A Problem in Paleobiology

Barry D. Hughes

Department of Mathematics and Statistics, University of Melbourne, Victoria 3010, Australia

William J. Reed

Department of Mathematics and Statistics, University of Victoria, Victoria, British Columbia, Canada V8W 3P4

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We present a stochastic model for the size of a taxon in paleobiology, in which we allow for the evolution of new taxon members, and both individual and catastrophic extinction events. The model uses ideas from the theory of birth and death processes. Some general properties of the model are developed, and a fuller discussion is given for specific distributions of the time between catastrophic extinction events. Long tails in the taxon size distribution arise naturally from the model.

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Random processes leading to probability distributions with slowly-decaying algebraic tails have been of considerable recent interest in physics, although they have been sporadically studied in other areas for many years. As probability laws with $\Pr\{X > x\} \propto x^{-\alpha}$ as $x \to \infty$ are naturally associated with scaling properties, self-similarity and fractals, it is tempting to propose fractal underlying mechanisms to explain the occurrence of these laws in particular contexts in nature.

We address a problem of interest in paleobiology, where long-tailed distributions arise, and propose a model that requires no explicitly fractal underlying mechanism to explain these distributions. The model predicts the distribution of the number of elements in a taxon, for example the number of species in a genus, and our analysis covers both the distribution of species currently in existence, and the distribution of all species in the genus that have ever existed, some of which may now be extinct.

Several other problems in taxonomy and genetics involve similar mathematical analysis, and the authors have briefly addressed elsewhere [1, 2] the fitting of models of this type to real biological data. More generally, the basic modelling approach in this paper involves killing at an exponentially distributed time a stochastic process for which the mean grows exponentially in time. The appearance of power-law distributions in such contexts has been discussed in general by the authors elsewhere [3], and has applications in social phenomena [4] and other contexts not covered in the present paper.

Modelling of taxon size has been of sporadic interest in the literature for some time [5, 6, 7], and there has been a steady accumulation of relevant data on both extinct and surviving taxonomic groups [8, 9]. We shall not address mechanisms for species interaction in an ecosystem that may drive extinction or species proliferation, nor shall we address the shape of evolutionary trees (cladograms).

In our model, a taxon comes into existence with a single representative species, genus or family at time $t = 0$. The number of members of the taxon grows with time as species mutate. Some species produce many new species, but any species may also become extinct, and a natural model for the proliferation and extinction of taxon members is the linear birth–death process (see, for example, [10], pp. 165–167 and pp. 265–266). A taxon member (referred to hereafter as a species) has in the time interval $(t, t + h)$ a probability $\lambda h + o(h)$ of 'giving birth' to a new species, and a probability $\mu h + o(h)$ of 'dying'. Assuming independence of speciation and extinction events, if there are n species present at time t, the probability of one speciation occurring in $(t, t + h)$ is $\lambda n h + o(h)$, and the probability of one extinction is $\mu n h + o(h)$. Let M_t denote the number of species that have ever existed (whether currently alive or not) at time t and N_t the number of species currently alive at time t, and write $p_{m,n}(t) = \Pr\{M_t = m, N_t = n\}$. Then for $h > 0$,

$$
\begin{aligned}
p_{m,n}(t + h) &= [1 - n(\lambda + \mu)h + o(h)]p_{m,n}(t) \\
&\quad + [\lambda h + o(h)](n - 1)p_{m-1,n-1}(t) \\
&\quad + [\mu h + o(h)](n + 1)p_{m,n+1}(t) + o(h).
\end{aligned}
$$

The first term on the right-hand side corresponds to no change in M_t or N_t in the time interval $(t, t + h)$, the second to one birth, and the third to one death. All other events have probability $o(h)$. Subtracting $p_{m,n}(t)$ from both sides, dividing by h and letting $h \to 0$, we deduce the differential-difference equation

$$
\begin{aligned}
\frac{d}{dt}p_{m,n}(t) &= -(\lambda + \mu)np_{m,n}(t) + \lambda(n - 1)p_{m-1,n-1}(t) \\
&\quad + \mu(n + 1)p_{m,n+1}(t).
\end{aligned}
$$

This equation is valid for all integer m and n provided that we adopt the convention that $p_{m,n}(t) = 0$ if $m \le 0$ or $n < 0$. We measure time from the appearance of the first individual, so that $p_{m,n}(0) = 1$ if $m = n = 1$; $p_{m,n}(0) = 0$ otherwise. Introducing the generating function $P(\xi, \zeta, t) = \mathbb{E}\{\xi^{M_t}\zeta^{N_t}\}$ (where $\mathbb{E}$ denotes expectation) one may readily derive [11] the partial differential equation $P_t = \{\xi\zeta^2\lambda - (\lambda + \mu)\zeta + \mu\} P_\zeta$ with initial condition $P(\xi, \zeta, 0) = \xi\zeta$. Using the method of characteristics one finds [11] that

$$
P(\xi, \zeta, t) = \xi \frac{z_2(\zeta - z_1)e^{\lambda\xi z_1 t} + z_1(z_2 - \zeta)e^{\lambda\xi z_2 t}}{(\zeta - z_1)e^{\lambda\xi z_1 t} + (z_2 - \zeta)e^{\lambda\xi z_2 t}}, \quad (1)
$$

where z_1 and z_2 denote the roots of the quadratic equation $\xi\lambda z^2 - (\lambda + \mu)z + \mu = 0$. Since the probability that M_t species have ever existed up to time t is given by $\Pr\{M_t = m\} = \sum_{n=1}^{\infty} p_{mn}$, setting $\zeta = 1$ in Eq. (1) we recover the generating function for the probability that M_t species have ever existed up to time t:

$$\mathbb{E}\{\xi^{M_t}\} = \frac{x_2(\lambda\xi - x_1)e^{x_1 t} + x_1(x_2 - \lambda\xi)e^{x_2 t}}{\lambda[(\lambda\xi - x_1)e^{x_1 t} + (x_2 - \lambda\xi)e^{x_2 t}]}.$$

For brevity we have let $x_i = \lambda\xi z_i$, so that x_1 and x_2 are the roots of $x^2 - (\lambda + \mu)x + \lambda\mu\xi = 0$. These roots are distinct for all μ and λ when $\xi < 1$. The roots become λ and μ when $\xi = 1$, so that the case $\lambda = \mu$ is degenerate for $\xi = 1$, but this presents no difficulties in the subsequent analysis. Using the results that $x_1 + x_2 = \lambda + \mu$ and $x_1 x_2 = \lambda\mu\xi$, establishes the form of the generating function needed below:

$$\mathbb{E}\{\xi^{M_t}\} = \xi + \frac{\lambda\xi(\xi - 1)[e^{(x_2 t} - e^{x_1 t}]}{(x_2 - \lambda\xi)e^{x_2 t} - (x_1 - \lambda\xi)e^{x_1 t}}. \quad (2)$$

To make contact with better known results on the number of species currently alive, we note that setting $\xi = 1$ gives $z_1 = 1$ and $z_2 = \mu/\lambda$ and Eq. (1) becomes [12]

$$\mathbb{E}\{\zeta^{N_t}\} = \begin{cases} \dfrac{\mu(1-\zeta) - (\mu - \lambda\zeta)e^{-t(\lambda-\mu)}}{\lambda(1-\zeta) - (\mu - \lambda\zeta)e^{-t(\lambda-\mu)}} & \text{if } \lambda \neq \mu, \\[2ex] 1 - (1-\zeta)/[1 + \lambda t(1-\zeta)]^{-1} & \text{if } \lambda = \mu. \end{cases}$$

That $\langle N_t \rangle = e^{(\lambda-\mu)t}$ follows by differentiation, while expansion of the generating function gives ([10], p. 166) $\Pr\{N_t = 0\} = (\mu - \mu e^{-t(\lambda-\mu)})/(\lambda - \mu e^{-t(\lambda-\mu)})$; for $n \geq 1$,

$$\Pr\{N_t = n\} = \frac{(\lambda - \mu)^2 e^{-t(\lambda-\mu)}}{[\lambda - \mu e^{-t(\lambda-\mu)}]^2} \left\{ \frac{\lambda - \lambda e^{-t(\lambda-\mu)}}{\lambda - \mu e^{-t(\lambda-\mu)}} \right\}^{n-1}.$$

In the limiting case $\lambda = \mu$, $\Pr\{N_t = 0\} = \lambda t/(1 + \lambda t)$ and $\Pr\{N_t = n\} = (\lambda t)^{n-1}/(1 + \lambda t)^{n+1}$ for $n \geq 1$. When $\mu = 0$ (that is, there is a pure birth process) the solution reduces to that found by Yule [5] in his model of species evolution under a speciation rate λ.

There is considerable evidence for major catastrophic extinctions occurring within a relatively short period, these extinctions having been attributed to various causes, including major meteorite impacts [13] and a hypothesised purely biotic mechanism called coevolutionary avalanches [14]. To include catastrophic extinctions in our model, we require the probability density function $f(t)$ for the time T between the start of a taxon and the next catastrophe. In the analysis below we carry a general $f(t)$ as far as possible. The three specific models discussed here are proposed with some diffidence, though each has a certain natural appeal, and each may apply to appropriate subsets of paleological data. The common thread to all three models is that as $t \to \infty$,

$$f(t) \sim \text{constant} \times t^q e^{-\theta t}, \quad (3)$$

with $1/\theta$ the mean time between catastrophic extinction events and either $q = 0$ or $q = -1$. The small-t behavior is different in the three models, but this difference does not affect the dominant asymptotic behavior of the taxon size distribution. Using Eq. (3) with some flexibility as to the value of q seems a reasonable approach.

(a) *The pure exponential model.* As a first model one may assume that $f(t) = \theta e^{-\theta t}$ for $t > 0$. This asserts that the waiting time for the next catastrophe is exponentially distributed, but effectively considers only one taxon: no account is taken of the fact that in a long time interval, many taxons should be initiated, while in a short time interval, it is likely that no taxons will be initiated. Subtle conditional probability effects are ignored.

For models (b) and (c) below, we assume that catastrophic extinction events occur in a Poisson process at rate θ, while taxon initiations occur in a Poisson process at rate ρ. Thus the probability density function for the waiting time between extinctions is $\psi(t) = \theta e^{-\theta t}$, $t > 0$, while the waiting-time density for the start of the next taxon is $\chi(t) = \rho e^{-\rho t}$, $t > 0$.

(b) *The first new taxon model.* Consider the time to the next catastrope for the *first* taxon initiated after the previous catastrophe. If we condition on the time T between catastrophes, the conditional waiting-time density for appearance of a taxon is $\rho e^{-\rho t}/(1 - e^{-\rho T})$, $0 < t < T$. The time between the appearance of the taxon and the next catastrophe therefore has the probability density function $\eta(t\,|\,T) = \rho e^{\rho(t-T)}/(1 - e^{-\rho T})$, $0 < t < T$. We now average over T to deduce for the time from taxon commencement to the next catastrophe the density

$$f(t) = \int_0^{\infty} \theta e^{-\theta\tau} \eta(t\,|\,\tau)d\tau = \rho\theta e^{\rho t} \int_t^{\infty} \frac{e^{-\rho\tau - \theta\tau}d\tau}{1 - e^{-\rho\tau}}.$$

It can be shown that $f(t) \sim \theta \ln[1/(\rho t)]$ as $t \to 0$, while $f(t) \sim [\rho\theta/(\rho + \theta)]\,e^{-\theta t}$ as $t \to \infty$.

(c) *Uniform taxon nucleation between catastrophes.* The probability that there is at least one taxon initiated in the time interval of duration τ between two successive catastrophes is $1 - e^{-\rho\tau}$. It is known [15] that for a Poisson process with rate ρ, conditional on there being n occurrences in a time interval of length τ, the occurrence times have the same distribution as the order statistics of a set of n independent times, each uniformly distributed on the interval of length τ. This suggests as a model for the probability density function for the time to the next catastrophe

$$f(t) = \frac{\rho + \theta}{\rho} \int_t^{\infty} \frac{[1 - e^{-\rho\tau}]}{\tau} \theta e^{-\theta\tau}d\tau.$$

The prefactor $(\rho + \theta)/\rho$ is inserted to ensure that $f(t)$ is non-defective, that is, integrates to unity. As $t \to \infty$,

$$f(t) = \frac{(\rho + \theta)e^{-\theta t}}{\rho t}\left[1 + O(t^{-1})\right]\left[1 + O(e^{-\rho t})\right].$$

The size of a surviving taxon. We address briefly the distribution of the number N of species in a taxon that

are living just before a catastrophic extinction event occurs; equivalently this is asking for the distribution of taxon size today, the detail residing in the probability density function $f(t)$ for the time since the taxon began. The case $\lambda < \mu$, in which a taxon is driven rapidly to extinction, is not considered. We shall consider only the case $f(t) = \theta e^{-\theta t}$, $t \geq 0$. Since relatively simple expressions for $\Pr\{N_t = n\}$ are available, the direct calculation of the distribution of

$$\Pr\{N = n\} = \int_0^\infty \Pr\{N_t = n\} f(t) dt$$

becomes possible; the details are equivalent to those in a model of live taxa where both species and genera proliferate [1] and will not be given here.

In the case $\lambda = \mu$, the distribution of N is reasonably rapidly decaying, though its dominant form is subtle:

$$\Pr\{N = n\} \sim \pi^{1/2}(\theta/\lambda)^{5/4} n^{-3/4} e^{-2(\theta/\lambda)^{1/2} n^{1/2}}.$$

The stretched exponential behavior is typical of the crossover behavior in problems of stochastic processes or statistical physics when exponential decay degenerates to algebraic decay as a parameter (here μ) passes through a critical value (here λ).

If $\lambda > \mu$, we find $\Pr\{N = n\} \sim \text{constant} \times n^{-1-\theta/(\lambda-\mu)}$, so that $\Pr\{N \geq n\} \sim \text{constant} \times n^{-\theta/(\lambda-\mu)}$ as $n \to \infty$. The mean taxon size is infinite if $\lambda \geq \mu + \theta$. Applications of these formulae to real data are given elsewhere [17].

Proliferation between catastrophes. The problem of greater palaeobiological interest concerns the number of species that ever belong to a taxon. As before, let $f(t)$ be the waiting-time density for the time T after the emergence of a taxon to the next global extinction. The case $f(t) = \theta e^{-\theta t}$ is of most interest, but we carry generality when we may. Let the random variable M be the number of species in a taxon that exists only between two successive catastrophes. With M_t the number of species that have ever existed up to time t, we have

$$p_m = \Pr\{M = m\} = \int_0^\infty \Pr\{M_t = m\} f(t) dt.$$

Using Eq. (2), the generating function for p_m is given by

$$\phi(\xi) = \sum_{m=1}^\infty p_m \xi^m = 1 + (\xi - 1)\{1 + \xi\chi(\xi)\}, \quad (4)$$

where

$$\chi(\xi) = \int_0^\infty \frac{\lambda[e^{x_2 t} - e^{x_1 t}]f(t)dt}{(x_2 - \lambda\xi)e^{x_2 t} - (x_1 - \lambda\xi)e^{x_1 t}}. \quad (5)$$

We need to determine the asymptotic behavior of $\chi(\xi)$ near $\xi = 1$. If the function $\chi(\xi)$ and its first derivative $\chi'(\xi)$, respectively, remain finite at $\xi = 1$, then the expected value $\langle M \rangle$ of M and the variance $\text{Var}\{M\}$ of M are finite, and we have $\langle M \rangle = 1 + \chi(1)$ and

$\text{Var}\{M\} = 2\chi'(1) + \chi(1) - \chi(1)^2$. The function $\chi(\xi)$ is symmetric under interchange of x_1 and x_2. We shall identify x_2 with the root that approaches λ as $\xi \to 1$, and x_1 with the root that approaches μ as $\xi \to 1$. Solving the quadratic equation for x_1 and x_2 exactly and expanding the solutions for $1 - \xi \to 0$, we record for later use that

$$x_1 = \mu - \lambda\mu(1-\xi)/(\lambda-\mu) + O([1-\xi]^2),$$
$$x_2 = \lambda + \lambda\mu(1-\xi)/(\lambda-\mu) + O([1-\xi]^2).$$

Provided that the integral in Eq. (5) converges for $\xi = 1$, we find that the expected value of M is

$$\langle M \rangle = 1 + \int_0^\infty \frac{\lambda[e^{(\lambda-\mu)t} - 1]f(t)dt}{\lambda - \mu}. \quad (6)$$

For $\lambda < \mu$, the mean is finite for every density $f(t)$. The degenerate case $\lambda = \mu$ can be analysed separately, or by taking the limit $\lambda \to \mu$ from below inside the integral in Eq. (6), giving $\langle M \rangle = 1 + \lambda\langle T \rangle$, so $\langle M \rangle$ diverges in the degenerate case $\lambda = \mu$ if the mean waiting time $\langle T \rangle$ for catastrophic extinctions is infinite.

For $\lambda > \mu$, the integral in Eq. (6) establishes that unless $f(t)$ has at least exponential decay, the mean is necessarily divergent. If $f(t) \sim \text{constant} \times t^r \exp(-\theta t)$ as $t \to \infty$, then the mean taxon size if finite so long as $\lambda < \mu + \theta$. Whether it is also finite in the critical case $\lambda = \mu + \theta$ depends on the value of r. In particular, for the exponential density $f(t) = \theta e^{-\theta t}$ we find that $\langle M \rangle = \infty$ if $\lambda \geq \mu + \theta$, while $\langle M \rangle = 1 + \lambda/(\theta + \mu - \lambda)$ if $\lambda < \mu + \theta$.

To analyse the case $\lambda > \mu$, we shall rewrite the integral for $\chi(\xi)$ in the equivalent form

$$\chi(\xi) = \int_0^\infty \frac{\lambda\{1 - e^{-(x_2-x_1)t}\}f(t)dt}{(x_2 - \lambda\xi) - (x_1 - \lambda\xi)e^{-(x_2-x_1)t}}.$$

The exponentials are decaying functions of time, since $x_2 - x_1 = \lambda - \mu + 2\lambda\mu(1-\xi)/(\lambda-\mu) + O([1-\xi]^2)$ as $1 - \xi \to 0$. Hence to leading order,

$$\chi(\xi) \sim \frac{\lambda}{\lambda-\mu} \int_0^\infty \frac{[1 - e^{-(\lambda-\mu)t}]f(t)dt}{\kappa(1-\xi) + e^{-(\lambda-\mu)t}},$$

where $\kappa = \lambda^2/(\lambda-\mu)^2$. In the case $f(t) = \theta e^{-\theta t}$, if we write $y = e^{-(\lambda-\mu)t}$, we find that

$$\chi(\xi) \sim \frac{\lambda\theta}{(\lambda-\mu)^2} \int_0^1 \frac{(1-y)y^{\theta/(\lambda-\mu)-1}dy}{\kappa(1-\xi) + y}.$$

Mellin transform methods (see, e.g. [16] or [18], Appendix 2) can be used to extract the asymptotic behavior of this integral and so determine the expansion for $\phi(\xi)$ near $\xi = 1$. We find that for $\lambda > \theta + \mu$,

$$\phi(\xi) = 1 - \frac{\pi\lambda[\kappa(1-\xi)]^{\theta/(\lambda-\mu)}}{\theta \sin[(\pi\theta)/(\lambda-\mu)]} + \cdots,$$

while $\phi(\xi) = 1 - (\lambda/\theta)(1-\xi)\ln[\kappa^{-1}(1-\xi)^{-1}] + \cdots$ for $\lambda = \theta + \mu$. This asymptotic behavior of $\phi(\xi)$ suggests the following behavior of p_m as $m \to \infty$:

$$p_m \sim \begin{cases} \text{constant} \times m^{-1-\theta/(\lambda-\mu)}, & \lambda > \theta + \mu, \\ \text{constant} \times m^{-2}\ln m & \lambda = \theta + \mu. \end{cases}$$

To derive this rigorously would require either a careful argument based around Darboux's Theorem [18], or the methods of Flajolet and Odlyzko [19], or Tauberian Theorems supplemented by information about the ultimate monotonic decay of p_m [18, 20]. We obtain the same asymptotic behavior for the total number of species that ever existed as that found for currently living species:

$$\Pr\{M \geq m\} \sim \begin{cases} \text{constant} \times m^{-\theta/(\lambda-\mu)}, & \lambda > \theta + \mu \\ \text{constant} \times m^{-1}\ln m, & \lambda = \theta + \mu. \end{cases}$$

More generally, note that as $\xi \to 1$,

$$\chi(\xi) \sim \frac{\lambda}{\lambda - \mu} \int_0^\infty \frac{f(t)dt}{\kappa(1-\xi) + e^{-(\lambda-\mu)t}}.$$

It can be shown that if $f(t) \sim \Theta t^r e^{-\theta t}$ $(r > -1)$ then

$$\chi(\xi) \sim \frac{\pi\lambda\Theta[\kappa(1-\xi)]^{\theta/(\lambda-\mu)-1}\{\ln[\kappa^{-1}(1-\xi)^{-1}]\}^r}{(\lambda-\mu)^{r+2}\sin[(\pi\theta)/(\lambda-\mu)]}$$

for $\lambda > \theta + \mu$. In the borderline case $\lambda = \theta + \mu$, we find

$$\chi(\xi) \sim \frac{\lambda\Theta}{(r+1)\theta^{r+2}}\{\ln[\kappa^{-1}(1-\xi)^{-1}]\}^{r+1}.$$

We predict the asymptotic forms

$$p_m \sim \begin{cases} \text{constant} \times m^{-1-\theta/(\lambda-\mu)}(\ln m)^r, & \lambda > \theta + \mu, \\ \text{constant} \times m^{-2}(\ln m)^{r+1}, & \lambda = \theta + \mu. \end{cases}$$

There has been a significant prior work on the modelling of populations subject to disasters in other contexts, with particular emphasis on the time to extinction in the process [21]. However, the principal conclusions of the present paper, especially those drawn for the properties of extinct taxa, appear to be new. We have shown that the competition between characteristic rates of species proliferation, individual species extinction, and large-scale catastrophic extinction is able to generate long-tailed distributions of taxon size and consequent scaling properties and fractal interpretations without the need to assume an underlying fractal model. The formalism covers both currently live taxa, and taxa destroyed out by previous global catastrophic extinction events. Our results are based on a null model for proliferations and extinctions. The validity of the model can be assessed by comparing the results established with empirical size distributions for living and fossil taxa (as in [1]). Models for evolution with an underlying dynamics have been proposed [22]. The null model provides a useful benchmark against which the predictions of more detailed models may be assessed and its concepts and analytical methods may have applications in other areas.

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