9–12] in their study of fossil records. When referring to this intermittent behavior of the single-species evolution, Gould speaks of “punctuated equilibrium”. It has been suggested that extinction events (at least the larger ones) are caused by external forces, such as changing sea levels [6] or big meteorites [7].

A great deal of effort has been invested in devising ingenious and at the same time *simple* theoretical models that may provide one with meaningful insights concerning punctuated equilibrium and other features of biological evolution [1–5,13]. Recently, a somewhat more realistic model than those previously in existence was introduced [14,15]. It deals with several *interacting species* and its intrinsic dynamics clearly exhibit the punctuated equilibrium phenomenon. More importantly, the model *predicts* that the laws governing the extinction distribution curves are power laws [14] and is also able to reproduce not only Sepkosky’s evolutive activity curves [12] but also lifetime species distribution ones [9,12], both kinds of curves constructed on the basis of fossil records. As reported in [14,15], the model’s workings are complex enough so as to be able to mimic some facets of actual biological evolution. On the basis of this model one may understand that several (simple) dynamical mechanisms exist that account for these (observed) facets without recourse to catastrophic events. It should be pointed out that the aforementioned predictions are of a mathematically robust nature [14,15].

For the convenience of the reader, we briefly summarize the findings of [14,15]:

- in [14], in addition to introducing the model, it was shown that it exhibits the features of punctuated equilibrium and power law behavior. Moreover, it is seen that critical behavior is a direct result of Darwinian competition (as simulated by the model workings). Elimination of such competition results in the disappearance of criticality.
- in [15], it was shown that, appearances notwithstanding, the model does not exhibit self-organized criticality (SOC) but a different type of critical dynamical evolution, that was mathematically grounded on phenotype–genotype correlations.

If one analyses the results reported in Refs. [14,15], some intriguing questions remain that deserve further clarification. In this vein we ask ourselves the following question: to what an extent additional features of (actual) biological evolution, not yet investigated in [14,15], such as symbiosis and the effects of a changing environment, have a counterpart in our model?

It is the aim of the present communication to answer these questions, in the understanding that they will help not only to clarify the inner workings of a rather successful model, but also to try and elucidate the roads one should traverse in an investigation of mathematical evolutive models. Additionally, we hope to be able to shed some modest amount of light on the actual biological process itself, as customarily expected from any *physical model*.

We begin the concomitant task with a brief recapitulation of the model under consideration.

## 2. The model

We deal [14,15] with  $M$  distinct, interacting biological species, each of which is represented by a vector in  $\mathcal{R}^N$ . The components  $V_\alpha^i$  of  $V^i$  represent different phenotypic features ( $\alpha, \beta, \dots$ ) that are to be affected and modified by the evolutionary process. The degree to which the  $i$ th species is “adapted” to the environment is represented by a quantity  $F_i$ , to be called its “fitness”, which is given by the expression

$$F_i = \sum_j^M \sum_{\alpha\beta}^N g_{\alpha\beta}^{ij} V_\alpha^i V_\beta^j + \sum_\gamma^N V_\gamma^i A_\gamma^i, \quad i = 1, \dots, M, \tag{1}$$

where the hyper-matrix  $g_{\alpha\beta}^{ij}$  provides the details of the inter-species interaction and the second term on the r.h.s. is an “environmental” one (see below). In [14] one assumed  $g_{\alpha\beta}^{ij} = -g_{\beta\alpha}^{ji}$ .

There is a correlation between the components of  $V^i$  which is represented by recourse to mappings between a set of  $k + 1$  real parameters and each of these components, i.e.

$$V_\beta^i = f_\beta(a_0^i, \dots, a_k^i), \tag{2}$$

with  $f_\beta$  an appropriate function. The set  $a_0^i, \dots, a_k^i$  defines in fact the  $i$ -species. As a result of biological mutations, these parameters are allowed to vary with time.

The conceptual difference between the  $a$ ’s (that span an “A-space”) and the  $V$ ’s (a “V-space”) should be emphasized here. The components of  $V$  denote different phenotypic features of the species that this vector represents. These features are correlated, via the  $a$ ’s, in the manner just described. Genetic changes, here mimicked by modifications in the  $a$ -values, drive the evolutionary process. The correlations just mentioned constitute an essential aspect of the model. Without them, a given species might (eventually) attain, after a series of appropriate mutations, *any* phenotypic feature whatsoever. This does not happen in nature.<sup>2,3</sup> Summing-up, changes in our  $a$ ’s are to be understood as reflecting uncorrelated genetic modifications (changes in one or more bases in one or more genes) while changes in the  $V$ ’s represent the concomitant phenotypic modifications that, to a greater or lesser extent, will be mutually correlated. The  $a_i$ ’s do not represent the genetic code in itself, but only the correlations introduced by its existence.

<sup>2</sup> This can be illustrated with reference to the following example [19]. Assume that a shellfish could reduce the weight of its shell, so that it might have a better chance of escaping from some fast-moving predator. However, a lighter, thinner shell would also decrease its resistance to *other* predators. A compromise must be reached (conflict of design), which would give rise to one of our correlations. Called stabilizing selections, *these* phenotypic correlations may keep species from evolving at all: they cannot go anywhere because moving in one direction has implications for its other competing functions. The two different shellfish features, speed and shell hardness, must change *together* because they depend upon common genes. One may imagine changes that would be simultaneously beneficial for both features, but they will be very rare, in general.

<sup>3</sup> Another example deserves to be cited here that shows how difficult it is to modify one feature without affecting others at the same time. Consider the *period* gene in the fruit-fly *Drosophila Melanogaster* [17], whose mutation affects not only the fly’s circadian rhythms (the timed cycles, such as for waking and sleeping, that are characteristic of all living things) but also the rhythm of the courtship song (and so the overall courtship routine and its efficacy).

Our model system evolves in the following fashion: we start with an arbitrary initial configuration (the  $a_i$ 's are randomly chosen within  $[-1, 1]$ ) and, in each of a series of time steps, mutation effects are mimicked by slightly modifying the  $a_i$ 's for the  $l$ th species. Both the selection of  $l$  and the nature of the changes are random. The condition  $|V^i| = 1$  is enforced so as to avoid unrestricted growth (with time) of  $|V^i|$ .

A particular mutation (change in a given  $a$ ) is “accepted” if it increases the corresponding fitness (as a consequence of such a mutation  $F_i$  grows). The  $a$ -change is in this case retained. Otherwise it is discarded and the  $a_i$ 's end up with their previous, old values.

As the features of each species are in a state of continuous change, there is a considerable amount of “evolutionary activity”, that we shall quantify with reference to the motion of a “center of mass”:

$$X_{CM} = \sum_{i=1}^M V^i \tag{3}$$

whose value is to be ascertained at a series of regularly spaced times. Then, we define the evolutionary activity ( $EA$ ) as

$$EA = |\delta_t X_{CM}|^2$$

where  $\delta_t$  represents variation in an arbitrary number  $t$  of time steps (in this and previous works we use  $t = 1000$ ).

For the sake of simplicity we took in [14,15] (i) our hyper-matrix in the form

$$g_{\alpha\beta}^{ij} = k_{ij} \delta_{\alpha\beta} , \tag{4}$$

and (ii)  $A_\gamma^i = 0$ . Thus, (1) reduces itself to

$$F_i = \sum_{j=1}^M k_{ij} V^i \cdot V^j, \quad i = 1, \dots, M , \tag{5}$$

where  $k_{ij} = -k_{ji}$ . These simplifications will be later removed.

The  $k_{ij}$  are randomly chosen within  $[-1, 1]$  (for  $i < j$ ) and are kept constant throughout. The functional form of (2) was chosen in the (quite general) fashion

$$f_\beta = \sum_{n=0}^k a_n x^n, \quad x = \beta/N \tag{6}$$

so that

$$V_\beta^i = \frac{\sum_{n=0}^k a_n^i (\beta/N)^n}{\sqrt{\sum_\beta \sum_{n,m=0}^k a_m^i a_n^i (\beta/N)^{n+m}}} . \tag{7}$$

### 3. Symbiosis and external environment

As previously stated, we also wish in the present effort to investigate two kinds of effects neglected in [14], namely (i) those of the external environment and (ii) those of symbiosis.

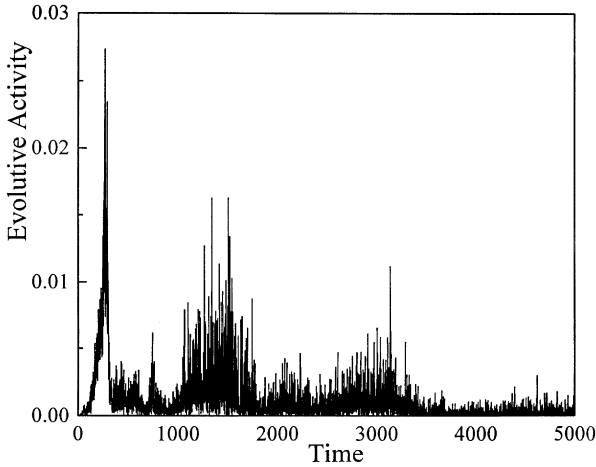


Fig. 1. Evolutive activity vs. time (arbitrary units) for  $Y = 100$  (see text),  $M = 25$ ,  $N = 17$ ,  $K = 5$ ,  $C = 0.5$ . Equilibrium is quickly attained. (Each point corresponds to 1000 time steps.)

### 3.1. Dynamical environmental effects

If we call  $Y$  the modulus of the vector  $A^i$  that represents the influence of the physical environment on the species  $i$  (for simplicity we will choose  $Y$  to be the same for all species), we clearly see that  $Y = 0$ , as chosen in [14], represents zero influence of the external environment. On the other hand, as  $Y$  grows, this influence will become more and more important. We also introduce the parameter  $C$ , which gives the fraction of non-vanishing  $k_{ij}$ 's.

When the external environment's influence is very strong (but constant), we observe that the dynamics of the entire system behaves in the following way: the ecosystem, after a relatively short period of time, reaches an "equilibrium state", after which no more sudden explosions of activity are to be detected. This is easily understood: the "environmental pushing" over a given species, say the  $i$ th one, is much stronger than the influence due to the other species. Once this species has become (well) adapted to the environment, it can only experiment minor changes, small fluctuations around the optimal state that are to be attributed to its interaction with the other species. Figs. 1 and 2 ( $Y = 100$ ,  $M = 25$ ,  $N = 17$ ,  $K = 5$ , and  $C = 0.5$ ) illustrate this point. Fig. 1 depicts global evolutive activity vs. time. We observe a behavior different to that reported in [14]. Initially, the activity pattern resembles that reported in [14]. As time elapses, however, mean amplitudes steadily decrease. Eventually, only (negligible) fluctuations are experienced. For small time values the evolutive activity distribution follows a power law, as in [14]. In the region of small fluctuations, a Gaussian-like distribution is obtained, which shows that the system's dynamics has *qualitatively* changed. The reasons that underlie this conduct of the global activity can be better understood with reference to the temporal behavior of the number of "beneficial" mutations ( $N_b$ ) (see Fig. 3).

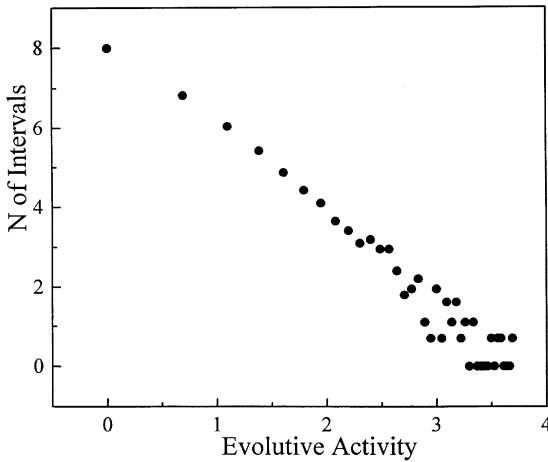


Fig. 2. Histogram constructed with the first part of the data displayed in Fig. 1 (log–log plot). A power law is well adjusted by the concomitant distribution of evolutionary activities.

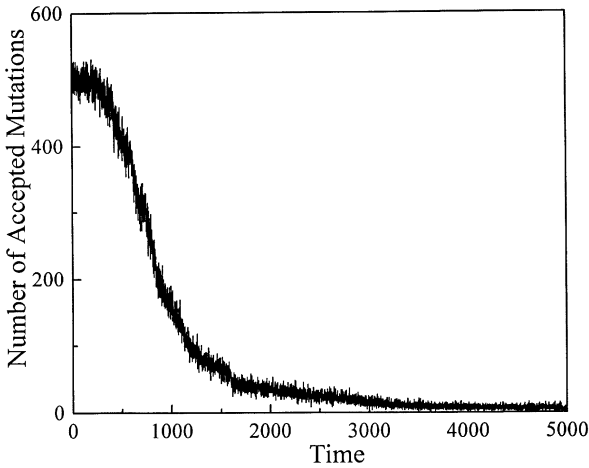


Fig. 3. Number of beneficial mutations ( $N_b$ ) vs.  $t$  for the scenario of Fig. 1 (see text). Each point represents 1000 time steps.

$N_b$  is the number of accepted mutations by a given species in a number of arbitrary time steps (here we take 1000 time steps), and they are beneficial in the sense that they produce an increase in fitness. Remember that when all the  $A_y^i$  vanish the mean value of  $N_b$  remains constant (does not depend upon  $t$ ). Here, however,  $N_b$  rapidly diminishes with  $t$ , reaching negligible values, a clear indication that the evolutionary process has stopped. Strong coupling to the external environment (large  $Y$  values) pushes the ecosystem towards an “equilibrium” situation. Inter-species interactions can only result in small fluctuations around this particular state.

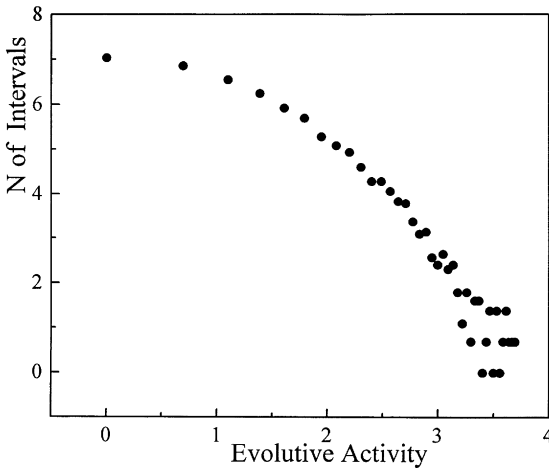


Fig. 4. Log–log plot of the distribution of evolute activities for  $Y = 100$  where strong random variations are involved (see text). We take  $M = 25$ ,  $N = 17$ ,  $K = 5$ ,  $C = 0.5$ . A deviation from a power law is to be observed.

For smaller  $Y$ -values than the ones discussed above the overall situation is qualitatively the same. The only difference can be found in the fact that fluctuations around the equilibrium state acquire larger amplitudes. Also,  $N_b$  is larger the smaller  $Y$  becomes.

Now, in the “real world” the environment does not remain constant (specially if geological time scales are envisioned). We can mimic this by letting  $Y$  become time dependent. For modest temporal variations ( $A^i$  are to be considered continuous functions of  $t$ ), the basic behaviors does not deviate from what has thus far been reported ( $Y$  independent of  $t$ ). Now, if the temporal dependence of the  $A^i$  is such that strong (and random) repeated oscillations are permitted, no equilibrium state is reached. The activity distribution (see the log–log graph of Fig. 4) exhibits a slight (“downwards”) concavity that resembles the one in Raup’s curve [10,18] (see graph on p. 269 of [18]). In both instances a deviation from what a power law would prescribe is to be appreciated. Big climate changes have indeed occurred on Earth as the juxtaposition of several effects such as equinox precession, perihelion precession, changes in the orbit’s eccentricity, etc. Even if each individual effect is of a periodic character, the superposition of them can become non-periodic in longer time intervals, so that our assumptions in drawing Fig. 4 are not of such an extreme nature as one might at first sight deduce.

We must also point out that, as one would expect, as  $Y$  becomes smaller the distribution of Fig. 1 becomes closer to a power law.

### 3.2. Symbiosis

In order to be in a position to deal with symbiotic or parasitic interactions we need to allow for a non-antisymmetric matrix  $k$ . This matrix has to be of a more general

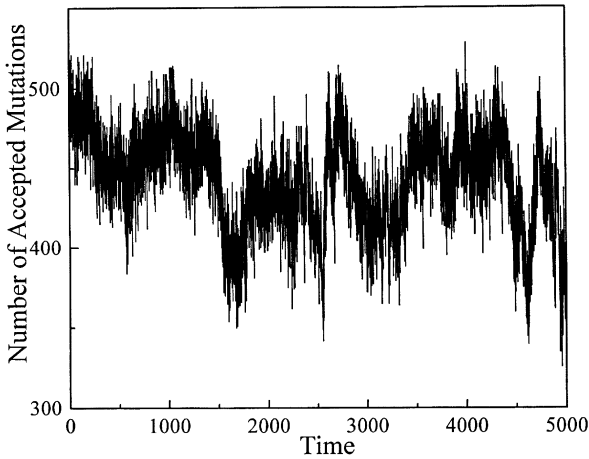


Fig. 5. Number of beneficial mutations ( $N_b$ ) vs.  $t$  for random values  $k_{ij}$ . Each point represents 1000 time steps.

character, and a way of removing the antisymmetry requirement is that of randomly selecting the matrix elements  $k_{ij}$  from the  $[0, 1]$ -interval. We shall set  $Y = 0$  so as to be able to focus our attention upon symbiotic effects, unencumbered by external influences.

We remember that for antisymmetric  $k$  matrices the number of beneficial mutations  $N_b$  is relatively stable. Let us discuss then the temporal behavior of  $N_b$  in the present circumstances. Large fluctuations ensue, as depicted in Fig. 5 for  $M=25$ ,  $N=17$ ,  $K=5$ , and  $C=0.5$ . This fluctuating behavior lends itself to interesting speculations concerning the origin of punctuated equilibrium. An old question is that of how to punctuate evolution. It has been argued [16] that species become caught in what is called “an adaptive grid lock”. Called stabilizing selection, this grid lock results because there is so much natural selection pushing a species to different directions. It cannot go anywhere because moving in one direction has implications for its other competing functions. For example, if a shellfish could reduce the weight of its shell, it might have a better chance of escaping from some fast-moving predators. But that evolutionary route could be closed because a lighter, thinner shell would also decrease its resistance to *other* predators, able to bore holes into their victims. So the species may remain unchanged for millions of years until a small population, isolated in a new environment, quickly evolves into a new species. Symbiosis is seen here to allow for this mechanism *without the isolation requirement*.

Of course, in the original model of [14] we did not need this mechanism to mimic punctuated evolution. The dynamical origin of the punctuated behavior in such a case was investigated in [15]. The interesting fact is that, as we enrich the model, we observe *new* mechanisms that contribute to “punctuate” the dynamics, some of which had already been theoretically predicted, although not (as far as we know) supported by numerical experiments of the nature we are presenting here.

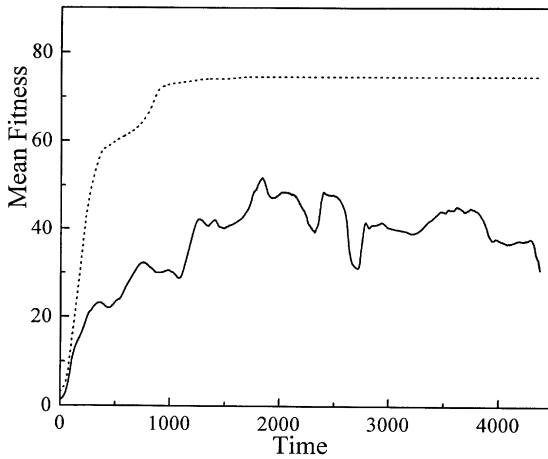


Fig. 6. Average fitness vs.  $t$  (arbitrary units). Dotted curve: symmetric  $k_{ij}$ -matrix. Full curve: random  $k_{ij}$ -values. See details in the text.

Another interesting fact to note is that such mechanisms can coexist without being of a mutually exclusive character, i.e., no single one of them bears sole responsibility for the “punctuation” phenomenon.

Symbiosis also changes the distribution of evolutive activities. The corresponding modifications imply slight deviations from what a power law prescribes, deviations that acquire the aspect of those reported in Fig. 4. In this respect, symbiosis plays a role similar to that of the external environment (i.e. deforms the power law distributions in order to endow the associated curve with a more “realistic” aspect).

We discuss next the effects of symbiosis upon the evolution of the average (over different species) of the corresponding fitnesses, to be denoted by  $F_{\text{average}}$ . It was shown in [14] that, for  $Y = 0$ ,  $F_{\text{average}}$  vanishes for all times  $t$ , as a direct consequence of the anti symmetric nature of the matrix  $k$ . In the present scenario (see Fig. 6),  $F_{\text{average}}$  grows with  $t$  until a certain plateau is reached. Afterwards, fluctuations of different magnitude ensue. The solid curve of Fig. 6 corresponds to  $k$ -matrix elements selected as indicated above, the dotted one to a *symmetric*  $k$ -matrix. The symmetric  $k$ -matrix represents the extreme case of a “totally symbiotic” system. We see from Fig. 6 that symbiosis allows for a better adaptive disposition of the whole ecosystem, as predicted by Maturana and Varela [19]. The “totally symbiotic” system (symmetric  $k$ -matrix) makes our “biological” system analogous to a spin glass (with a different time evolution law, though). In Fig. 7 we show the time evolution of  $N_b$  versus  $t$  for this system. From Fig. 7 we appreciate the fact that in this case an equilibrium state (local minimum of the system’s energy) is rapidly reached and the system then “freezes up”. This can be seen as a rather spectacular effect of the above-mentioned grid lock mechanism. It has to be pointed out that the distribution of evolutive activity does not follow a power law for the frozen system. It is also important to point out that all previous results do not appear to strongly depend on neither  $M, N, K$ , or  $C$ .

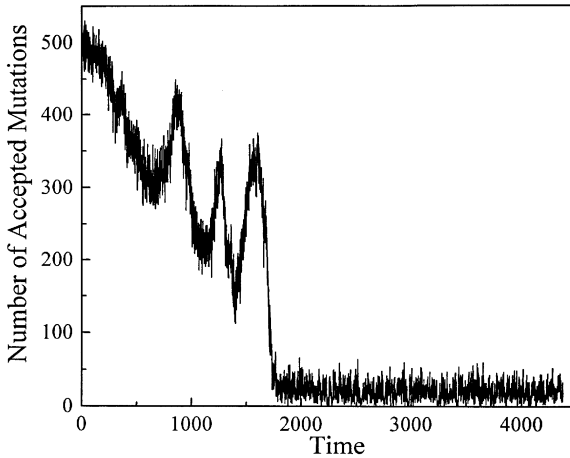


Fig. 7. Number of beneficial mutations ( $N_b$ ) vs.  $t$  for a symmetric  $k_{ij}$  matrix (see text). Each point represents 1000 time steps. Notice that, after some time has elapsed, a rather spectacular gridlock effect can be observed.

## 4. Discussion

### 4.1. Environmental effects

We conclude that the essential features of the model introduced in [14] remain basically the same after inclusion of both environmental and symbiotic effects. The distribution of evolutive activities continues following a power law, with just slight deviations that tend to bring it in closer agreement with fossil records' results. This "robustness" of the power law character of the concomitant curve would tend to lend support to the idea that punctuated behavior is a purely dynamical effect. One does not need catastrophic external events in order to attain it.

However, it is to be pointed out that the introduction of environmental effects tends to improve agreement with the fossil records, as just stated. The model seems thus to be able to smoothly integrate these external effects into a coherent dynamical picture, à la Maturana [20]: the ecosystem it describes attains its characteristic "deformed" power law distributions on account of both inter-species interactions and ambient (external) influences. That such an integration of both types of influences is attained should be of importance because, due to the smoothness of the distribution of extinction events at all scales (as revealed by fossil records), it has been argued that there should be just *one* mechanism responsible for it (either external influences, or the intrinsic nature of the concomitant dynamics). However, we have shown here that both mechanisms can be seen to work together at all scales.

This smooth integration of both kind of influences is extremely important, because due to the smoothness of the distribution of extinction events at all scales (obtained from fossil records) it has been argued that there is only one mechanism responsible

for it (either external influences, or rather the internal dynamics by itself). However, we have seen here that both mechanisms can smoothly work simultaneously at all scales.

#### 4.2. *Symbiosis as a facilitator of the adaptive grid lock mechanism*

Symbiosis is seen to be important indeed (modifying the power law distribution), which adds up to the realistic features of the model [19]. The original version of the model was characterized by an almost constant number of beneficial mutations  $N_b$  with  $t$ . The introduction of symbiotic mechanisms alters this picture and gives numerical support to earlier speculations [16] concerning an “adaptive grid lock” mechanism, that assumed that rapid evolution could occur, but only in isolation (think of the Galapagos case). Here symbiosis is seen to enrich the dynamics of the model in such a fashion that the grid lock effect is incorporated, but, after some time, the species can escape it, even in the presence of other competing species.

### 5. Conclusions

Summing up, a simple mathematical model is here seen to account for some major features of biological evolution, which should reinforce the idea that natural phenomena, no matter how complex, are amenable to be treated à la Galileo. Of course, the analogies drawn in the present work between evolutive dynamics and simple dynamical trends are to be regarded as being of a mere illustrative character. Anyway, they may be of some help in trying to unravel a small portion of the complexity that characterizes very important kinds of dynamical processes: the biological ones.

### Acknowledgements

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