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Statistics of certain models of evolution

Russell K. Standish*
High Performance Computing Support Unit, University of New South Wales, Sydney 2052, Australia

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In a recent paper, Newman [J. Theo. Bio. **189**, 235 (1997)] surveys the literature on power law spectra in evolution, self-organized criticality and presents a model of his own to arrive at a conclusion that self-organized criticality is not necessary for evolution. Not only did he miss a key model (Ecolab) that has a clear self-organized critical mechanism, but also Newman's model exhibits the same mechanism that gives rise to power law behavior, as does Ecolab. Newman's model is, in fact, a ‘‘mean field'' approximation of a self-organized critical system. In this paper, I have also implemented Newman's model using the Ecolab software, *removing* the restriction that the number of species must remain constant. It turns out that the requirement of constant species number is nontrivial, leading to a global coupling between species that is similar in effect to the species interactions seen in Ecolab. In fact, the model must self-organize to a state where the long time average of speciations balances that of the extinctions; otherwise, the system either collapses or explodes. In view of this, Newman's model does not provide the hoped-for counterexample to the presence of self-organized criticality in evolution, but does provide a simple, almost analytic model that can be used to understand more intricate models such as Ecolab. [S1063-651X(99)09702-0]

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I. INTRODUCTION

Over the last five years, the notion that biological evolution is a *self-organized critical phenomenon* has gained currency and, in particular, has been championed by Bak [1] and Kauffman [2]. Self-organized critical phenomena are characterized by a frustration between two processes. The archetypical example is that of a sandpile, where the process of adding sand to a sandpile to make the slope of that pile steeper is opposed by the instability of the sandpile, which works to make the sandpile flatter once the slope passes a critical angle. One of the most obvious manifestations of criticality is a power law spectral behavior, although criticality is by no means necessary for this power law behavior to be manifested.

In a recent paper, Newman [3] surveyed the field to conclude that the mechanism by which ecosystems are driven to criticality is not well understood, but that the evidence in the fossil record for power law spectra of extinction event size and species lifetimes is good. Solé *et al.* [4] present the best evidence yet that these distributions are power laws. However, Newman missed an important model of evolution, *Ecolab* [5,6], that is more general than those surveyed, and gives us the best idea yet of how evolution could be a self-organized critical phenomenon.

Newman goes further to introduce his own model of evolution to make the point that the coevolutionary avalanches that all the other models (including Ecolab) exhibit are not necessary for the observed power law behavior. He further claims that his model is not critically self-organized. However, the mechanism that leads to power law behavior in Newman's model is precisely the same as that in Ecolab, and that mechanism is of the nature of a frustration between two processes that characterizes Bak's sandpile model.

II. ECOLAB

In this section, we consider a model of evolution called *Ecolab*. Ecolab (perhaps unfortunately) is both the name of a model and a simulation system written by the author to implement that model. The ecology is described by a generalized Lotka-Volterra equation, which is perhaps the simplest ecological model to use:

$$\dot{n}_i = r_i n_i + \sum_{j=1}^{n_{\rm sp}} \beta_{ij} n_i n_j . \tag{1}$$

Here **r** is the difference between the birth rate and death rate for each species, in the absence of competition or symbiosis. $\boldsymbol{\beta}$ is the interaction term between species, with the diagonal terms referring to the species' self-limitation, which is related in a simple way to the carrying capacity K_i for that species in the environment by $K_i = -r_i\beta_{ii}$. In the literature (e.g., Strobeck [7], Case [8]) the interaction terms are expressed in a normalized form, $\alpha_{ij} = -K_i/r_i\beta_{ij}$, and $\alpha_{ii}=1$ by definition. **n** is the species density.

These equations are simulated on a simulator called *Ecolab* [9]. The vectors **n** and **r** are stored as dynamic arrays, the size of which (i.e., the system dimension) can change in time.

A. Linear stability analysis

Linear analysis starts with the fixed point of Eq. (1):

$$\hat{\mathbf{n}} = -\boldsymbol{\beta}^{-1}\mathbf{r}, \tag{2}$$

where $\dot{\mathbf{n}}=0$. There is precisely one fixed point in the interior of the space of population densities (i.e., **n** such that $n_i > 0$) provided that all components of $\hat{\mathbf{n}}$ are positive, giving rise to the following inequalities:

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*Electronic address: R.Standish@unsw.edu.au

$$\hat{n}_i = (\boldsymbol{\beta}^{-1}\mathbf{r})_i > 0, \quad \forall\ i. \tag{3}$$

This interior space is denoted $\mathbb{R}_+^{n_{\mathrm{sp}}}$ mathematically.

There may also be fixed points on the boundary of $\mathbb{R}_+^{n_{\mathrm{sp}}}$, where one or more components of **n** are zero (corresponding to an extinct species). This is because the subecology with the living species only (i.e., with the extinct species removed) is equivalent to the full system.

The *stability* of this point is related to the negative definiteness of derivative of $\dot{\mathbf{n}}$ at $\hat{\mathbf{n}}$. The components of the derivative are given by

$$\frac{\partial \dot{n}_i}{\partial n_j} = \delta_{ij}\left(r_i + \sum_k \beta_{ik} n_k\right) + \beta_{ij} n_i . \tag{4}$$

Substituting Eq. (2) gives

$$\left.\frac{\partial \dot{n}_i}{\partial n_j}\right|_{\hat{\mathbf{n}}} = -\beta_{ij}(\boldsymbol{\beta}^{-1}\mathbf{r})_i . \tag{5}$$

Stability of the fixed point requires that this matrix be negative definite. Since the $(\boldsymbol{\beta}^{-1}\mathbf{r})_i$ are all negative by virtue of Eq. (3), this is equivalent to $\boldsymbol{\beta}$ being negative definite or, equivalently, that its n_{sp} eigenvalues all have negative real parts. Taken together with the inequalities (3), this implies that $2n_{\mathrm{sp}}$ inequalities must be satisfied for the fixed point to be stable. This point was made by Strobeck [7], in a slightly different form. (Note that Strobeck implicitly assumes that $\Sigma_i r_i \hat{n}_i / K_i > 0$, so comes to the conclusion that $2n_{\mathrm{sp}} - 1$ conditions are required.) If one were to randomly pick coefficients for a Lotka-Volterra system, then it has a probability of $4^{-n_{\mathrm{sp}}}$ of being stable, i.e., one expects ecosystems to become more unstable as the number of species increases [10].

B. Permanence

While stability is a nice mathematical property, it has rather less relevance when it comes to real ecologies. For example the traditional predator-prey system studied by Lotka and Volterra has a limit cycle. The fixed point is decidedly unstable, yet the ecology is *permanent* in the sense that both species' densities are larger than some threshold value for all time. Hofbauer, Hutson, and Jansen [11] and Law and Blackford [12] discuss the concept of *permanence* in Lotka-Volterra systems, which is the property that there is a compact absorbing set $\mathcal{M} \subset \mathbb{R}_+^{n_{\mathrm{sp}}}$, i.e., once a trajectory of the system has entered $\mathcal{M}$, it remains in $\mathcal{M}$. They derive a sufficient condition for permanence due to Jansen [13] of the form

$$\sum_i p_i f_i(\hat{\mathbf{n}}_B) = \sum_i p_i\left(r_i - \sum_j \beta_{ij} \hat{n}_{Bj}\right) > 0, \quad \exists\ p_i > 0 \tag{6}$$

for every $\hat{\mathbf{n}}_B$ equilibrium point lying on the boundary ($\hat{n}_{Bi} = 0\ \ \exists\ \ i$), provided the system is *bounded* (or equivalently *dissipative*). (Boundedness is ensured in this model by choosing the β_{ij} such that $\beta_{ij} + \beta_{ji} \leqslant 0,\ \forall\ \ i,j$. This precludes symbiosis, but does allow for unstable behavior. See [9] for a discussion of boundedness.) This condition is more general than stability of the equilibrium—the latter condition implies that a local neighborhood of the equilibrium is an absorbing set. Also, the averaging property of Lotka-Volterra systems implies that the equilibrium must lie in the positive cone $\mathbb{R}_+^{n_{\mathrm{sp}}}$. So Eq. (3) must still hold for permanence.

Consider the boundary points $\hat{\mathbf{n}}_B$ that are missing a single species *i*. Then Jansen's condition for these boundary points is

$$r_i - \sum_j \beta_{ij} \hat{n}_{Bj} > 0. \tag{7}$$

This set of conditions is linearly independent. Let the number of such boundary points be denoted by $n_B \leqslant n_{\mathrm{sp}}$. Then the set of conditions (6) will have rank $n_B \leqslant \nu \leqslant n_{\mathrm{sp}}$ (the number of linearly independent conditions), so that the system has at most a probability $2^{-n_{\mathrm{sp}}-\nu}$ of satisfying Jansen's permanence condition if the coefficients are chosen uniformly at random. Since stability is also sufficient for permanence, the probability lies between $4^{-n_{\mathrm{sp}}}$ and $2^{-n_{\mathrm{sp}}-\nu}$.

Another rather important property is *resistance to invasion* [8]. Consider a boundary equilibrium $\hat{\mathbf{n}}_B$. If it is proof against invasion from the missing species, then the full system cannot be permanent. For the boundary points that miss a single species, this implies that condition (7) is necessarily satisfied for permanence, along with Eq. (3). The probability of permanence is then bounded above by $2^{-n_{\mathrm{sp}}-n_B}$.

The important point to take away from this section is that while a randomly selected ecology is more likely to be permanent than to have a stable equilibrium, the likelihood decreases exponentially with increase in species number.

C. Mutation

Adding mutation involves adding an additional operator to Eq. (1):

$$\dot{\mathbf{n}} = \mathbf{r} * \mathbf{n} + \mathbf{n} * \boldsymbol{\beta}\mathbf{n} + \texttt{mutate}(\boldsymbol{\mu}, \mathbf{r}, \mathbf{n}), \tag{8}$$

where * refers to elementwise multiplication. This operator extends the dimension of the whole system, so is rather unusual. The precise form of `mutate` is not germane to the present argument; the interested reader is referred to the previous publications describing it [5,6,9]. Suffice it to say that it adds new species according to a stochastic mechanism, and that we would expect the criticality result to be robust with respect to changes of mutation algorithm employed.

D. Self-organized criticality

Let us consider what happens to the largest eigenvalue of $\boldsymbol{\beta}$. Suppose that initially the system has a stable equilibrium, in which case all the eigenvalues have negative real part. As mutations are added to the system, the largest eigenvalue will increase towards zero. As it passes zero, the system destabilizes, and the system will start to exhibit limit cycles or chaotic behavior. As further mutations are added to the system, permanence is no longer satisfied and an extinction event will occur. This will restore permanency to the system, and possibly even stability. So we have two frustrated processes opposed to each other, the first, mutation, which

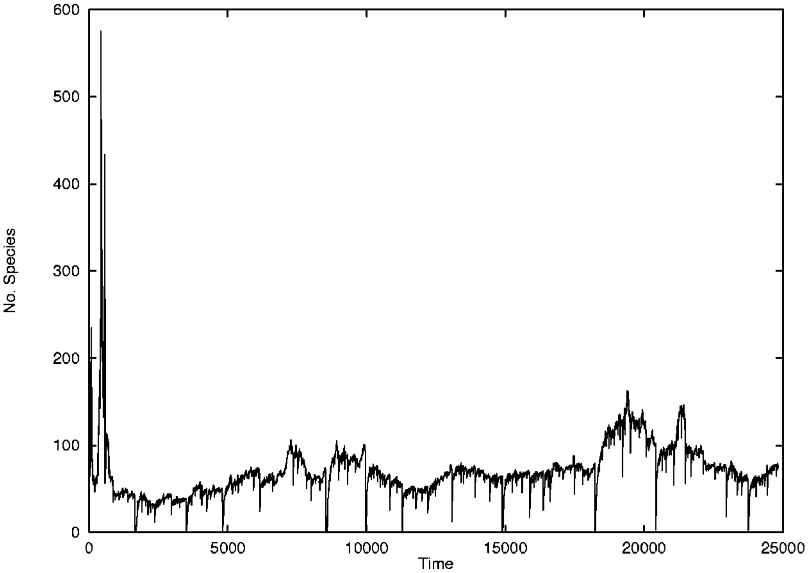

FIG. 1. n_{sp} as a function of time in the generalized Newman model. Time units are in time steps.

builds up ecosystem complexity, and the second being the trend toward impermanency as the ecosystem becomes more complex. This is analogous to the sand being added to the top of the pile, and the stability of the sandpile slope in Bak's sandpile model.

III. THE NEWMAN MODEL

Newman has presented his model of evolution in a number of papers [14,15,3]; this model is largely equivalent to an earthquake model presented in [16,17]. In the biological context, the model has a fixed number of species, all of which feel environmental stress, denoted by $\eta(t)$, which is random variate with distribution $p_{\mathrm{stress}}(\eta)$. Each species has an individual threshold x_i such that if $\eta > x_i$, species i becomes extinct. These extinct species are then replaced by new species, with thresholds randomly assigned from some distribution $p_{\mathrm{thresh}}(x)$. There is one further twist to the model, in that the threshold values are allowed to drift over time in order to prevent the model from stagnating with every species having the maximum threshold.

The Ecolab software allows us to build a variant of this model that allows the number of species to vary over time. When the model was first implemented, the system underwent a ''mutation catastrophe,'' in which the number of species exploded. This is similar to what happens in the Ecolab model when the mutation rate is set too high. Normally, one would expect that the number of speciation events should be proportional to the number of species. However, this leads to an excess of speciation over extinctions.

The resolution of this conundrum is to require that the stress values η be proportional to the number of species, i.e., $\eta = n_{\mathrm{sp}}\eta'$, where η' is drawn from some distribution $p_{\mathrm{stress}}(\eta')$. The justification for making this assumption can be seen by considering a simplified model of Ecolab (called Ecolab−−), described in the next section. Of course, in Newman's original model, n_{sp} is a constant, and so his model is consistent with this modification.

Wilke and Martinetz [18] examined a similar model, in which they label the mutation rate g, and consider finite f rather than $f = 0$ as I do here. They too note the conundrum of exponential growth in species number, and resolve it by introducing an arbitrary logistic constraint. My argument is that the reason for this logistic constraint is that species must interact with each other, and the greater the number and strengths of these interactions, the greater the stresses are that are felt by the ecosystem.

It could be argued that the *raison d'être* of the Newman model is to study the effect of coherent extinction through exogenous causes. However, these will always give rise to stress distributions that are independent of species number. However, the stress distribution will ultimately be dominated by the term that does depend on the species number.

Once the stress values depend on species number, the system self-organizes so that speciations and extinctions balance on average. A trace of n_{sp} can be seen in Fig. 1, and the distribution of lifetimes is seen in Fig. 2. The peak in the curve at $\tau = 10$ is an artifact of the simulation, and should be ignored. The distribution actually has two regions, the inner one $10 \ll \tau \ll 10^3$ having a power law with exponent ≈ -1, and the outer region $\tau \gg 10^3$ having exponent ≈ -2. By running the experiment at different mutation rates, the lifetime λ at which the distribution changed from τ^{-1} to τ^{-2} was found to be inversely proportional to the mutation rate.

In comparing the result of my variation with the original Newman model, it should be noted that the power law exponent in Newman's original model is -1 out to a time $1/f$, and decays exponentially after that. In my version, the same power law exponent was observed out to $1/g$, and then appears to change to a faster power law decay, although the error bars are sufficiently large not to rule out an exponential decay. In each of these models, the lifetime $1/f$ or $1/g$, respectively, is roughly the lifetime that a maximally fit organism (one with a maximal value x_i) can survive before succumbing to mutation pressures.

IV. THE ECOLAB−− MODEL

In this section, we will consider a simplification of the Ecolab model where the interaction terms $\Sigma_j \beta_{ij} n_j$ are replaced by a random variate $\eta_i(t)$ from a suitable distribution:

$$\dot{n}_i = (r_i - \eta_i) n_i . \tag{9}$$

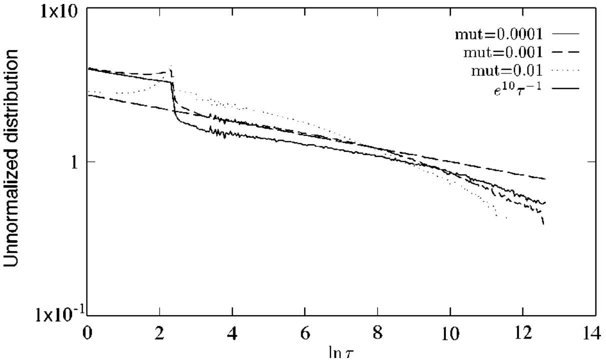

FIG. 2. Distribution of species lifetimes in the generalized Newman model with Gaussian stress distribution.

Since η_i is effectively the sum of a large number of independent quantities, its distribution will tend to be normal, and the deviation (controlling how large η_i gets) will be proportional to $n_{\rm sp}$, the connectance (proportion of nonzero elements in $\boldsymbol{\beta}$) and the interaction strength. This is why stresses in the Newman model must be proportional to $n_{\rm sp}$. When η_i exceeds r_i for any significant period of time, species i becomes extinct. Since $\eta_i(t)$ is a continuous function of $\mathbf{n}(t)$ which is itself a continuous function of t, there will be a correlation $\eta(t)\eta(t+\tau)>0,\ \forall\tau<\tau_0,\ \exists\tau_0>0$. Equation (9) connects the full Ecolab model with the Newman model.

In order to make the analysis simpler, we assume that n_i are real values, rather than integers as in Ecolab. In order to detect when extinction happens, we take an arbitrary threshold σ such that if $n_i<\sigma$, species i is extinct.

V. DISTRIBUTION OF SPECIES LIFETIMES

Figure 2 shows the distribution of species lifetimes (time from speciation to extinction) in the augmented Newman model. This figure is not normalized, since a power law x^α has an infinite integral. So the abscissa of the graph is not significant but the slope is. The lines are fitted by linear regression. Authors often quote a correlation coefficient; however, this is generally meaningless on a log-log plot. Even the value of the slope is meant to be an indication only, as the large relative error at high lifetime values can lead to significant errors in the computed slope.

Figure 3 shows the lifetime distribution for Ecolab, which has a slope of -2 for lifetimes less than 100 but -1 for larger lifetimes. At still larger times ($\tau \gg 0.1/\mu$), the distribution turns over, decaying exponentially. Previously published versions of this graph [6] only show the smaller lifetime behavior.

Consider now the probability $p(>\tau|x)$ that a species with threshold x will become extinct after time $t=\tau$ in the Newman model. Since time is discrete in this model, this is simply the probability that the stress η does not exceed x for the first τ steps:

$$p(>\tau|x)=\left[\int_0^x p_{\rm stress}(\eta)d\eta\right]^\tau. \tag{10}$$

Now the distribution $p(>\tau)$ of species having lifetimes τ is just the above quantity, integrated over the distribution of thresholds:

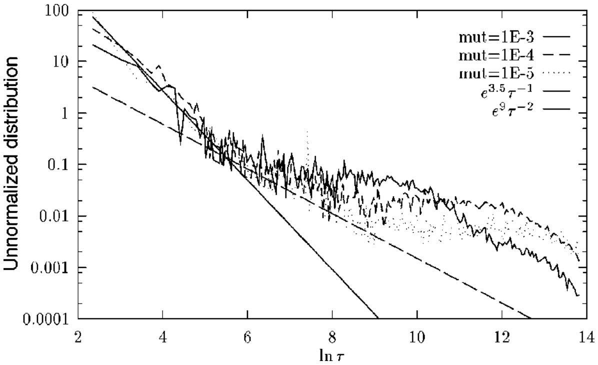

FIG. 3. Distribution of species lifetimes in Ecolab.

$$\begin{aligned}p(>\tau)&=\int p(x)p(>\tau|x)dx\\&=\int p_{\rm thresh}(x)\left[\int_0^x p_{\rm stress}(\eta)d\eta\right]^\tau dx\\&=\int_0^1 p_{\rm thresh}(x)\xi^\tau\frac{dx}{d\xi}d\xi,\end{aligned} \tag{11}$$

where $\xi=\int_0^x p_{\rm stress}(\eta)d\eta$.

Assume the following inequalities hold:

$$\begin{aligned}p_{\rm thresh}(x)&\leq K_1 p_{\rm stress}(x),\ \forall\ x,\\&\geq K_0 p_{\rm stress}(x),\ \forall\ x<x_c,\ \exists\ x_c.\end{aligned} \tag{12}$$

Without loss of generality, $p_{\rm thresh}(x)$ is taken to be the uniform distribution between 0 and 1, and is zero outside this interval. $p_{\rm stress}(x)$ is positive for all positive x, with the large x tail needed to establish power law behavior [15]. In this case, the constants K_0 and K_1 correspond to the inverses of the maximum and minimum of $p_{\rm thresh}(x)$ over the unit interval, and $x_c=1$. Let us introduce $\xi_c=\int_0^{x_c}p_{\rm stress}(x)dx$ as being the change of variable equivalent of x_c. In the case of uniform threshold distribution, and monotonic stress distribution, $1-\xi_c$ is the proportion of stress events that overwhelm the hardiest of species. The inverse of this proportion is a time scale above which the lifetime distribution must decay exponentially. In order to observe power law behavior, the stress distribution must be chosen so that $\xi_c\approx 1$.

Substituting Eq. (12) into Eq. (11) generates the following inequality:

$$\begin{aligned}&K_0\int_0^{\xi_c}p_{\rm stress}(x)\xi^\tau\frac{dx}{d\xi}d\xi\\&\quad\leq p(>\tau)\leq K_1\int_0^1 p_{\rm stress}(x)\xi^\tau\frac{dx}{d\xi}d\xi,\\&K_0\frac{\xi_c^{\tau+1}}{\tau+1}\leq p(>\tau)\leq K_1\frac{1}{\tau+1},\end{aligned} \tag{13}$$

since $p_{\rm stress}(x)=d\xi/dx$ and where $\xi_c=\int_0^{x_c}p_{\rm stress}(x)dx$.

Now $p(\tau)=p(>\tau-1)-p(>\tau)$, so the following inequality is obtained:

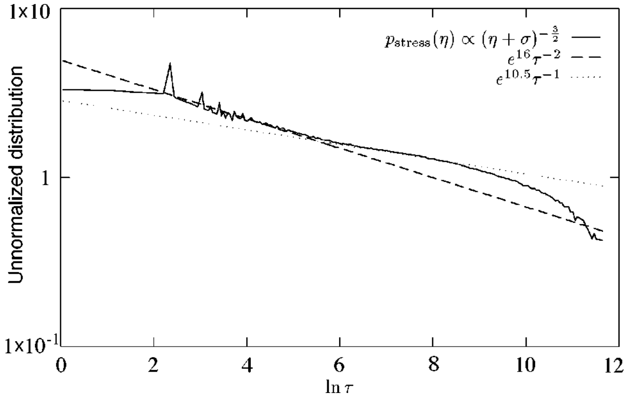

FIG. 4. Distribution of species lifetimes in the generalized Newman model, with $p_{\rm stress}(\eta) \propto (\eta+\sigma)^{-3/2}$.

$$\frac{(K_0\xi_c^\tau - K_1)\tau + K_0\xi_c^\tau}{\tau(\tau+1)} \leqslant p(\tau) \leqslant \frac{(K_1 - K_0\xi_c^\tau)\tau + K_1}{\tau(\tau+1)}. \tag{14}$$

Assuming that $\tau \ll (1-\xi_c)^{-1}, \xi_c^\tau = [1+\tau(1-\xi_c)] + \cdots \approx 1$, this inequality may be simplified:

$$\frac{(K_0 - K_1)\tau + K_0}{\tau(\tau+1)} \leqslant p(\tau) \leqslant \frac{(K_1 - K_0)\tau + K_1}{\tau(\tau+1)}. \tag{15}$$

This result indicates that there are two domains, the first being when $\tau < K_0/(K_1 - K_0)$, where the lifetime distribution is a power law with exponent -2. This domain is more pronounced the closer K_1 is to K_2, i.e., the closer $p_{\rm thresh}(x)$ is to $p_{\rm stress}$. The other domain occurs when $\tau > K_1/(K_1 - K_0)$, where any power law will have an exponent less than -1. In between, there will be a transition between the two domains. This result is not terribly strong, as the inequality can also be satisfied by any distribution falling off faster than a power law. However, it does contradict the results of the *time-average approximation* (TAA) theory of Sneppen and Newman [17] in the case of the Lorentzian distribution, where a power law with exponent 0 (i.e., a flat distribution) is predicted. While a flat distribution is manifestly ridiculous, others are not. The TAA predicts a power law of 1/3 for a power law stress distribution with exponent $-3/2$. Figure 4 shows the observed lifetime distribution in this case, and the distribution never flattens out more than τ^{-1}.

Now lets us turn our attention to the Ecolab-- model to see if a similar relationship can be derived. In what follows, the species index i is dropped. Integrating Eq. (9) gives us

$$n(t) = n_0 e^{\int_0^t r - \eta(s) ds},$$

and taking logarithms gives

$$\ln n(t) = \int_0^t r - \eta(s) ds,$$

since $n_0 = 1$ for all new species.

For the species to become extinct after time $t = \tau$, we require

$$\int_0^t r - \eta(s) ds > \ln \sigma, \quad \forall \quad t < \tau. \tag{16}$$

Since time is discrete in this model, $\eta(s)$ is a piecewise constant function; therefore, the integral can be replaced by a sum so that

$$\sum_{i=0}^{t-1} \eta_i < rt - \ln \sigma, \quad \forall \quad t < \tau. \tag{17}$$

Now inequality (17) defines a set $\mathcal{M} \subset \mathbb{R}^\tau$, and the probability of a species having a lifetime greater than τ if its reproduction rate is r is given by

$$p(>\tau | r) = \int_{\mathcal{M}} \prod_{i=0}^{\tau-1} p_{\rm stress}(\eta_i) d\eta_0 d\eta_1 \cdots d\eta_{\tau-1}. \tag{18}$$

Lets us first deal with sufficient conditions for inequality (17) to be satisfied, which are

$$\eta_i < r - \ln \sigma/\tau, \quad \forall \quad i \leqslant \tau \tag{19}$$

$$< r, \text{ as } \sigma < 1. \tag{20}$$

Therefore, a lower bound for $p(>\tau|r)$ is

$$p(>\tau|r) \geqslant \left[\int_{-\infty}^{r} p_{\rm stress}(\eta) d\eta \right]^\tau. \tag{21}$$

Now consider the following relation:

$$n(t+1) = (1 + r - \eta_t) n(t).$$

For the species not to go extinct before $t = \tau$, we require $\eta_t < 1 + r, \ \forall \ t \leqslant \tau$. Therefore,

$$p(>\tau|r) \leqslant \left[\int_{-\infty}^{(r+1)} p_{\rm stress}(\eta) d\eta \right]^\tau. \tag{22}$$

Now find constants K_0 and K_1 so that

$$\begin{aligned} K_0 p_{\rm stress}(r) \leqslant p_r(r), \quad \forall \quad r < r_c, \ \exists \ r_c, \\ \leqslant K_1 p_{\rm stress}(r+1), \end{aligned} \tag{23}$$

where $p_r(r)$ is the probability distribution of reproduction rates. Since $p(>\tau) = \int p_r(r) p(>\tau|r) dr$, we find

$$\begin{aligned} K_0 \int^{r_c} p_{\rm stress}(r) \left[\int_{-\infty}^{r} p_{\rm stress}(\eta) d\eta \right]^\tau dr \leqslant p(>\tau) \\ \leqslant K_1 \int p_{\rm stress}(r+1) \left[\int_{-\infty}^{(r+1)} p_{\rm stress}(\eta) d\eta \right]^\tau dr, \end{aligned}$$

$$\frac{K_0 \rho_c^\tau}{\tau} \leqslant p(>\tau) \leqslant \frac{K_1}{\tau}. \tag{24}$$

Now, since $p(\tau) = p(>\tau) - p(>\tau+1)$,

$$\frac{K_0 \rho_c^\tau}{\tau} - \frac{K_1}{\tau+1} \leqslant p(\tau) \leqslant \frac{K_1}{\tau} - \frac{K_0 \rho_c^\tau}{\tau+1}, \tag{25}$$

$$\frac{(K_0\rho_c^\tau - K_1)\tau + K_0\rho_c^\tau}{\tau(\tau+1)} \leqslant p(\tau) \leqslant \frac{(K_1 - K_0\rho_c^\tau)\tau + K_1}{\tau(\tau+1)}. \tag{26}$$

Again, like the Newman model, we have two domains of power law possible, an inner domain where the power law is -2, and an outer domain where any power law is capped by -1. This is what is seen in Fig. 3.

VI. CONCLUSION

The Newman model owes its power law behavior to much the same mechanism as does Ecolab, although the assumption of constant species number hides essential interspecies connections. Both models demonstrate a power law exponent near -2 at small time scales, agreeing with the fossil record (after Sneppen *et al.* [19]), turning into a gentler power law with exponent less than -1 at longer times.

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