

Species lifetime distribution for simple models of ecologies

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Interpretation of empirical results based on a taxa's lifetime distribution shows apparently conflicting results. Species' lifetime is reported to be exponentially distributed, whereas higher-order taxa, such as families or genera, follow a broader distribution, compatible with power-law decay. We show that both forms of evidence are consistent with a simple evolutionary model that does not require specific assumptions on species interaction. The model provides a zero-order description of the dynamics of ecological communities, and its species lifetime distribution can be computed exactly. Different behaviors are found as follows: an initial $t^{-3/2}$ power law, emerging from a random walk type of dynamics, which crosses over to a steeper t^{-2} branching process-like regime and finally is cut off by an exponential decay that becomes weaker and weaker as the total population increases. Sampling effects also can be taken into account and shown to be relevant. If species in the fossil record were sampled according to the Fisher log-series distribution, lifetime should be distributed according to a t^{-1} power law. Such variability of behaviors in a simple model, combined with the scarcity of data available, casts serious doubt on the possibility of validating theories of evolution on the basis of species lifetime data.

biodiversity | birth and death equations | branching processes | fossils analysis | stochastic processes

Ecosystems have become paradigmatic examples of complex systems, showing organization and collective dynamics across very different time and spatial scales (1). These features are captured by nontrivial relationships among measurable quantities, which take forms familiar to statistical physics. Well-known examples include the species-area scaling relationship (2, 3), allometric relations (4–7), and the occurrence of power laws in the distributions of species lifetime and size of extinction events (8–10). These statistical laws have been measured over many orders of magnitude and exhibit similar patterns across very different living ecosystems and also in different quantitative studies of fossil records (11). The ubiquity of these patterns (12) suggests that they may be amenable to be studied in a general and aspecific framework.

In this work, we will address the issue of species (or more general taxa) lifetime distribution. Although the analysis of fossil records has recently highlighted several patterns in the evolution of biodiversity, and motivated the proposition of different mechanisms that may have caused these patterns, the functional form of the species lifetime distribution remains a debated issue. According to several studies (13), species lifetime seems to be exponentially distributed. Others have found evidence of power-law behavior with exponent close to -2 if genera, and therefore longer time scales, are considered (ref. 12; see also ref. 11 and references therein). Keitt and Stanley (14) analyzed data sets from the North American Breeding Bird Survey (www.pwrc.usgs.gov/bbs) finding a power-law distribution for species lifetime (in their study defined as the time between colonization and local extinction) with an exponent close to $-3/2$. In fact, the detailed analysis of Newman and Sibani (15) of the data by Raup

and Sepkoski (16) has shown how both these hypotheses consistently fit the data, and, when a power-law fit is applied, an exponent between $-3/2$ and -2 is estimated.

On the theoretical side, these different, not to say contrasting, findings have been invoked to support different macroecological theories. The power-law behavior with exponent -2 is to be expected when species dynamics can be regarded as a critical branching process (17) where two or more species can originate at a random moment from a common ancestor and, also randomly, become extinct. An exponential behavior in the lifetime distribution is often referred to as Van Valen's law (18). The mechanism proposed by Van Valen in support of this view is commonly known as the Red Queen effect: there may not be enough time for a species to gain evolutionary advantage over competing species before the rapidly changing environment completely redraws the fitness landscape. As a consequence, the extinction probability of any species does not depend on time, and an exponential behavior for lifetime distribution easily follows. Several data sets support these conclusions (refs. 19–22; see also ref. 23 for further analysis of the same data). More recently, the occurrence of power-law distributions with non-trivial exponents has attracted particular attention because of an ongoing debate on whether the observed patterns are caused by a self-organized critical dynamics (8–10) that would naturally lead to the notion of punctuated equilibrium (24). In this framework, an ecosystem is depicted as a system of interacting species whose dynamics converges spontaneously close to a critical point (12); the extinction of a given species may trigger a cascade of extinction events starting from the species that depend on, or directly interact with, the species just extinct and leading to fluctuations of any size in the number of extinction occurrences that may contiguously take place.

The aim of the present work is to show that all of the behaviors mentioned above for the lifetime distribution are captured by a simple model of noninteracting species. We conclude, therefore, that it may be problematic, if not inappropriate, to discriminate between existing macroecological theories on the basis of existent data sets. The framework we adopt here is inspired by the ecological neutral theory proposed by Hubbell (25) and thereafter extended and analytically studied in refs. 26–30. This class of models assumes that individuals in an ecological community are fully equivalent and that the population of a species is essentially subject to a birth and death process. Then, each species undergoes the same dynamics: the reproductive success of each individual depends only on the species population size and not on the particular species considered. Competition among species is taken into account explicitly only through a constraint on the total population of the community and implicitly through averages of birth and death rates.

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From the point of view of evolutionary theory, the hypothesis of species equivalence may be still justified by a Red Queen effect (18), which is able to forbid the acquisition of a large evolutionary advantage (i.e., a significantly higher fitness level) of a species over its competitors. In the framework of population dynamics, this hypothesis implies that demographic stochasticity is the main driving force for the assembly of ecological communities, meaning that its effect is overwhelmingly strong compared with that of fitness differences among species, which, although present, may be neglected. It is worthwhile to stress that, in principle, complex ecological mechanisms acting on long time scales are not ruled out by these stochastic models, as far as they can be included in effective birth and death rates. This consideration opens the issue of determining whether these theories are able to assess realistic predictions on large time and geographical scales, such as those relevant for the fossil observations. It is widely believed (1) that statistical physics may provide the tools to bridge these very different scales. In this perspective, it is encouraging that Conette and Lieberman (31), based on the studies of the biodiversity time series compiled by Sepkoski and coworkers (32, 33), recently concluded that a random-walk-like model is not inconsistent with the observed biodiversity time patterns.

The model we consider here is analytically solvable and is introduced in the next section. The resulting lifetime distribution interpolates, through a scaling function, between the behaviors of two well-known stochastic processes: exit time problem for the one-dimensional random walk (34) and the critical Galton–Watson branching process (17). Our results show that, even in a simple model in which interactions among species are included only in an averaged way, a variety of different behaviors for the distribution of extinction time are possible. In particular, depending on the relevant time scales, we find an exponential, or a power-law, behavior. The latter can either occur with exponent -2 , typical of branching processes (17), or, for shorter time scales, with a random-walk-like exponent $-3/2$. In addition, if we assume that the abundance of species is distributed according to a Fisher log-series (35), in the Galton–Watson case, we find a power-law distribution of extinction times with exponent -1 .

As we will discuss in the conclusion, these results stress the importance of time scales and sampling effects in the analysis of lifetime distributions. This theory also can easily accommodate the contrasting empirical observations of refs. 11–13 and 15 by assuming that, whereas species lifetimes probe the exponential regime of the theory, genera lifetimes fall in the power-law range. The fact that power laws arise in an “effective” single-species theory, combined with the sparseness of available empirical data, suggests that it may not be possible to validate (or discard) ecological or evolutionary mechanisms like self-organized critical dynamics (12) on the basis of an observed nonexponential behavior in the lifetime distributions.

Description of the Model

According to the assumption of neutrality (25, 26), the dynamics of our model is uniquely specified by the effective birth and death rates $b^{(n)}$ and $d^{(n)}$ that depend exclusively on the population size n .

We refer to the functions $b^{(n)}$ and $d^{(n)}$ as effective because they may embody, in a cumulative way, a variety of ecological causes that may, in principle, influence the increase/decrease over time of the number of individuals in a species or, more generally, in a given taxon. The framework is therefore ample enough to describe a population dynamics that is not simply dominated by demographic stochasticity, but also, for example, by immigration, emigration, or niche assembly. We can safely assume that $b^{(n)}/n$ and $d^{(n)}/n$, the birth and death rates per individuals, can

be expanded in a power series in $1/n$ around their asymptotic values b_1 and d_1 (28)

$$\begin{aligned} b^{(n)}/n &= b_1 + b_0/n + b_{-1}/n^2 + \dots \\ d^{(n)}/n &= d_1 + d_0/n + d_{-1}/n^2 + \dots \end{aligned} \quad [1]$$

The nonzero coefficient in this Taylor series can be generally related to various kind of ecological effects giving advantages (or disadvantages) to a less abundant species with respect to a more abundant one. In Hubbell’s theory (25, 26), the terms b_0 and d_0 may be interpreted as the result of an immigration/emigration mechanism that couples the community to a meta-community living on a larger geographical scale. The mechanisms described by higher power in $1/n$ in Eq. 1 are relevant only for small population sizes, and they are unable, reasonably, to affect properties observed on large spatial scales and long time scales. In the following, therefore, we will study the dynamics described only by the first two terms in the expansion of Eq. 1:

$$\begin{aligned} b^{(n)} &= b_0 + b_1 n \\ d^{(n)} &= d_0 + d_1 n, \end{aligned} \quad [2]$$

for all $n \geq 1$. Despite the simple form of the birth and death rates, and the simplicity of the assumptions, this class of models is able to provide very good fits of species abundance relations (26–28), which can be related to the probability P_n of having species with population size n . This probability, P_n , evolves with time according to a birth and death master equation

$$\frac{d}{dt} P_n(t) = b^{(n-1)} P_{n-1}(t) + d^{(n+1)} P_{n+1}(t) - (d^{(n)} + b^{(n)}) P_n(t). \quad [3]$$

We impose $b_1 < d_1$, ensuring that the average number of individuals is finite and there is no “demographic explosion.” The ratio $\alpha = b_1/d_1$ fixes, in fact, the average population per species (27, 28).

To study the lifetime distribution, we consider an absorbing barrier at $n = 0$, imposing $b^{(0)} = d^{(0)} = 0$. The initial condition is that the new species at time $t = 0$ has just one individual

$$P_n(0) = \delta_{n,1}. \quad [4]$$

Making these assumptions, $P_0(t)$ represents the probability of being already extinct at time t , and the lifetime probability distribution function (or exit time distribution), $p(t)$, is just the time derivative of $P_0(t)$

$$p(t) = \frac{d}{dt} P_0(t). \quad [5]$$

We will first examine the two limit cases $b_1 = d_1 = 0$ and $b_0 = d_0 = 0$ and then move to the general case.

Results

When $b_1 = d_1 = 0$, the number of individuals belonging to a given species undergoes a random walk in n space where b_0 (d_0) is the probability per unit time to jump one step to the right (left). A species lifetime therefore would correspond to the time it takes for the random walk to reach $n = 0$, i.e., to exit the positive axis. The problem of exit time distribution for a random-walk process has been widely studied in the literature (see, for example, ref. 34). In particular, it is well known that in the critical case $b_0 = d_0$ the lifetime follows a distribution of the form $p(t) \sim t^{-3/2}$. Indeed, it is easy to verify that the solution of Eq. 3, in the present case, is

$$P_0(t) = 1 - \exp(-2t)(I_0(2t) + I_1(2t)) \quad [6]$$

$$P_k(t) = \exp(-2t)(I_{k-1}(2t) - I_{k+1}(2t)) \quad k > 0,$$

where $I_k(z) = (1/\pi) \int_0^\pi \exp(z \cos(\theta)) \cos(k\theta) d\theta$ are modified Bessel functions of integer order, and the unit of time has been chosen such that $b_0 = d_0 = 1$. Since for large z , $I_0(z) \propto e^z/\sqrt{z}$, from Eqs. 5 and 6, it follows that $p(t) \sim t^{-3/2}$ asymptotically.

Let us now analyze the case $b_0 = d_0 = 0$. This limiting case is interesting from an ecological point of view because the d_0 and b_0 terms happen to be small when one looks on a very large scale (such as a continental scale). The dynamics is equivalent to a Galton–Watson process in continuous time (17): the asymptotic behavior of the lifetime distribution is a classic result of the theory of critical branching processes (36).

Also in this case, the birth and death equation can be analytically solved; defining the characteristic function $G(x, t) = \sum_{n=0}^\infty P_n(t)x^n$, the birth and death equation can be transformed into a first-order partial differential equation for the function G , which can be integrated by the characteristics method. In the following, without loss of generality, we set $d_1 = 1$, and the initial condition in Eq. 4 translates in $G(x, 0) = x$. As shown in detail in *Supporting Text*, which is published as supporting information on the PNAS web site, the exact solution is

$$p(t) = \left(\frac{1 - \alpha}{e^{(1-\alpha)t} - \alpha} \right)^2 e^{(1-\alpha)t}. \quad [7]$$

This distribution has an exponential-like shape when $(d_1 - b_1)$ (or $1 - \alpha$) is not too small. On the other hand, when b_1 approaches d_1 , the distribution has a power-law behavior with exponent -2 and a characteristic time scale $t^* = 1/(1 - \alpha)$. The distribution $p(t)$ can be cast in a more appealing form by using the language of critical phenomena in statistical mechanics. For large t and t/t^* fixed, it follows, from Eq. 7, that

$$p(t) = \frac{1}{t^{*2}} f\left(\frac{t}{t^*}\right), \quad [8]$$

where $f(x) = [x/(1 - e^{-x})]^2 e^{-x}$. Thus, plotting $t^2 p(t)$ vs. t/t^* , one gets, in the scaling region, a universal curve where all of the model details are absorbed in the characteristic time scale, t^* . When dealing with observational data, an estimate of t^* can be obtained by the ratio of two consecutive moments, $\langle t^k \rangle (k \geq 1)$, of lifetime probability distribution function.

It also is interesting to investigate the role of the initial condition on the lifetime p.d.f. Taking into account an effective speciation rate, one can show, for the particular case at hand, that the resulting stationary distribution (26) is the celebrated Fisher log series (35)

$$P_n = \mathcal{N} \frac{\alpha^n}{n}, \quad [9]$$

where $n > 0$ and \mathcal{N} is a normalization constant. By using the result above, it is therefore possible to calculate the expected extinction time of a species that is chosen at random in the ecosystem. Setting as initial conditions the characteristic function associated to the distribution in Eq. 9, $G(x, 0) = \log(1 - x\alpha)/\log(1 - \alpha)$, one finds

$$G(0, t) = \frac{1}{\log(1 - \alpha)} \log \left[\frac{(1 - \alpha)e^{(1-\alpha)t}}{e^{(1-\alpha)t} - \alpha} \right]. \quad [10]$$

In this case, again $p(t) = \partial G(0, t)/\partial t \sim e^{-t/t^*}$ when $t \gg t^*$, whereas $p(t) \sim t^{-1}$ when $t \ll t^*$, which means that the critical exponent for the lifetime p.d.f is now -1 .

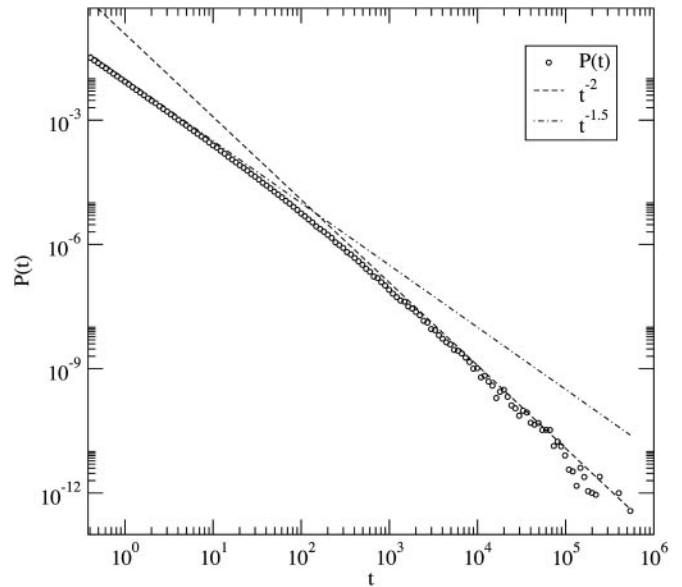


Fig. 1. Numerical sample of the lifetime probability distribution function with parameters $d_1 = 1$, $b_1 = 1 - 5 \times 10^{-5}$, $b_0 = d_0 = 10$. Notice the crossover between the two power laws (shown; notice the log-log scale) and the beginning of the exponential regime.

We now discuss, qualitatively first, the solution in the general case when all of the coefficients are different from zero and $b_0 \sim d_0$, $b_1 \sim d_1$. Heuristically, long-living species typically have a large number of individuals. For such species, the b_0 and d_0 terms can be reasonably neglected. Thus, one expects a crossover from the $t^{-3/2}$ to the t^{-2} behavior at a certain characteristic time and finally an exponential decay beyond another characteristic time scale. Numerical simulations do support this hypothesis, as shown in Fig. 1, and suggest that the crossover time is proportional to the ratio b_1/b_0 .

In *Supporting Text*, we provide the analytical solution of the general case, proving rigorously both the asymptotic critical behaviors and the scaling of the solution with the ratio b_0/b_1 . In the following, we discuss the main results and their consequences. In terms of the Laplace transform of $P_0(t)$, $\tilde{P}_0(s) = \int_0^\infty P_0(t)e^{-ts}$, the exact solution for the critical case $b_0 = d_0 = r$ and $b_1 = d_1 = 1$, is given by

$$s\tilde{P}_0(s) - 1 = \frac{\int_1^\infty \frac{dy}{y} e^{-sy} \left(1 - \frac{1}{y}\right)^r}{\int_1^\infty dy e^{-sy} \left(1 - \frac{1}{y}\right)^r} = \frac{1}{\partial_s \log N(s, r)}, \quad [11]$$

where we have defined $N(s, r) = \int_1^\infty (dy/y) e^{-sy} (1 - (1/y))^r$. For small s the function $N(s, r)$ diverges as $-c \log s$, where c depends only on r ; this divergence implies that $\tilde{P}_0(s)$ behaves as $\tilde{P}_0(s) \sim (1/s) + c \log s$. The Tauberian theorem ensures in this case that $P_0(t)$ behaves like $1 - ct^{-1}$ for large t , implying that the lifetime distribution has a t^{-2} power-law tail.

To derive the crossover to the $t^{-3/2}$ behavior, we need to focus on time scales $t \ll 1/r$ for $r \ll 1$. This scale is related to the limit $s \rightarrow 0$ with rs fixed in the solution, for which one obtains

$$N(s, r) = \int_0^\infty \frac{dx}{x} e^{-\sqrt{rs}(x + \frac{1}{x})} = 2K_0(2\sqrt{rs}), \quad [12]$$

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