A Physical Basis of Evolution and Speculation on an Evolutionary Basis of Physics

K. Michaelian

Instituto de Física, Universidad Nacional Autónoma de México A.P. 20-364, 01000 México D.F., Mexico

January 31, 2003

Abstract

It is suggested that natural selection and free energy minimization are the same phenomena. Such a supposition leads to a physical basis for the dynamics of evolving systems and to a speculation concerning the description of physical processes from an evolutionary perspective. A model is presented to describe the evolutionary dynamics of a community of species under the mandate of free energy minimization. Many important dynamical signatures of natural ecologies are reproduced by the model.

Biology has resisted an interpretation based on the concepts of physics and the two disciplines have, for the most part, had separate histories since the beginning of science. This dichotomy can surely be attributed to the anthropocentric egotism of man, the epitome of biology, designed for some special purpose in the universe. Interestingly, the practice of science began in agriculture, in the artificial selection of food crops, a science which would only attain a partial formal logical structure some 4000 years later! Although the time was spent in slowly developing the tools of science, like observation, hypothesis making, and experimentation, a great deal more effort and time was spent in refuting dogmatic, but more practical, views held, and still held, by the majority. The simple anthropic explanations of the physical world, which all lead to one or more gods or uniqueness theorems as the supersymetry principle, were more complete and readily understood by everyone.

In the last century, the tools of science have developed to such an extent that they are more advanced than required to dissolve the dichotomy between physics and biology and to retire to history once and for all the anthropocentric view in whichever manifestation. What is still lacking, however, is a consensus on the physical basis underlying the structure and dynamics of biological systems. This consensus has been hampered by a number of widely held misconceptions. The object of this paper is to review two of the most important misconceptions which have played a major role in maintaining the dichotomy to recent times. Their clarification allows a unification of the two disciplines by suggesting a physical basis for evolutionary theory and an evolutionary basis for physical theory.

1 Misconceptions

The greatest misconception inhibiting the description of biology from a physical perspective had its origin at the beginning of the last century with the development by Clausius of the concept of entropy and the formulation of the second law of thermodynamics in the development of the theory of heat engines. Boltzmann later gave the concept of Clausius a microscopic basis by relating the entropy of a system to the probability of the macroscopic state based on the number of equivalent microscopic states which render the macroscopic state indistinguishable. Unfortunately, however, from here the quantitative developments of the theory were based on the model of an ideal gas with non-interacting components. This lead to much confusion in applying the concept of the second law of thermodynamics to real systems, in particular to biological systems which have little similarity to an ideal gas [1]. Entropy, unfortunately, became associated with disorder, the antithesis of complexity. How was it possible that biological systems appeared to increase their complexity, reduce disorder, when the 2nd law demanded its destruction? Many seemingly valid explanations, however incomplete, were given. The most accepted being that the 2nd law applies only to closed systems and biological systems were *not* closed and could therefore increase their order (reduce their entropy) at the expense of the environment, which, taken together, did form a closed system. It appeared, however, that only biological systems had this special ability and thus there was still an argument for uniqueness in biology. Distinguished physicists such as Schrödinger [2] and Wigner [3], for example, postulated that there were as yet *undiscovered* biological laws operating.

Others argued that complexity and order in the universe could increase even though entropy increased by assuming that the number of micro states defining a given macro state also increased with time [4]. Order was defined as 1 - D where the disorder Dwas given by

$$D = S/S_{max} = S/k \log n_{max} \tag{1}$$

where n_{max} is the maximum possible number of micro states consistent with the macrostate. Assuming that the maximum number of micro states can increase with time $n_{max}(t)$ and that $k \log n_{max}$ increases faster than S(n), it is possible to have order increase even though entropy increases. Two of the postulated mechanisms for increasing the number of micro states were, the expansion of the universe, and the production of elementary particles [5].

The real problem, and its solution, of course, has to do with the introduction of the concepts of order/disorder, or complexity, taken from common experience but never incorporated into the formal structure of science [6], and its association with entropy, one of the basic, and well founded, elements of a scientific description of nature. The common conception of complexity, prevalent among physicists, is based on the notion of a noninteracting ideal gas. It is only in this case that the association with entropy has some legitimacy. In the real world, interactions are an integral part of the ordering of material particles, interactions which, in fact, give rise to the material.

If our concept of order or complexity were to be associated with not only entropy but also with the internal interactions, then there would be no confusion about increasing order together with increasing entropy. In fact, this definition of order had been given long ago by Helmholtz in his definition of the free energy and the observation that, when left alone, all systems tend to more stable states of greater longevity by reducing their free energy F, as defined by

$$F = E - TS \tag{2}$$

where E is the internal energy of the system due to interactions between the internal constituents and T is the temperature. Increasing the entropy decreases the free energy of the system and thus increases the order of the system. In this scheme, order has a very natural description, increasing the order of the system makes it more stable, longer lasting in time, or more viable in the biological sense. This is true of either the ideal gas approaching equilibrium, the crystallization of matter, or the evolutionary dynamics of a community of interacting biological systems.

Meanwhile, on the biological side, an equally great misconception was being played out. Darwin's theory for species change gained rapid acceptance for its simplicity, generality and logical structure. However, one very important question remained unanswered. What was natural selection selecting? This seemingly innocent question led to a similar amount of confusion as did the concept of order. Biologist maintained that what was being selected was that which was more fit. Insistence on explaining what was meant by "fit", would inevitably lead to "that which survived", be it the fastest, strongest, cleverest, etc. This answer, of course, leads to the tautological statement that natural selection leads to "survival of the survivors", and therefore, in the view of Popper evolutionary theory was a metaphysical program [7]. This proclamation, unfortunately, led to the awakening of the resting anthropocentric philosophers who found vindication in the criticism of the, by then, accepted scientific dogma. Poppers criticism, and the ensuing denials of evolutionary theory being a scientific theory, also led, however, to many important attempts to place evolutionary theory on a more fundamental physical basis with a more formal logical structure. The terms fastest, strongest, cleverest, gave way to, most energy efficient, minimal entropy producing, greatest power producing [8], etc.

However, there is a more encompassing association of survival in biology with a universal concept in physics which does not depend on the system being in a particular thermodynamic state [9]. We have noted above that survival, or being stable over time, in the physical world is associated with free energy minimization. Now, the dichotomy between physics and biology, at least in one very important aspect, can be resolved. Natural selection and free energy minimization are one and the same. They are equivalents in different languages. Accepting this postulate leads to many interesting new insights into both evolutionary theory and physical theory. In this paper we will consider in detail these insights into evolutionary theory and leave that of physical theory to a few speculative comments in the conclusions to be further developed in a forthcoming paper.

2 A Physical Basis for Evolutionary Theory

If we select a particular species and ask whether this species is fit, whether it will be observable in say one million or even one thousand years from now, assuming a constant environment, it is inevitably realized that the answer to this question depends not only on the inherent structure of the species but on the environment, both physical (abiotic) and biotic, and the interaction between species and the environment. That is, the fitness of the species is not an inherent characteristic, rather it is a condition of the community of the species together with the environment.¹ The species is one of a finite number of elements of a larger organism, the community plus the local environment. In turn, communities and the environment are elements of a still larger organism, the biosphere [11]. At each level, specie, community, or biosphere, the dynamics of the system is governed by the same physical laws which underlie the structure and dynamics of all finite systems. In particular, the minimization of free energy (the condition of fitness) given the restrictions of the resource space, governs the dynamics of the exploration of this space and hence the evolution of the strengths of the interactions between species and between species and environment.

To demonstrate this, in the following we consider a physical model for determining the evolutionary dynamics at the community level, based on free energy minimization. This will be accomplished by formalizing an exact analogy between a cluster of atoms interacting in physical space and a cluster (community) of species interacting in an abiotic resource space. Movement of the species in this space implies changing the abiotic resource gradient requirements of the species as well as changing the interaction strengths with the other species and thus is representative of evolutionary change. Such change will become part of the community, be selected, if the movement results in lowering the free energy of the system as a whole. In this case the stability of the community as a whole will improve. Natural selection in the model is thus based on a global criterium. To speak of the individual fitness of a species makes as little sense as it does to talk of the free energy of an individual atom in the atomic cluster. A valid question, however, is; how important is this species to the stability of the community?

The analogy to be presented can be more formally summarized as follows: Cluster physics, deals with one, or at most a few, "species" of particles interacting through, generally, isotropic potentials in a three-dimensional, infinite, physical space. Stable configurations, or morphologies, at zero temperature are determined by minimizing the potential energy of the system [12]. At finite temperatures, the free energy of the system is minimized by including the entropy of the vibrational and rotational modes of the system, leading to a most probable morphology at the given temperature. At a sufficiently high temperature, depending on the "connectivity" of the atoms (through the form of the interaction potential), melting occurs and the system executes a series of morphological changes, moving in a relatively free but discrete manner over minima on the free energy surface accessible at that temperature.

Ecology deals with a community of biotic species interacting through anisotropic potentials in a many-dimensional, finite, abiotic resource hyper-space. Stable community structures at zero temperature (the static case of no evolution or movement in resource hyper-space and no change in the abiotic resources) will be those corresponding to local minima in the surface defined by the internal energy of the biotic-abiotic system. At low temperature, the system will vibrate around an equilibrium configuration. At a sufficiently high temperature melting occurs, and the system explores, in a time-wise discrete manner, the free energy local minima accessible, implying episodes of evolution (mutation, speciation, changes in the connectivity of the ecocluster, and population changes between the extremes of extinction and the maximum carrying capacity of the space). Table 1 lists the correspondences between quantities in the atomic and ecological cluster models. The details of this model have been given in a separate publication [13]. Here a brief outline of the model and some of the results will be given.

¹This immediately renders of questionable value all those recent theories in which fitness is inherent to the species [10].

	Atomic Cluster	Ecocluster
basic unit	atom	specie
space	3D infinite physical	nD finite resource hyper-space
interaction	pair or n-body	pair or n-body, anisotropic
temperature	kinetic energy of atoms	mutation, abiotic resource fluctuation
minimization of H	stability	viability of ecosystem
dynamics	molecular dynamics	genetic algorithm
collective movement	isomerization	evolutionary episode

Table 1: Correspondence between quantities of the atomic cluster and the ecological cluster.

2.1 The Model

A species is represented by its position vector $\vec{r_i}$ in an n-dimensional resource space. The projection of the species point on an axis of the space represents the gradient of the particular resource required by an average member of that species. The Helmholtz free energy of the ecocluster is a sum of the internal energy E minus the product of the temperature T and the entropy S of the cluster. The internal energy and the entropy are appropriate functions of the coordinates $\vec{r_i}$ of the points in resource space representing the n species, and their populations p_i ,

$$H = E(\vec{r_1}, \vec{r_2}, \cdots, \vec{r_n}, p_1, p_2, \cdots, p_n) - TS(\vec{r_1}, \vec{r_2}, \cdots, \vec{r_n}, p_1, p_2, \cdots, p_n).$$
(3)

Except for the special case where H is at a local minimum in the free energy surface, the \vec{r} and p are functions of time, representing the evolution and population dynamics respectively.

The internal energy E consists, principly, of three components:

- 1. The total of the interactions of each species i with its abiotic environment.
- 2. The inter-specific interaction between species i and j, be it competition, parasitism, or symbiosis.
- 3. The intra-specific interaction between members of the same species i due to competition arising from the limited carrying capacity of the local abiotic environment.

The second term of eq. (3) represents, for a finite "temperature" T, the contribution to the free energy arising from the entropy S of the vibrational and rotational modes of the cluster in its particular configuration in resource space. In this analogy, the temperature of the cluster is attributed to two components; the natural random mutation rates of the species, and to the (assumed random) variability of the abiotic environment, affecting the resource gradients.

If the above listed contributions of internal energy to the free energy of the cluster are pair-wise additive among the individuals of the interacting species, then the first contribution should be proportional to p_i , the second to $p_i p_j$ and the third to $p_i (p_i - 1)/2$ ($\sim p_i^2/2$ for large populations). The free energy can then be written in the form

$$H = \sum_{i}^{n} \left[p_{i} E_{1}(\vec{r_{i}}) + \sum_{j \neq i}^{n} p_{i} p_{j} E_{2}(\vec{r_{i}}, \vec{r_{j}}) + \frac{p_{i}^{2}}{2} E_{3}(\vec{r_{i}}) \right] - TS(\vec{r_{1}}, \vec{r_{2}}, \cdots, \vec{r_{n}}, p_{1}, p_{2}, \cdots, p_{n})$$
(4)

where the E's are related to the respective individual or pair contributions of the three components of the internal energy listed above.

For the special case of the cluster in thermodynamic equilibrium, it has been shown in reference [13], that equation (4) leads to the well know Lotka-Volterra equations giving the equilibrium populations of the species. In order to study the general behavior of the cluster out of equilibrium, in terms of its evolutionary dynamics, it is necessary to specify the functional dependence of the E's and entropy S in equation (4) on the species positions $\vec{r_i}$ in resource space. In other words, we must now quantify the contributions to the free energy due to the interaction between species, and between species and the abiotic environment. This must incorporate the physical and chemical exchanges (metabolic pathways) amongst individuals and with the abiotic environment. This task for complex organisms is far beyond the scope of present biochemical and biophysical understanding. However, we can grossly simplify the interaction scheme, but keep it general enough to allow some important characteristics of the cluster model to be delineated.

First, we assume that all abiotic resource gradients are independent and have been normalized such that displacement of a given species point along any of the k coordinates is equally important to the function describing the free energy of the community. Also, the resource gradient limits are restricted such that the allowable volume of resource space is the physically meaningful positive quadrant of a k-dimensional sphere of radius a.

Next, we assume that the effect on the internal energy of the system for an individual of species i, due to its interaction with the abiotic environment, is proportional to the resource gradient required,

$$E_1(\vec{r_i}) = A_i r_i,\tag{5}$$

where A_i is a constant and $r_i = |\vec{r_i}|$ is a root mean square value of the resource gradient.

The interaction energy E_2 between species should be a function of the distance between them in resource space. Because of competition for resources between species located close together in resource space, this function should be repulsive (increasing the free energy) at short distance. Species could acquire symbiotic or parasitic interdependence, implying association in real physical space and thereby leading to some attraction at intermediate distance in resource space. Different species could also be in competition for the same biotic resources (n-body effects) in which case there would be a repulsive or destabilizing effect on the community. At large distance the local abiotic environments would be significantly different and the species interaction would be expected to be small. An interaction energy functional representing the effect of an individual of species j on one of species i ($i \neq j$), with the required dependence on species separation $r_{ij} = |\vec{r_i} - \vec{r_j}|$ in resource hyper-space, is

$$E_2(\vec{r_i}, \vec{r_j}) = r_i r_j (B_{ij} \exp[-p(r_{ij} - 1)] - C_{ij} \exp[-q(r_{ij} - 1)]).$$
(6)

The constants B_{ij} are positive, giving the first term a positive definite value, representing repulsion due to competition for abiotic resources. The exponential nature of this term, and a large value for p and a small value for q (chosen to be = 10 and = 2 respectively for all inter-specie interactions in this model) give it a short range character implying importance only for two species attempting to occupy the same resource hyper-space volume. The second term represents competition for biotic resources (C_{ij} and C_{ji} negative), parasitism (C_{ij} positive, C_{ji} negative, or vice-versa), symbiosis (C_{ij} and C_{ji} positive), or independent (C_{ij} and C_{ji} zero) and supplies the interdependence or the binding of the community. The factor $r_i r_j$ multiplying the above term represents the increasing interaction strength between species *i* and *j* as either species *i* or *j* increases its abiotic resource gradient requirement. The exponential nature chosen for this term is in accord with the results of niche overlap studies from the field [14, 15].

The intra-specific interaction term, E_3 , is proportional to the resource consumption of an individual and to the inverse of the carrying capacity K_i of the resource hypervolume occupied by species *i* (see reference [13]). The carrying capacity is taken to go to zero at the resource boundary limits (0 and *a*) and to be inversely proportional to the amount of resource consumed by an individual between these limits, giving,

$$E_3(\vec{r_i}) = B_{ii}r_i^2 \quad 0 < r_i < a$$

$$= +\infty \quad r_i \le 0, r_i \ge a$$
(7)

where B_{ii} is a positive species specific constant. This term is positive definite and avoids species evolving characteristics which the environment cannot support.

With the free energy as given by equation (4), and incorporating the interaction functionals E_1 , E_2 and E_3 as given by equations (5), (6) and (7), and an expression for the vibrational and rotational entropy, we can now proceed to study the dynamics of the ecocluster out of equilibrium. As in nature, a genetic algorithm is used to govern the movement of the cluster over the free energy surface [13]. The system, being not initially in equilibrium, will take an overall trajectory in the direction of reducing its free energy, be it changes in connectivity, extinction or generation of new species. The ecocluster will thus move through a set of quasi-equilibrium states (local minima) with the time spent in each state related not only to the height of the energy barriers, but also to the vibrational and rotational entropy of the state.

The variables of the genetic algorithm to be optimized are the species populations and their positions in resource space. The initial populations of all possible species precursors is zero and their initial positions are generated at random. A species comes into existence when its population evolves to a finite positive value. Interaction strengths between species and between species and the abiotic resources, as defined by equations (5) through (7) once suitable values of the A_i, B_{ij} and C_{ij} are chosen [13], are free to evolve with the changing configuration of the community in resource space.

2.2 Results

In figure 1 we present the free energy as a function of time of a cluster evolving in a 3-dimensional resource space. The free energy of the community is not a smooth function of time, as found in the genetic optimization of atomic clusters [16, 17], but demonstrates abrupt changes as reconfigurations of the cluster, due to the appearance of new species, and increases in the populations of existing species, change the local topology of the free energy surface.

Figure 2 show the increase in the total number of species as a function of time. The increases are generally less than linear, as can be derived from the empirical observations that, extinction declines on average over time, diversity increases, and no species lives forever [18]. Figure 3 shows the sum total of the population of all species as a function of time. In the particular trajectory of the ecocluster shown here, there are three regimes of population growth which are mirrored in the free energy changes (Fig. 1).

In figure 4 we plot the individual movements, with respect to the origin of the resource space, of four randomly selected species as a function of time. During the early exploration of resource space, while the number of species is small, the movements (evolutionary events) are substantial over short time periods. At later times, while the number of species is large, the cluster visits more stable configurations with fewer lower energy minima accessible and evolution is more gradual. The model thus predicts punctuated equilibrium type of evolution [19] in small and young communities and more gradual evolution in large, more established communities.

We can now give a simple answer to two major evolutionary problems, that of stasis (the maintenance of stability within species) and that of coherence across taxa of punctuational events [20]. When the ecocluster is configurated near a local minimum on its free energy surface, the configuration is fixed and the species points are in stasis, only vibrating about fixed points. A particular fluctuation, however, could allow the cluster to escape the local minimum, causing a collective movement of the species (coherent punctuational event), and move it into another saddle connected minimum, giving stasis once again.

In figure 5 we have plotted the sum of the displacements of all species over a fixed time interval as a function of time. Large collective movements of the species points in resource space is equivalent to mass extinction events in which the species undergo substantial change in short time. Figure 5 is a record of the number and size of extinction events over the evolutionary history of the cluster. We note that, in general, the extinction rate and magnitude of the events decrease over time. This has been found in nature on a global scale [21].

The probability (frequency) of extinction events as a function of extinction size is given in figure 6. The relation between the probability and the size is a power law of form $P(s) \propto 1/s^{\tau}$, with $\tau = 2.29 \pm .04$ for the three dimensional resource space. The power τ has a dependence on the dimensionality of the space in which the species are interacting, it is large for low dimensional spaces and small for high dimensional spaces [13]. The power law behavior is indicative of scale invariance. Considering that, on average, in nature each species interacts strongly (nearest neighbor in this model) with no more than 3 or 4 others [22], the results for the 3 dimensional resource space are in good agreement with data from the field which give $\tau = 1.9 \pm 0.4$, $\tau = 2.0 \pm 0.2$ [23] and $\tau = 1.95$ [24].

3 Conclusions

Two widely held misconceptions concerning fundamental concepts from physics and biology were responsible for maintaining the dichotomy between these two disciplines. Recognizing this leads to an interesting unification of physics and biology. In particular, we have suggested that the concept of natural selection in biology is equivalent to free energy minimization in physics. Each leads to states of a system of greater longevity, or viability in the biological sense. A physical model was presented to gain insight into the evolutionary dynamics of a community of species based on the global criterium of free energy minimization of the system as a whole. The model reproduces well many of the important dynamical signatures of real ecologies, in particular, the less than linear increase in species diversity as a function of time, the reduction in the rate of extinction as a function of time, the power law distribution of size of extinction events, and punctuated equilibrium. As well, a simple explanation of stasis and coherence of evolutionary events over taxa and time was given.

The apparent symmetry in the concepts of natural selection and free energy minimization, which govern the dynamics of systems of their respective disciplines, leads us to speculate that the dynamics of physical systems can also be viewed from the perspective of evolutionary theory. Specifically, the dynamics of physical processes entails responses to particular situations, not in a continuous, causal determinism but rather in a discrete, stochastic manner. A multitude of system states exist, consistent with local restrictions, but for the observed trajectory through phase space, one is naturally selected according to a probability determined by the resulting change in the free energy of the system. As a specific example, the quantum tunneling of a particle through a finite energy barrier, and the mutation of a species from one fitness peak to another across a fitness minimum, bear an extraordinary resemblance. There are many details of this view which remain to be developed, however, here we will be content with this brief mention and leave the development of these ideas to further works.

4 Acknowledgements

The author would like to gratefully acknowledge the financial support of DGAPA-UNAM, grant no. IN101297, and CONACyT, grant no. 25083E.

References

- S. D. Haitun, Entropy and Disorder: The Evolution of Views Concerning their Connection, p. 220-227 in Thermodynamics: History and Philosophy, eds. K. Martinas, L. Ropolyi and P. Szegedi, (World Scientific, Singapore, 1990).
- [2] E. Schrödinger, *What is Life*, (Cambridge University Press, Cambridge, 1944).
- [3] E.P. Wigner, *Symmetries and Reflections*, (Indiana University Press, Bloomington, Indiana, 1967).
- [4] P. T. Lansberg, Can Entropy and "Order" Increase Together, Phys. Lett. A 102, 171 (1984).
- [5] S. Frautschi, Entropy in an Expanding Universe, Science 217, 593 (1982).
- [6] J. Maddox, Complicated Measures of Complexity, Nature 344, 705 (1990).
- [7] For an interesting discussion on the debate of tautology in traditional evolutionary theory, see Wilkins, J. http://www.talkorigins.org/faqs/evolphil.html.
- [8] J. L. Torres, Natural Selection and Thermodynamic Optimality, Nuovo Cimento 13, 177-185 (1991).
- D. Jou, J. Casas-Vázquez and G. Lebon, *Extended Irreversible Thermodynamics*, Rep. Prog. Phys. 51, 1105-1179 (1988).
- [10] Models in which fitness is assigned to individual species can be found in; Bak, P. and Sneppen, K. Phys. Rev. Lett. **71**, 4083-4086 (1993); Solé, R. V. and Bascompte, J. Proc. Roy. Soc. **B 263**, 161-168 (1996); Solé, R. V., Bascompte, J. and Manrubia, S. C. Proc. Roy. Soc. **B 263**, 1407-1413 (1996); Abramson, G.

Phys. Rev. E **55**, 785-788 (1997); Wilke, C. and Martinetz, T. Phys. Rev. E **56**, 7128-7131 (1997); Boettcher, S. and Paczuski, M. Phys. Rev. Lett. **76**, 348-351 (1996).

- [11] For an interesting introduction to the hypothesis of "Gia", in which the biosphere is considered to be a single living organism, see the article; R. J. Charlson, J. E. Lovelock, M. O. Andreae, S. G. Warren, Oceanic Phytoplankton, Atmospheric Sulfur, Cloud Albedo and Climate, Nature 326, 655-661 (1987).
- [12] K. Michaelian, N. Rendón, I. L. Garzón, Structure and Energetics of Ni, Ag, and Au Nanoclusters, Phys. Rev. B 60, 2000 (1999).
- [13] K. Michaelian, A Cluster Model of Ecologies, submitted for referee.
- [14] R. M. May, Will a Large Complex System be Stable, Nature 238, 413-414 (1972).
- [15] R. M. May and R. H. MacArthur, Niche Overlap as a Function of Environmental Variability, Proc. Nat. Acad. Sci. 69, 1109-1113 (1972).
- [16] K. Michaelian, Evolving Few-Ion Clusters of Na and Cl, Am. J. Phys. 66, 231-240 (1998).
- [17] K. Michaelian, A Symbiotic Algorithm for Finding the Lowest Energy Isomers of Large Clusters and Molecules, Chem. Phys. Lett. 293, 202-208 (1998).
- [18] M. E. J. Newman and P. Sibani, Extinction, Diversity and Survivorship of Taxa in the Fossil Record, Proc. R. Soc. London B 266, 1593-1600 (1999).
- [19] N. Eldredge and S. J. Gould, Punctuated Equilibrium Prevails, Nature 332, 211-212 (1988).
- [20] S. J. Gould, and N. Eldredge, Puntuated Equilibrium Comes of Age, Nature 366, 223-227 (1993).
- [21] D. M. Raup and J. J. Sepkoski Jr., Mass Extinction in the Marine Fossil Record, Science 215, 1501-1503 (1982).
- [22] G. Sugihara, K. Schoenly and A. Trombla, Scale Invariance in Food Web Properties, Science 245, 48-52 (1989).
- [23] M. E. J. Newman, Proc. R. Soc. Lond. B **263**, 1605-1610 (1996).
- [24] R. V. Solé and J. Bascompte, Are Critical Phenomena Relevant to Large-Scale Evolution?, Proc. Roy. Soc. B 263, 161-168 (1996); R. V. Solé, J. Bascompte and S. C. Manrubia, Extinction: Bad Genes or Weak Chaos, Proc. Roy. Soc. B 263, 1407-1413 (1996).



Figure 1: The free energy of the ecocluster for a particular trajectory on the free energy surface as a function of time for a 3 dimensional abiotic resource hyper-space.



Figure 2: The number of viable species (with a population greater than 10) as a function of time for a 3 dimensional abiotic resource hyper-space.



Figure 3: The total population of the community (number of individuals) as a function of time for a 3 dimensional resource hyper-space.



Figure 4: The movement (as measured as distance from the origin) of 4 randomly chosen species in the 3 dimensional abiotic resource space as a function of time. Punctuated equilibrium is clearly observed in the early stages of these evolutionary histories.



Figure 5: Extinction event size as a function of time for the ecocluster evolving in a 3 dimensional abiotic resource hyper-space.



Figure 6: Frequency of extinction events as a function of event size for the ecocluster evolving in a 3 dimensional dimensional resource hyper-space. The error bars are statistical (the square root of the number of events). The line is the best χ^2 fit power law (straight line on log-log graph).