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Review Article

ON THE FRACTAL NATURE OF ECOLOGICAL AND MACROEVOLUTIONARY DYNAMICS

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Abstract

In recent studies, a new class of models dealing with evolutionary processes on the large timescale have shown that many of the general traits of the fossil record can be reproduced under some simple assumptions. Additionally, the study of living ecosystems and their network organization, as well as the time series analysis of population fluctuations, points in the direction that complex ecosystems are organized close to instability points where extinction of species and ecological turnover would be the rule. In this paper, we further explore these ideas and their implications for our understanding of evolution as a complex dynamical process with some universal features linked with network-level properties. In particular, a source for the decoupling between micro- and macroevolutionary mechanisms is provided.

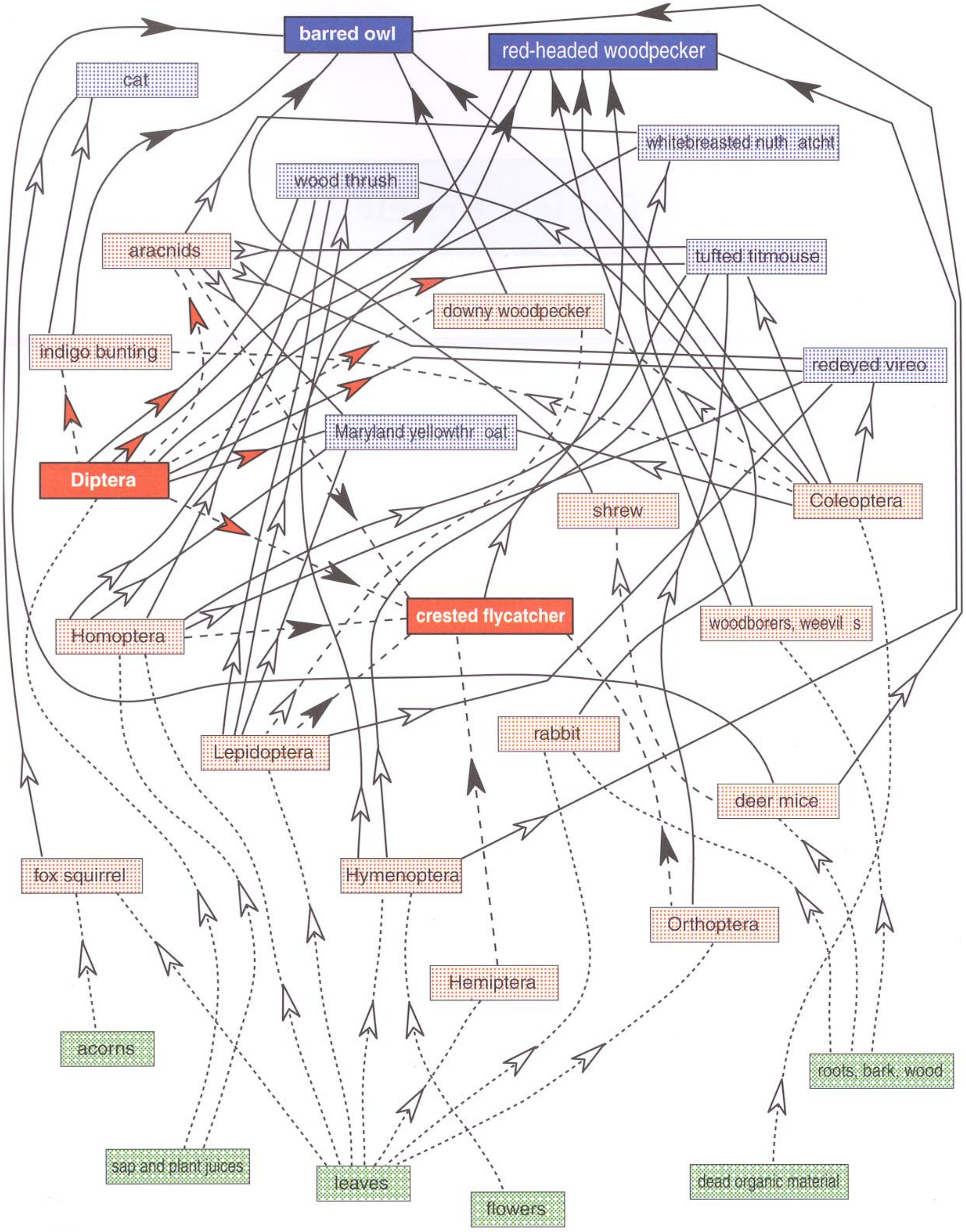

Fig. 1 A food web from Trelease Woods, Illinois [data from Cohen *et al.* (1990)[15]]. Many different types of interactions are included as arrows connecting different compartments. Some of the nodes are in fact clusters of a number of species and contain many different groups of organisms. The network here shown is a simplified one. Although direct interactions are easily recognized, the relevance of higher-order links can only be assessed as evolution proceeds. Basal species (those that do not have preys) have green background, top species (do not have predators) have blue background, and intermediate species (have both predators and preys) are represented with red background. The links indicate the predator-prey relationship, arrows go from prey to predator: Dotted links start in basal species, solid line links go to top species, and links between pairs of intermediate species are dashed. The most predated group corresponds to Diptera (outgoing arrows in red), while most diverse predators have ingoing arrows in black (crested flycatcher, red-headed woodpecker and barred owl).

1. INTRODUCTION: ECOSYSTEMS AS COMPLEX SYSTEMS

Biological species have been traditionally treated as isolated entities, and pictured as simple elements somehow influenced by an external constant or slightly fluctuating environment. Classical studies on population genetics have dealt with basic models of specific traits of fixed species, and the underlying ecological structure has been often forgotten. In fact, this simplification is unavoidable, since the full consideration of all species in an ecology goes beyond any reasonable mathematical treatment. As a consequence, in most cases, and in spite of the clear success of this approximation, the link between population genetics and ecology becomes far from satisfactory.[1]

Ecosystems have a well-defined web structure (Fig. 1) and several key regularities which suggest the presence of constraints operating at higher levels.[2–4] As a starting point, many classical studies have considered the Lotka-Volterra S-species equations,

$$\frac{dN_i}{dt} = N_i\left(\epsilon_i - \sum_{j=1}^{S}\gamma_{ij}N_j(t)\right) \tag{1}$$

where $\{N_i\}$, $i = 1, \ldots, S$ are the populations of each species and N_i represent their relative abundances. These models have been explored in depth, and two main qualitative problems have been considered: (i) small-n problems, involving two or three species and (ii) large-n models, involving a full network of interacting species. In the last case, the problem of stability versus complexity[5–7] still remains open. The so called community matrix $\Gamma = (\gamma_{ij})$ is the basic subject of all these studies.

A first look at a complex web of interactions immediately tells us that many indirect effects might be present.[8,9] In fact, not only the direct links between pairs of species are relevant, but also the way these links organize, the architecture of the very network, can play a main role in the subsequent evolution of the system. This observation, which can be quantified in several ways,[10] immediately poses the question: How relevant are indirect effects? This is an extremely relevant point.[11,12] Indeed, their relevance depends on the collective phenomena arising from the wiring structure of the web; and recent studies show, in fact, that a network-dependent response of ecosystems to perturbations is a common phenomenon.[13] Using an experimental system where the energy transfer between different species was measured (i.e. the energetic strength of the links), it was shown that links supporting relatively small energy flows can have a large impact on the rest of the system when varied or removed, while interactions carrying an important flow of energy can have a smaller impact [an illustrative example is described in Ratcliffe (1979)].

The pattern of connections must be related with the abundance of species S in the ecosystem. In this context, we should mention some regularities arising from the observation of real ecologies. In fact, it seems that the degree of connectivity among species in an ecosystem follows a well-defined (and highly non-trivial) dependence with S, as will be discussed later. On the other hand, complex ecological systems are formed by a large number of species whose abundances typically follow a log-normal distribution [example Fig. 2, see also Preston (1962)]. The shape of this long-tailed distribution is a characteristic feature of many ecosystems and reminds us that rarity is a dominant characteristic of most species (and an essential contribution to the overall diversity in world ecologies).

The problem of diversity is intimately linked to the last observation. High diversity levels are a common trait in a great number of situations, among which rainforests and coral reefs are major representatives. This is the baroque of nature in the words of the ecologist Ramon Margalef.[18] But why is nature diverse? We could imagine a planet where life is restricted to a continuous sheet of photosynthetic, single-celled organisms without further complexity. Nonetheless, it seems clear that because of the intrinsic trend to change arising from mutational forces, variation is an unavoidable outcome of living systems. Variation leads to new species, and these species compete for resources. Competition then appears as an important driving mechanism able to remove less-fit competitors from the ecology. Nevertheless, there are several ways to escape from competitive exclusion. One is the presence of mechanisms that enable different species with different ways of exploiting the same resources to co-exist (like trade-offs between dispersal and colonization). Another is the presence of spatial degrees of freedom: It can be shown that the simple introduction of space for competitors to move may lead to a situation where no exclusion takes place.[20,21]

But clearly, because no arbitrary high levels of diversity would be tolerated, thresholds to the maximum number of species are expected. This is an

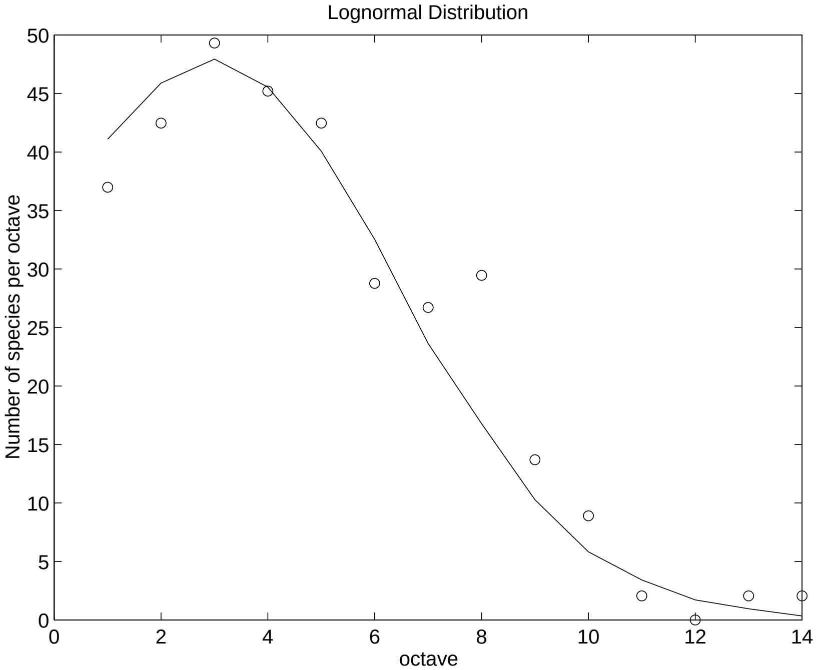

Fig. 2 Species abundances in a collection of moths caught in light trap [redrawn from Pielou (1969)]. When observations are grouped by octaves (which is equivalent to plotting on semilogarithmic scale using logarithms to base 2), the histogram obtained looks as though it would be well fitted by a symetrical normal curve truncated on the left and a long tail representing the few abundant species.

immediate conclusion obtained from microcosm experiments as well as from field data. An instance of threshold phenomena in ecology has been recently reported by Keitt and Marquet (1996) in relation with the avifauna of Hawaiian Islands. It was shown that after a gradual accumulation of introduced bird species, numerous extinction events occurred once a critical number of introduced species was reached.[22] The distribution of extinction events and the waiting times to extinction were shown to be power-law distributed. Perhaps the accumulation of species (by speciation events or natural immigration from a species pool) could also drive a given natural ecosystem towards the instability point, where extinctions would be triggered.

We start with a brief review of available field data describing ecosystems at two different time scales. The first time scale is relatively short and considers changes in population abundances and their spatial variation, the second one is larger and might represent a coarse-grain in time and space of the previous one. At the macroevolutionary level, only the presence or absence of species is relevant, and space is not an explicit variable. While the shortest time scale is characterized by ecological dynamics (i.e. the system may be described by a set of coupled equations of the Lotka-Volterra type for each of the populations present, for instance), we will argue that the second one is a consequence of the organization of the network of interactions close to instability points (where scaling properties are observed) and is essentially decoupled from the dynamics at the ecological time scale. To this end, we will analyze the collective behavior arising from different models formed by many species in interaction. A particular feature of these models is that they involve the presence of a transition point between two different regimes of behavior characterized by stable and by unstable dynamics, respectively.[23,24] Such a point has particular stability properties that might play a crucial role in our understanding of why ecosystems are so diverse and unpredictable.

2. SCALING PROPERTIES OF SPECIES IN INTERACTION

The complexity of an ecological system can be described through different statistical measures which quantify its degree of diversity (and its dependence with time or space), the organization of the biological interactions (e.g. predation), or the response of the system to perturbations.

2.1 Scaling in Ecosystems

Probably one of the best known quantitative measures in ecology is the species-area law, which relates the variation in the number of different species S with the area A available to them. The most common way of representing the relation between species and area is in the form of a power-law,

$$S \propto A^{-z} \tag{2}$$

where the exponent z depends on the geographical characteristics of the area (particularly on the degree of isolation of the ecosystem) and on the taxonomic group analyzed.[25] Recently, it has been found that the relation (2) can be obtained from ecological dynamics,[26] and is indeed the functional form to be expected in any complexely wired ecosystem where the available resources scale proportional to the area A. This statistical measure is complemented with local records of species abundances. In many cases, the number of individuals belonging to a given species present in a monitored (relatively small) area fluctuates strongly in time, pointing to a high local turnover and to an important dynamical exchange of species in space. Indeed, recent studies have quantified the permanence time of species in local patches. In particular, Keitt and Stanley (1998)[27] have examined the dynamics of breeding bird populations, and found that the distribution of species lifetimes (i.e. the time between colonization and local extinction) follows a power-law with a cutoff due to the finiteness of the time series. Also the analysis of temporal series of population abundances carried out by Pimm and Redfearn (1988) revealed that non-trivial time correlations are present.

A consequence of the system's dynamics and of the organization of network of interactions is that the probability $q(N)$ that a given species is represented by N individuals is

$$q(N) \propto N^{-\eta} \tag{3}$$

with $\eta \simeq 1 - 1.25$.[17] Recent approaches recover this relation,[26,29] as well as the functional form of the permanence time reported in Ref. 27. Equation (3) might indeed be the result of the intrinsic multiplicative nature of the reproduction process inside each species.

It has been observed that complex ecosystems respond in a highly nonlinear way to perturbations. Keitt and Marquet[22] have re-analyzed the effect of the introduction of new species into Hawaiian islands. Their results point to a threshold-like phenomenon: Apparently, the island community is organized close to its maximum capacity, and the introduction of new species above a certain threshold triggers avalanches of various sizes (see Fig. 3).

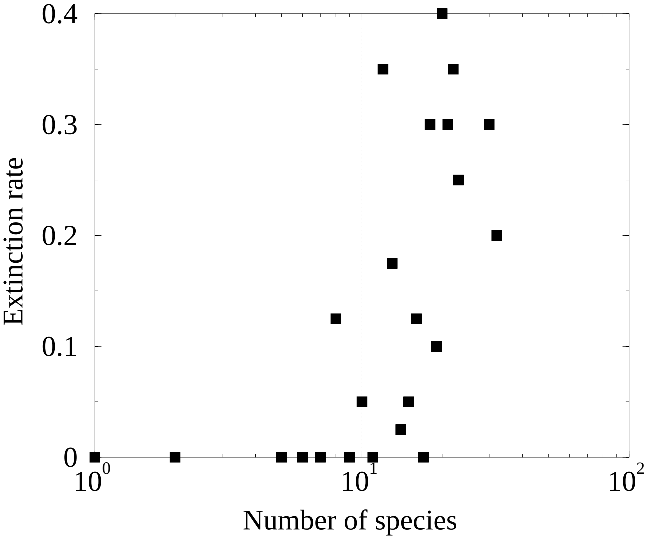

Fig. 3 Response of the introduced Hawaiian avifauna to a number M of introduced bird species (in the horizontal axes). The system does not "react" until a critical number ($M \sim 10$) is reached. Data from Ref. 30 as represented in Ref. 22.

All the properties discussed here portray ecosystems as complex and highly dynamical systems, far from the static picture which once characterized theoretical ecology.

2.2 Scaling in Macroevolution

The analysis of fossil data is a valuable source of information about the organization of ecosystems at a large time- and space-scale. Here, one is no longer concerned with the spatial distribution of a population or with its fluctuations, but just with the moment in time at which a species "appears" (meaning it has accumulated enough mutations to be substantially different from its parent species) and goes extinct. This process can be pictured as a tree where each branch represents a species, new branches appear at speciation points and end when the species dies out, and where distance between branches stands for the similarity between species.

This simple image allows us to estimate a number of quantities which are representative of the macroevolutionary process. Suppose that each of the branches stands for a genera (formed by a group of related species). Sepkoski (1993)[31] compiled data for more than 14 000 genera, which show that the distribution of lifetime of genera (i.e. of the lengths of these branches), follows a clear power-law with an exponent close to −2.[32] The self-similar properties of taxonomy have been also analyzed. Since species are grouped into genera, genera into families, families into orders, etc. the question arises: What is the probability $G(S)$ of having S subtaxa (e.g. species) within a given taxa (e.g. genera)? Bruno Burlando studied the geometry of taxonomic systems by means of various criteria (apart from standard taxonomy) to group subtaxa in higher-level taxa.[33] He systematically obtained a power-law dependence,

$$G(S) \propto S^{-\gamma} \tag{4}$$

with an exponent $\gamma \simeq 1 - 2$, typically. This value of γ seems to depend on the group considered and on the taxonomic level. Recent analysis gives a simple explanation for the lower values of γ by means of branching processes.[34] Although appealing, due to its simplicity, this mechanism would fail to explain any value of γ appreciably departing from unity (as is observed).

Traditionally, the size of an extinction event classified it as a *background extinction* (continuous and low-intensity extinction) or as a *mass extinction* (catastrophic and usually related to external disturbances), and different mechanisms were ascribed to them. The supposition of a linear dependence between cause (perturbations) and effect (extinctions) was behind the theory. A better measure of the distribution $p(E)$ of extinctions of size E returns a continuous and broad distribution,[35,36] and the possibility of a single (even internal) mechanism able to explain the whole range of responses has been put forward. We will discuss some concrete models in the forthcoming sections.

A threshold effect similar to that discussed in the previous section is also observed in the relation between originations of species and extinctions within a geological stage. The main difference (apart from the timescale) comes from the fact that in the ecological systems, new species were introduced through immigration, while in the present case, it is speciation inside the system which acts as a source of novelty (and possibly perturbation). We represent in Fig. 4, the percent of extinction in families (vertical axes) due to the origination of a number of families shown in the horizontal axes. These data correspond to marine organisms, and have been obtained from Benton (1995).[37] This relation is again indicative that some threshold phenomenon could be at play in macroevolution (although not all the sets in Ref. 37 offer such a clear relation).

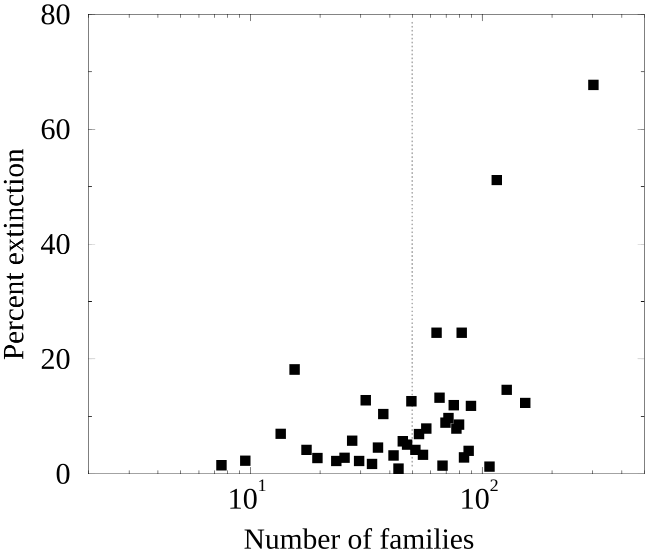

Fig. 4 Percent of extinction in marine families in the same geological stage where a number of families (shown in the x-axes) appeared through speciation. The response of the system seems to increase notably after a threshold of around 50 new originations is overcome.

A last set of scaling observations in the fossil record corresponds to the presence of slowly decaying correlations in the time series for extinctions and originations. Recently, this has been a matter of great interest and also of controversy. First studies[38] pointed to a correlation extending up to 200 million years. These results were criticized due to the methodology employed,[39] but more careful analysis still support the presence of very large correlation times.[40] Independent measures suggest that the correlation might extend *only* for around 40 million years.[41] More recently, it has been claimed that there are no significant correlations in time if trends (like an increase in diversity) are eliminated from the original data.[42] Although the diversity of organisms has been increasing since the origin of pluricellular life (a fact reflected in any related time series), it is not yet clear if this trend is a property of the system or is indeed the origin of all correlations,

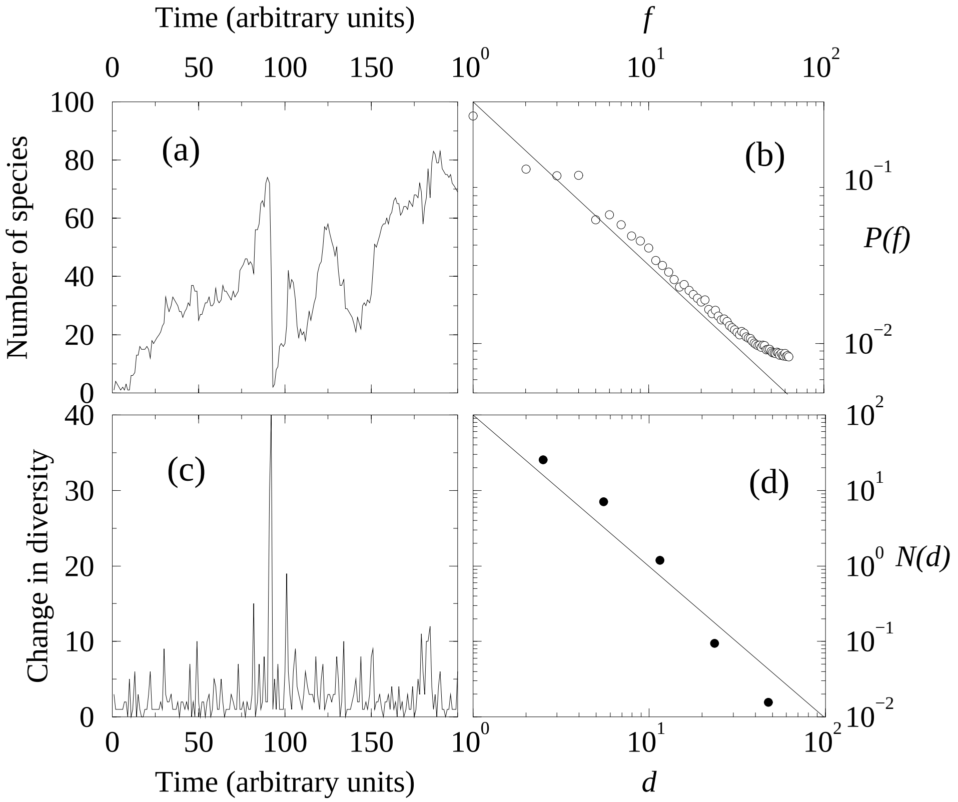

Fig. 5 Diversity of planktic foraminiferal species from Jurassic to present. (a) Number of species recorded; and (b) corresponding power spectrum, of the form $P(f) \simeq 1/f$. In (a), each point in the series corresponds to a stratigraphic unit (Ref. 45). (c) Changes in diversity, computed as the absolute difference between two consecutive points in (a); and (d) corresponding distribution.

being the remaining data uncorrelated.[a] Consider the record of the number of planktic foraminiferal species shown in Fig. 5 (data from Ref. 45). There is a large extinction event at the end of the Cretaceous which brings the system back to a very low degree of diversity. Starting there, diversity can only be recovered at a much slower pace than is eliminated. This time series shows $1/f$ noise and the distribution of its corresponding increments decays as a power-law with an exponent close to -2. Only new and more accurate data can help set the answer to the question on whether extinction and speciations are highly correlated or essentially independent in time.

The macroevolutionary scale again presents us with a highly dynamical, continuously changing system. We should remember that at least 99% of the species that ever existed are extinct. Evolutionary pathways can be understood, to a large extent, as "arms races" where only those who keep on adapting to an ever-changing environment can survive. It has been observed that the probability that a taxon goes extinct at a certain time does not depend on the time that this group has been thriving around. In other words, the accumulation of mutations (which at the short time scale allow adaptation and hence survival) does not produce any absolute improvement. This is the Red Queen effect, essential to understanding the dynamics of macroevolution, and which will be discussed in detail in Sec. 4.

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[a] A clear example of trend intrinsic to the system (at short time scales) is the kind of dynamics observed in stick-slip processes (see for example Ref. 43 and Fig. 2 in Ref. 44). Imagine a block of wood on a rough surface trying to move under the action of a spring which pulls it. The force felt by the block steadily increases until the block suddenly moves and a certain amount of stress is released. At short timescales, it might seem that the force would only increase, and that the "real" dynamics is hidden by this trend. But if a larger time series is available, one realizes that long periods of steady increase are compensated by sudden releases of the accumulated stress, and both phenomena are just two outputs of the same process.

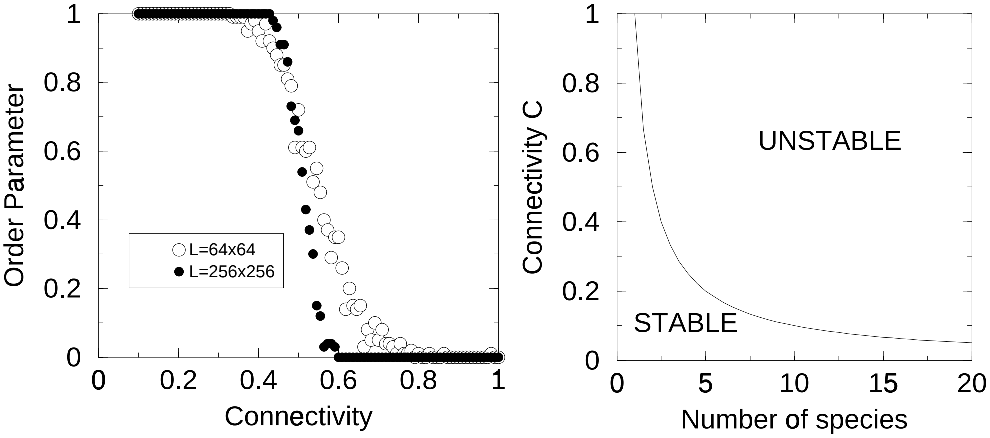

Fig. 6 Phase transition in the linear stability analysis of a randomly wired model ecosystem. The probability of having the system stable is plotted versus the connectivity of the $S \times S$ matrix. The variance α^2 is fixed so that transition takes place at the 0.5 connectivity value. The probability is computed after repeating the numerical stability analysis a hundred of times for each connectivity value. As S grows, the curves show a sharper transition.

3. CONNECTIVITY AND STABILITY IN ECOSYSTEMS

One of the first classical studies on the collective properties of food webs was carried out by Robert May in 1972.[5] May's observation comes from the classic results by Gardner and Ashby (1970)[46] concerning the stability properties of large, randomly wired differential systems of the kind

$$\frac{d\mathbf{x}}{dt} = \underline{\mathrm{A}}\mathbf{x}\,. \tag{5}$$

These authors showed that the larger the system, the less stable it was.[46] May further extended their ideas to the ecological context and found deep implications concerning the problem of stability-connectivity in complex communities.[5,47]

Let us consider [following Hasting (1982)] the discrete counterpart of an S-dimensional system, described by

$$\mathbf{x}_{t+1} = \underline{\mathrm{B}}\mathbf{x}_t \tag{6}$$

where $\underline{\mathrm{B}}$ is an $S \times S$ matrix whose entries are generated at random. Specifically, the matrix has a connectivity $C \in (0, 1)$, i.e. the total number of nonzero connections is CS^2 (the rest of the links is absent). The weight of the connections follows a distribution with zero mean and variance α^2. As usual, (3) can be understood as an equation for the evolution of small perturbations around a stability point. In this context, the entries of the $S \times S$ matrix, $\underline{B}_{ij}$, symbolize the effect of small departures from the stability value of population j on species i.

Let us denote the probability of stability of the previous system (in the linear stability analysis sense) as $P(S, \alpha, C)$. Then, the May-Wigner theorem establishes that,

$$\text{if } \alpha^2 SC < 1, \quad \text{then } P(S, \alpha, C) \to 1 \quad \text{as } S \to \infty$$

$$\text{if } \alpha^2 SC > 1, \quad \text{then } P(S, \alpha, C) \to 0 \quad \text{as } S \to \infty\,.$$

In terms of statistical physics, this system (in the thermodynamic limit $S \to \infty$) exhibits a phase transition at $\alpha^2 SC = 1$ (Fig. 6).

In order to gain some insight into the derivation of the previous result, consider the following approximation. Suppose that the disturbance from the stability population abundances of our species verifies the constraint

$$\mathbf{x}^2 \equiv x_1^2 + x_2^2 + \cdots + x_S^2 = 1\,. \tag{7}$$

Considering that the entries of the $S \times S$ matrix are independent, identically distributed stochastic variables, the average $\langle(\underline{\mathrm{B}}\mathbf{x})^2\rangle$ can be written in this case as

$$\begin{aligned}\langle(\underline{\mathrm{B}}\mathbf{x})^2\rangle &= \langle(\underline{\mathrm{B}}\mathbf{x}_1)^2 + (\underline{\mathrm{B}}\mathbf{x}_2)^2 + \cdots + (\underline{\mathrm{B}}\mathbf{x}_S)^2\rangle \\ &= \sum_{i=1}^{S}\langle(\underline{\mathrm{B}}\mathbf{x}_i)^2\rangle \end{aligned} \tag{8}$$

where $\mathbf{x}_i$ is a column vector whose components are $\delta_{ij}x_i$ with $j = 1, 2, \ldots, S$. Then each term can be obtained as

$$\langle(\underline{\mathrm{B}}\mathbf{x}_i)^2\rangle = \left\langle \sum_{j=1}^{S}(\mathrm{B}_{ji}x_i)^2 \right\rangle. \tag{9}$$

Now, remembering again that the elements of $\underline{\mathrm{B}}$ are independent, the crossed terms can be ignored and then

$$\langle (\underline{\mathrm{B}}\mathbf{x}_i)^2 \rangle = \left\langle \left(\sum_{j=1}^{S} \mathrm{B}_{ji} x_i \right)^2 \right\rangle . \tag{10}$$

For large S, the last expression stands for the variance of a sum of SC independent stochastic variables, each of them following a distribution with zero mean and equal variance $\alpha^2 x_i^2$. Then

$$\langle (\underline{\mathrm{B}}\mathbf{x}_i)^2 \rangle = SC\alpha^2 x_i^2 \,. \tag{11}$$

Using the constraint (7), the average $\langle (\underline{\mathrm{B}}\mathbf{x})^2 \rangle$ can be written as

$$\langle (\underline{\mathrm{B}}\mathbf{x})^2 \rangle = \alpha^2 SC \tag{12}$$

and we can see that if $\alpha^2 SC < 1$, then $\langle (\underline{\mathrm{B}}\mathbf{x})^2 \rangle < 1 (= \mathbf{x}^2)$, thus the system will be stable (for a detailed general analysis, see Ref. 48).

The May-Wigner result describes the general conditions for a randomly wired community to be stable. This requirement (random wiring) is a rather strong one, since communities are, in principle, the result of co-evolutionary interactions and selection pressures. But further elaborations of the previous set of conditions, involving much more reasonable biological constraints, lead to the same basic trade-off between connectivity and species number. If some kind of global constraint to ecosystem stability was operating, real (and so assumed stable) ecologies should be observed in the (S, C) plane *below* the critical line defined by the curve

$$S < \frac{1}{\alpha^2 C} \,. \tag{13}$$

But this is not what we find: most ecosystems are in fact placed *on* the critical line. This is an interesting observation and can be interpreted in a rather clear way. Ecosystems are driven to larger diversity by means of two basic mechanisms: immigration at the short, ecological time scale, and speciation at the larger, evolutionary time scale. This is typically a slow driving process which leads to an increase in diversity. Hence, diversity might be an unavoidable outcome of complex systems displaying intrinsic variability. At this point, higher-order mechanisms start to operate: ecologies are formed by interacting species and arbitrary interactions are not permitted. This is basically what the previous $S - C$ plot tells us: there are intrinsic regularities controlling the global properties of complex ecosystems.

Complex ecologies would result from the conflict between the driving mechanism, leading to increases in diversity and the instability arising from the global constraints. Once the stability threshold is reached, global constraints start to operate. Complex fluctuations arise and no stable structures can be sustained beyond the threshold. Is there evidence for such edge-of-instability behavior in real ecologies? The answer is yes. Remarkable studies on the nonlinear dynamics of both laboratory and field populations has shown that the available data are consistent with a system poised close to instability points.[49] Ellner and Turchin (1995)[49] have estimated the largest Lyapunov exponent (LLE) from ecological time series by means of the so-called response surface method (a powerful technique to analyze short time series from real data). Criticality (i.e. the transition regime separating ordered from chaotic behavior or ordered from disordered dynamics) is typically characterized by an LLE close to zero, indicating that the system is neither stable nor unstable. The Turchin-Ellner analysis revealed that in fact the measured LLEs are clustered around zero, strongly supporting the presence of a marginal stable state.

4. THE RED QUEEN

Beyond the ecological time scale, there is a larger temporal scale where evolutionary changes in species (and thus in the parameters) occur. At this scale, species seem to evolve and go extinct at a constant pace, independent on their lifetime. In other words, apparently it does not matter how long a species has been thriving around and "adapting." It keeps on evolving and its chances to go extinct are the same as for a recently generated species. This observation motivated the metaphore of the Red Queen[50] as an *ad hoc* explanation for this counterintuitive result.

A model was developed by Maynard Smith and co-workers (see Stenseth and Smith (1984)[51] and references therein) in order to test the plausibility of the previous picture, namely, the continuous coevolution of species even in a constant environment. Their model considers a fixed number S of interacting species. It is assumed that some fitness measure ϕ can be defined, and a maximum fitness ϕ_i^* is

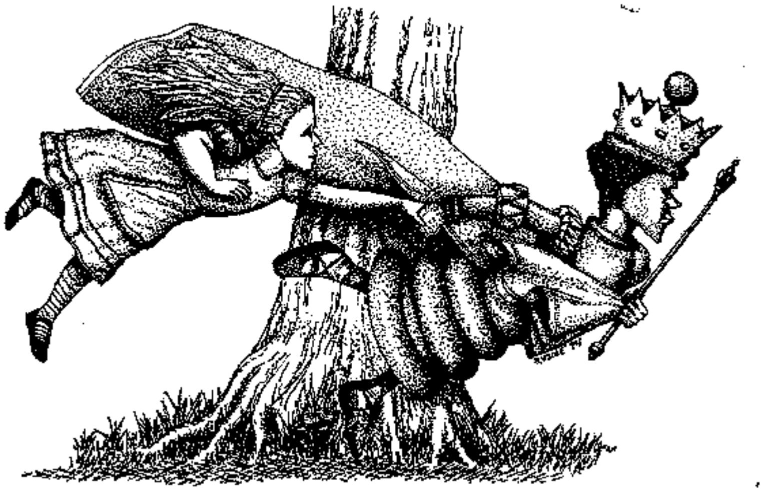

Fig. 7 Alice and the Red Queen. In Lewis Carroll's *Through the Looking Glass*, the Red Queen told Alice "Now, you see, it takes all the running you can do, to keep in the same place."

supposed to exist for every species in a given fixed, external biotic environment. At a given time, the fitness ϕ_i and the maximum ϕ_i^* take different values, and each species tries to reduce the so called *lag load*, defined as

$$L_i = \frac{\phi_i - \phi_i^*}{\phi_i}; \qquad i = 1, \dots, S\,. \tag{14}$$

If β_{ij} is the change in the lag load L_i due to a change in L_j, then a mean-field equation for the average lag load $\langle L \rangle = \sum_i (L_i)/S$ can be derived. This is done by first separating, for each species, changes due to "microevolution of co-existing species" from those linked with its own microevolution.[51] The whole equation for the lag load variation in a given species is

$$\delta L_i = \delta_c L_i - \delta_g L_i \tag{15}$$

which simply says that the lag load typically increases due to changes in the other species and decreases due to microevolutionary changes in the species under consideration. This can be written in the following way,

$$\delta L_i = \sum_{j=1}^{S} \beta_{ij} \delta_g L_j - \delta_g L_i \tag{16}$$

where β_{ij} (with $\beta_{ii} = 0$) is the increase in L_i due to a (unit) change in L_j. If we assume that most species are close to their adaptive peaks, any evolutionary change in one species will have a deleterious effect on the rest of species. The time continuous equivalent formulation of this model is

$$\frac{dL_i}{dt} = \sum_{j=1}^{S} \beta_{ij} k_j L_j - k_i L_i\,. \tag{17}$$

By taking the average in both sides of the previous equation, we obtain the following expression for the evolution of the average lag load:

$$\frac{d\langle L \rangle}{dt} = \frac{1}{S} \sum_{i=1}^{S} \left\{ \sum_{j=1}^{S} \beta_{ij} k_j L_j - k_i L_i \right\}. \tag{18}$$

Assuming now that $k_i = k$ for all $i = 1, \dots, S$, the average lag load equation can be written as

$$\frac{d\langle L \rangle}{dt} = \frac{k}{S} \sum_{j=1}^{S} (\Psi_j - 1) L_j \tag{19}$$

and it has a steady-state solution if $\Psi_j = 1$ for all $j = 1, \dots, S$. In other words, if

$$\Gamma \equiv \sum_{i=1}^{S} \beta_{ij} = 1; \qquad \forall\, j\,. \tag{20}$$

Otherwise, it can be shown that $\langle L \rangle$ will decrease (increase) for $\Gamma < 1 (\Gamma > 1)$. The previous identity is telling us that the equilibrium state of this system is reached through a balance between the reduction of the individual lag load of each species and the increases due to co-evolutionary changes in the remaining partners. And the main result of this model is that the Red Queen picture, in which evolution of species proceeds at an approximately

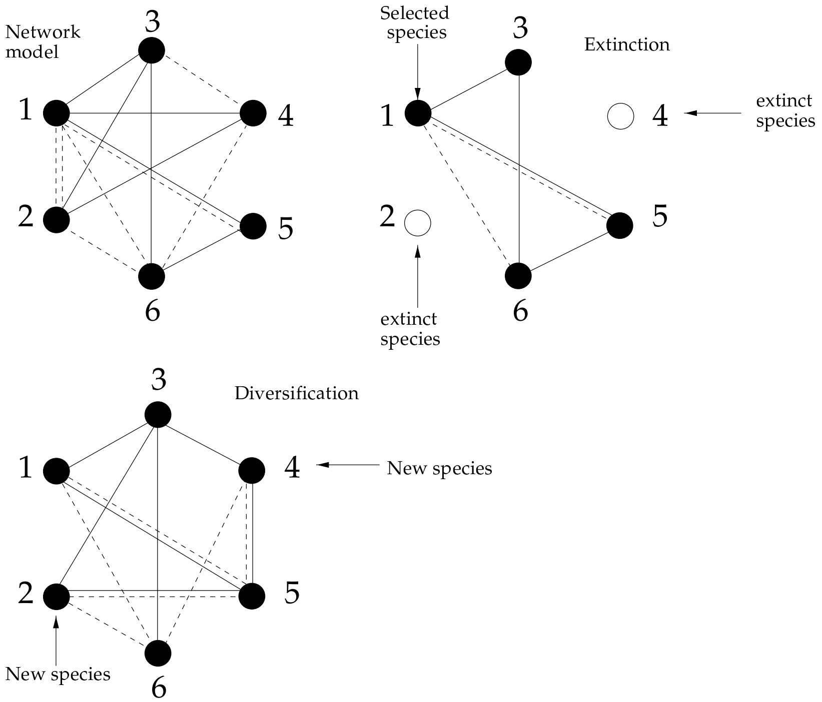

Fig. 8 Basic set of rules of the evolution model shown for a $N = 6$ species ecosystem. The first rule involves randomization of connections (see text) followed by the extinction of some of the species (empty circles). The final step considers diversification: We choose one of the survivors at random and copy it and its connections into the empty sites.

steady rate, is indeed feasible even in the absence of changes in the physical environment.

There is a deep connection between this result and the presence of a critical boundary outlined in the previous section. As species co-evolve, their interactions with other species change. Additionally, immigration from outside the ecosystem will occur, thus introducing further changes in diversity and connectivity. These connections can simply change in time or some new ones can appear or disappear, as new ways of exploiting other species emerge or as new specializations arise. A given tree species in the rainforest can become resistant to some plague or more able to disperse its seeds. A consequence of this evolutionary adaptation will be an increase of population size. But in a rich ecosystem, larger populations sooner or later translate into more opportunities for parasites to take some profit. Larger populations thus are only transient phenomena as far as emerging parasites or competitors will find their way to exploit the successful species. Increasing number of connections will be unavoidable because diversity is usually linked with the emergence of a web of interactions. But after the threshold is reached, both increasing numbers of links or changes in their strengths will lead to instability. The system is always forced to change and species turnover will be the rule.[52]

5. EVOLUTION MODEL

If we look at the large-scale pattern of species generation and extinction, as revealed by the fossil record of life, the shape of the pattern is fuzzier and often only reveals a small information about the underlying community structure and its interactions.[53] The impression from our discussion about available data is that large-scale evolution is still an open problem. How much can we infer from the analysis of the fossil record? The analysis of field data has been complemented in recent years with several theoretical approaches[54–58] [for a recent review of current models, see Newman and Plamer (1999)[59]]. Models based on either external perturbations or internal dynamics are not new. Raup (1996) and Sepkoski (1984) have pioneered the formulation of both externally-driven extinction dynamics as well as competition-dependent dynamics.[60,61]

Beyond the limitations implicit in the incompleteness of the fossil record, the available data provide clear indications of the relevance of the ecological scale.[62] It seems clear that external perturbations have been important, but their effects do not appear to scale proportionally to the size of the perturbation. Some mass extinctions have more profound effects than others,[63] and cascade effects have been reported from several well-known extinction episodes. This is the case of the collapse of marine food chains with the end-Cretaceous phytoplankton crisis[64] or more recently, with the extinction of megaherbivores at the end-Pleistocene.[65] This last case is particularly well-documented and shows the decline and successive extinction of many vertebrates after the extinction of large-sized mammals, which brought extensive vegetational changes. Such changes eventually triggered the concomitant disappearance of many other species. A well-defined chain of ecological effects is seldom accessible from the remote past, but as far as we know, ancient ecosystems were as diverse and complex as current ones, and the laws of ecological interactions should be the same.[66]

The Lotka-Volterra equations (1) are too difficult to manage if Γ is formed by time-dependent terms. We would like to retain the basic qualitative approach, but shift our interest from the ecological timescale to the speciation-extinction timescale. In this last picture, where the structure of the network of interactions is believed to play a main role, species are represented through a binary variable: $S_i = 0$ (extinct) or $S_i = 1$ (alive). The state of such species evolves in time (now assumed discrete) according to

$$S_i(t+1) = \Phi\left(\sum_{j=1}^{n} \gamma_{ij}(t) S_j(t)\right) \tag{21}$$

with $i = 1, \ldots, N$. Here $\Phi(z) = 1$ if $z > 0$ and zero otherwise. Equation (21) can be understood as the discrete counterpart of (1), but involving a much larger time scale. In this model,[67,68] the ith species is in fact represented by the set of connections $\{\gamma_{ij}, \gamma_{ji}\}$, $\forall\ j$. The elements γ_{ij} are the *inputs* and define the state of the species. The elements γ_{ji} are the *outputs* and represent the influence of this species over the remaining ones in the system.

The dynamics is defined in three steps:

(1) *Changes in connectivity.* At each time step, each species i experiences a change in one of its inputs j, which is chosen at random. The connection $\gamma_{ij}(t)$ is assigned a new value $\gamma_{ij}(t+1)$ randomly drawn from a uniform distribution in the interval $[-1, 1]$. This slow change in the global system can be ascribed either to external causes or might be the result of modifications due to co-evolution. With this rule, small random changes are introduced into the network. It should be noted that this rule involves both external and internal perturbations. A given keystone species that sends several positive inputs to others can at some point disappear as a consequence of a strong change in one of its input connections. Although single changes in connections are apparently small, they can actually induce strong changes.

(2) *Extinction.* The local fields $\mathcal{F}_i = \sum_j \gamma_{ij}(t) S_j(t)$ are computed, and all species are synchronously updated. If the kth species goes extinct, then $S_k = 0$ and all the connections that define it are set to zero: $\gamma_{kj} = \gamma_{jk} \equiv 0$, $\forall j$. This updating introduces extinction as well as selection of species. In fact, those sets of connections which make a species stable will remain. But in removing a given species, some positive connections (mainly being *outputs* of k) with a stabilizing effect on other species can also disappear, and this renders the system more unstable.

(3) *Replacement.* Some species are now extinct and empty sites are available for colonization. Diversification is introduced as follows. A living species is picked up at random and "copied" in the vacant spaces. The new species are identical to the one randomly choosen: note that after their origination, our rule (1) causes their differentiation. Let S_c be the parent species. For each extinct species S_j (vacant spaces), the new connections γ_{ij} and γ_{ji} are given by $\gamma_{kj} = \gamma_{cj}$ and $\gamma_{jk} = \gamma_{jc}$. In this way, the new species are the result of the speciation of one of the survivors.

6. CRITICALITY AND UNPREDICTABILITY

In this section, we analyze the way in which the critical state is reached and the interpretation of the resulting dynamical pattern. The random changes in the network of connections, together with the non-trivial correlations introduced through the replacement step, make the trophic links between species more and more complex. We can quantify their complexity by means of an adequate statistical measure, as follows. Let us first consider the time

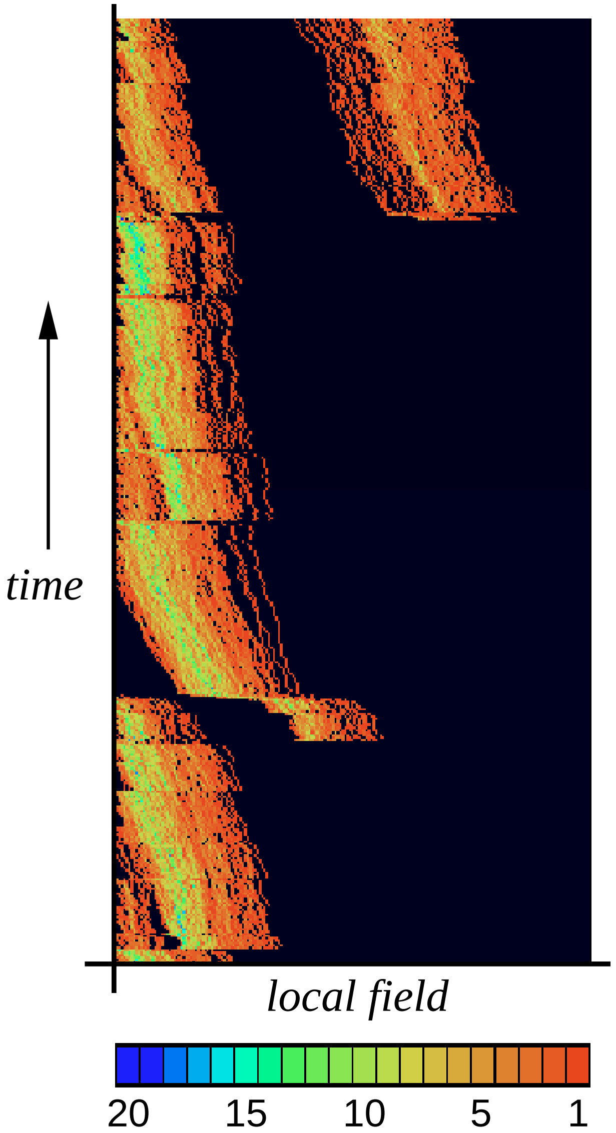

Fig. 9 Evolution towards the instability (left margin). We represent the evolution of the local fields for a system with 200 species after the transient, and for 400 time steps. Time runs from bottom to top, and the horizontal axes varies between 0 (extinction threshold, left side) and 200 (right side). The color code stands for the number of species with a given value of the local field (black corresponds to non-represented values of the local field). This simulation corresponds to the model of Sec. 5 [as described in Manrubia and Paczuski (1998).[14]].

evolution of the connections. We call $P(\gamma^+)$ and $P(\gamma^-) = 1 - P(\gamma^+)$ the probability of positive and negative connections, respectively. The time evolution of $P(\gamma^+, t)$ is defined by the master equation

$$\frac{\partial P(\gamma^+, t)}{\partial t} = P(\gamma^-, t)P(\gamma^- \to \gamma^+) - P(\gamma^+, t)P(\gamma^+ \to \gamma^-)\,. \qquad (22)$$

From the definition of the model, we have a transition rate per unit time given by $P(\gamma^+ \to \gamma^-) = P(\gamma^+ \to \gamma^-) = 1/(2N)$ which leads to an exponential relaxation $P(\gamma^+, t) = (1 + (2P_0 - 1)\exp(-t/N))/2$, where $P_0 = P(\gamma^+, 0)$. This result is immediately reflected into an exponential decay in the local inputs, $\mathcal{F}_i(t) \propto \exp(-t/N)$. As a result, the system evolves towards a critical state where the global input coming from the co-evolving partners has a value close to zero, and thus small changes involving single connections can trigger extinction events.

We can use the entropy of connections per species, i.e. the Boltzmann entropy

$$\begin{aligned} H(P(\gamma^+, t)) &\\ = -P(\gamma^+, t)\log(P(\gamma^+, t)) &\\ - (1 - P(\gamma^+, t))\log(1 - P(\gamma^+, t)) & \quad (23) \end{aligned}$$

as a quantitative characterization of our dynamics. The Boltzmann entropy gives us a measure of disorder but also a measure of uncertainty.[69] It is bounded by the limits $0 \leq H(P(J^+, t)) \leq \log(2)$, which correspond to a completely uniform distribution of connections (i.e. $P(\gamma^+, t) = 1$ and $P(\gamma^-, t) = 0$, having zero entropy) and to a random distribution with $P(\gamma^\pm, t) = 1/2$ (maximum entropy), respectively. Our rules make possible the evolution to the maximum network complexity, here characterized by the upper limit of the entropy.

The entropy $H(P(\gamma^+, t))$ grows, after a large extinction event, towards its maximum value $H^* = \log(2)$, with sudden drops near large extinctions. This means that our system slowly evolves towards an "attractor" characterized by a randomly connected network. At such state, small changes of strength $1/N$ can modify the sign of $\mathcal{F}_i$ and extinction may take place. At this point, one clearly sees what is the role that external perturbations play. For them to trigger a large extinction, it is necessary that they act on a system located close to the critical state (here, the network close to the maximum entropy). A large extinction will never be found in a system with a low entropy of connections even if the external perturbation is reasonably large. This is a key property of self-organized critical (SOC) systems.[70] More specifically, an SOC system has an *order parameter* that defines the transition displayed by the system (in our case the change from no-extinctions to extinctions) as a continuous phase transition. This order parameter has been shown to be the extinction rate, while the control parameter is the average value of the connections $\langle \gamma_{ij} \rangle$.[68] For $\langle \gamma_{ij} \rangle > 0$, no extinction will be found for a large enough system, while for $\langle \gamma_{ij} \rangle < 0$, extinctions of all sizes (up to system size) can be found.

Several of the features observed in the fossil record are reproduced with a good accuracy by our model. First, a wide distribution of extinction events is obtained.[b] It has a power-law profile of the form $p(E) \approx E^{-\tau}$ with $\tau = 2.05 \pm 0.06$, which is consistent with the information available from the fossil record.[32,35,71]

Second, due to the replacement of extinct species with surviving ones, the species tend to form groups with similar local field $\mathcal{F}_i$. If we consider a snapshot of the system at time t, we observe several such groups containing different numbers of species, and separated by empty intervals without species (in the $\mathcal{F}_i$-space). Subsequent evolution shows that these groups are long-lived entities which keep a fairly constant number of species (up to extinctions and new originations from time to time) for a long time. These groups can be identified with a higher level in the taxonomical hierarchy, namely genera. The computation of the number of genera $G(S)$ formed by S species returns the dependence $G(S) \propto S^{-2}$,[44,73] which is in good agreement with part of the measurements on real taxonomy.[33] As a consequence, the taxonomical "classification" might be a result of the self-organization inside the system, of the correlations arising from the very dynamical rules, and even an unavoidable output of the evolutionary process.

Also the Red Queen effect discussed in Sec. 4 has its counterpart analyzed in this model. Consider a system formed by a large number of species which, due to the replacement rule, would be spontaneously grouped into a variable (still large) number G_t of genera, as discussed previously. We can define a "pseudocohort" in our system as the number of genera G_0 present in the simulation at time t_0, and follow its evolution. It is easy to compute, at each time step $t > t_0$, how many of the initial genera still have at least one species present in the system. In Fig. 10, we plot different curves corresponding to time steps $t_1 < t_2 < \cdots < t_{10}$ in a system with $S = 2500$ species. The number of genera initially present in each of the ten curves varies between 16 and 163. The almost linear decay in the log-linear plot, punctuated by large extinction events, very much resembles the pattern observed in the fossil record.[71]

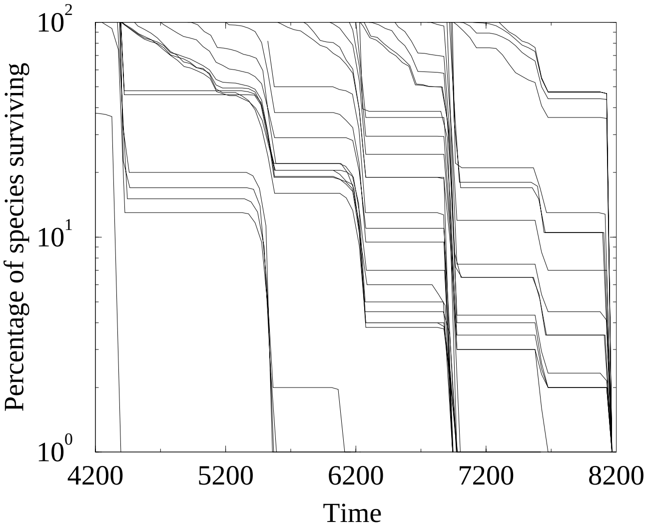

Fig. 10 Survivorship of genera in the evolutionary model described in Sec. 5. Each line starts with all the genera present in the system at that point in time, and shows the remaining survivors as evolution proceeds. Mass extinctions appear as drops in survivorship and are very reminiscent of the pattern observed in the fossil record. Each point corresponds to an average of over 100 time steps.

7. SUMMARY

We have analyzed the presence of instability points in three different types of models. Our main point was the observation that complex ecologies involve complex patterns of interaction that might be interpreted in terms of critical states. Several sets of evidence from field studies give support to the view of real ecologies as complex systems poised close to marginal stability boundaries.

A very important consequence of this marginal state is that close to instability points (where typically scaling of relevant quantities appears), fluctuations play a leading role. The relaxation time towards equilibrium (even in the presence of a very small driving) becomes very large and in this context the final outcome of ecological interactions can be extremely delayed. What is the consequence of this long-transient behavior? The main consequence is that marginal stability might be the

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[b] Also the model by Newman and Roberts, which considers external causes to be the main motor generating extinction events, returns an exponent compatible with field data,[58,72] while other models give values clearly different: $\tau \approx 1.1$ for the quenched Bak-Sneppen model,[55] and $\tau = 1$ for Kauffman-Johnsen's one.[54]

final cause of large diversity in natural ecologies. The reason is that, together with the driving, the extremely long transient times (which would eventually eliminate some species from the system) are in fact only counter-balanced by immigration/speciation events. This would explain the fact that a very large number of rare species is always present. These rare species are not eliminated because large fluctuations close to the marginal state imply the propagation of effects through the whole network in a highly unpredictable way.

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