Extinction, diversity and survivorship of taxa in the fossil record

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Abstract

Using data drawn from large-scale databases, a number of interesting trends in the fossil record have been observed in recent years. These include the average decline in extinction rates throughout the Phanerozoic, the average increase in standing diversity, correlations between rates of origination and extinction, and simple laws governing the form of survivorship curves and the distribution of the lifetimes of taxa. In this paper we derive mathematically a number of relations between these quantities and show how these different trends are inter-related. We also derive a variety of constraints on the possible forms of these trends, such as limits on the rate at which extinction may decline and limits on the allowed difference between extinction and origination rates at any given time.
1 Introduction

Traditionally, studies of origination and extinction have focussed on single taxa or groups of taxa, in an attempt to determine the causes of particular extinction events. In the latter half of the twentieth century, the larger mass extinction events have also drawn a considerable amount of attention from researchers curious about their scope and origin. However, it has only been in the last twenty-five years or so that fossil data have been available of sufficient quality to allow statistical investigation of large-scale patterns in the extinction and origination record. One of the earliest statistical studies was that of Van Valen (1973), who looked at “survivorship curves” for a large number of different groups of organisms and conjectured possible mechanisms to explain what he saw. More recently, a variety of authors have looked at other trends in the fossil record, and proposed simple empirical laws governing various aspects of taxon origination and extinction. Of particular interest to us in this paper, in addition to Van Valen’s work, will be work on the distribution of the lifetimes of taxa (Sneppen et al. 1995), the increase in diversity towards the recent (Benton 1995), and the decline in extinction rates (Sibani et al. 1995, Newman and Eble 1998).

Our concern in this paper is with overall statistical trends in the fossil record of the last 600 million years (My) or so. For instance, it has been observed that the mean extinction rate for genera (or families) appears to decline during the Phanerozoic. There is certainly a great deal of fluctuation about this mean, with many intervals of time in which extinction increases rather than falls off. We however will look only at the general trend and not at these fluctuations. Thus our work does not for example address the appearance of mass extinction events in the record, or such controversial issues as the causes of particular events or the number of taxa killed.

In this paper we present a mathematical treatment of the trends in the fossil record and show that they are not independent but are in fact closely related to one another. Starting with only a few very basic and uncontentionous observations about patterns of extinction and diversity, we derive quite strict limits on the way in the fossil record can behave. We show for instance that the origination rate for families must be equal to the extinction rate at all times to within about one family per million years—a similar result pertains for genera or any other taxonomic subdivision—and that although the average extinction rate declines during the Phanerozoic, there is a limit on how fast it can decline. These and other conclusions are derived in Section 3.

Table 1 lists the quantities which will appear in our discussion of extinction
and origination, along with some hypotheses about their behaviour based on fossil evidence.

(1) We denote by $x(t)$ and $y(t)$ the number of taxa becoming extinct and originating per unit time, respectively, as a function of time $t$. As mentioned above, it is widely believed that the extinction rate has declined on average during the Phanerozoic. This decline is clear in Figure 1, which shows the extinction rate for marine families, drawn from an updated version of the compilation of fossil data by Sepkoski (1992). It has been suggested that on average this decline takes the form $x(t) \sim 1/t$, provided the origin of time is suitably chosen (Newman and Eble 1998). For origination the case is less clear, but again it appears (Van Valen and Maiorana 1985, Sepkoski 1998) that the rate is falling off over time (see the inset to Figure 1).

(2) Frequently one measures the fractional (or percentage) extinction rate in the fossil record, which is the ratio of the number of taxa becoming extinct per unit time to the total number in existence. Another way of looking at this quantity is as the probability per unit time of the extinction of any one taxon. We denote this quantity $p(t)$. By studying its time-integrated value, Sibani et al. (1995) determined that $p(t)$ declines approximately according to a power law $p(t) \sim t^{-\alpha}$. The most recent data indicate that the integrated form grows roughly logarithmically in time (see the inset to Figure 2), and hence that $\alpha = 1$. The data are also compatible with slightly smaller values of $\alpha$ in the region of 0.8 or 0.9.

(3) The variable $D(t)$ represents the number of taxa alive at time $t$, the so-called “standing diversity”. Overall, it appears from the fossil record that this quantity has increased towards the recent. Benton (1995) has

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Table 1 The various quantities appearing in our theory.

| variable | meaning          | conjectured form | reference                  |
|----------|------------------|------------------|----------------------------|
| $x(t)$   | extinction rate  | $t^{-1}$         | Newman & Eble 1998         |
| $y(t)$   | origination rate | declines         | Van Valen & Maiorana 1985  |
| $p(t)$   | percent extinction | $t^{-1}$       | Sibani et al. 1995        |
| $D(t)$   | standing diversity | $\exp(t/t_D)$   | Benton 1995                |
| $w(t)$   | survivorship     | $\exp[-\tau/\tau_w(t)]$ | Van Valen 1973            |
| $R(\tau)$ | lifetime distribution | $\tau^{-\beta}$ | Sneppen et al. 1995       |
suggested that it does so exponentially $D(t) \sim \exp(t/t_D)$, although there is sufficient variation in the data that they can also be reasonably well fit by a linear form $D(t) \sim a + bt$. The diversity is shown in Figure 2 using data from the compilation by Sepkoski (1992) again.

(4) The variable $w_t(\tau)$ represents the “survivorship curve”—the probability that a taxon which was alive at time $t$ is still alive a time $\tau$ later. Van Valen (1973) suggested on the basis of fossil data analyses that this curve takes the form $w_t(\tau) \sim \exp[-\tau/\tau_w(t)]$ for genera or families within single orders or phyla. In other words, it falls off exponentially in $\tau$ with a rate constant $\tau_w$ which depends on $t$. ($\tau_w(t)$ is also equal to the mean taxon lifetime at time $t$.) This result is often referred to as Van Valen’s law. As Raup (1991) has shown, this result appears to be true also for larger groups. In the inset to Figure 3 we show the survivorship curve for all known genera of marine organisms which were alive 150 million years ago (Ma). As we can see it follows the predicted exponential form quite
Figure 2  Main figure: the number of known families of organisms as a function of time during the Phanerozoic. The dotted (curved) line is the best fit exponential and the dashed (straight) one is the best linear fit. Inset: the integrated percentage extinction of families. Data from Sepkoski (1992).

closely. Van Valen’s law has gained theoretical support from a model of extinction advanced by Raup (1978) and by Baumiller (1993). This model is based on a simple time-homogeneous birth/death process for the species within a genus and contains two parameters $\lambda$ and $\mu$, which measure the rates at which species appear and disappear. In the case where $\lambda \ll \mu$, the survivorship curve takes the form postulated by Van Valen. On the other hand if $\lambda \simeq \mu$ then the survivorship curve takes the form $w_t(\tau) \sim 1/(1 + \lambda \tau)$.

The variable $R(\tau)$ denotes the probability distribution of species lifetimes $\tau$ averaged over the entire fossil record. It has been suggested (Sneppen et al. 1995) that this distribution has a power-law form $R(\tau) \sim \tau^{-\beta}$, with an exponent $\beta$ somewhere in the range from $\frac{3}{2}$ to 2, although the data are probably just as well fit by an exponential (see Figure 3).
Figure 3  Main figure: Histogram of the lifetimes of marine genera during the Phanerozoic. The solid line is the best power-law fit to the points between 10 and 100 My. The dotted line is the best exponential fit to all the points. Inset: the number of genera of marine organisms surviving out of an initial group of 740, over a period of 150 My up to the present. The dotted line is the best fit exponential. Data from Sepkoski (1992).

We should emphasize that we are not making any statement here about the causes of the trends described above. The mathematical developments of the following sections are equally valid whether the trends are the result of biological effects such as true extinction or pseudoextinction or are artifacts of things like taxon sorting, preservational bias or taxonomic classification (Raup and Sepkoski 1982, Flessa and Jablonski 1985, Pease 1992, Gilinsky 1994). Our theory makes statements only about the appearance and disappearance of taxa in the fossil record, and not about causes.

In this paper we present an analysis of the relationships between the quantities in Table 1, and discuss the implications of the conjectures listed in the third column. Our theory makes only two quite simple assumptions.
(1) We assume that on average the extinction rate is not increasing and that standing diversity is not decreasing. These results seem to be widely accepted in the palaeontological community and are well supported by fossil data.

(2) We assume that all species ultimately become extinct. Empirically, this seems to be a reasonable assumption. The mean lifetime of a species in the fossil record is in the range from 4 to 11 My (Valentine 1970, Raup 1991), and there are no known examples of species which have lived longer than 100 My.

The outline of this paper is as follows. In Section 2 we derive a number of relations between the quantities defined in Table 1 and specify under what conditions these relations should hold. In Section 3 we apply our theory to the empirical trends noted above, and explain the implications of our analysis for fossil extinction and origination. In Section 4 we give our conclusions.

2 Theoretical framework

Consider then a record of the origination and extinction of a large number of taxa spanning a time interval from an earliest time $t_0$ to a latest time $t_1$. If our time interval is the entire Phanerozoic, for instance, then $t_0 \approx 545$ Ma and $t_1$ is the present. We will write our theory in terms of general “taxa”. Exactly the same relations between quantities apply whether these taxa are species, or some proxy for species, such as genera or families, or still higher taxonomic groups such as classes or orders.

2.1 Standing diversity and extinction probability

Given a time-varying taxon extinction rate $x(t)$ and origination rate $y(t)$, as defined in Section 1, the standing diversity of taxa $D(t)$ is simply the difference between the integrated number of originations since the start of our time interval, and the integrated number of extinctions. In other words

$$D(t) = \int_{t_0}^{t} [y(t') - x(t')] \, dt'.$$  \hspace{1cm} (1)
And the fractional (or percentage) extinction per unit time \( p(t) \) is the ratio of the rate of extinction to the number of extant species:

\[
p(t) = \frac{x(t)}{D(t)},
\]

(2)

As we mentioned, \( p(t) \) may also be regarded as the probability per unit time of the extinction of any one species. Assumption (1) from Section 1 implies that \( p(t) \) must be a constant or decreasing function of time.

### 2.2 Survivorship curve

The survivorship curve \( w_t(\tau) \) is related to \( p(t) \) by the differential equation

\[
\frac{dw_t}{d\tau} = -p(t + \tau)w_t(\tau),
\]

(3)

with the initial condition \( w_t(0) = 1 \) for all values of \( t \). Essentially, this equation says that out of a given initial group of taxa, the number becoming extinct in any small interval of time is equal to the number still alive multiplied by the probability of any one of them becoming extinct in that interval. The solution of this equation is

\[
w_t(\tau) = \exp \left[ -\int_{t}^{t+\tau} p(t') \, dt' \right].
\]

(4)

Now our second assumption from Section 1 comes into play. In order that all species ultimately die, we require that \( w_t(\tau) \to 0 \) as \( \tau \to \infty \), which is only possible if the integral in Equation (4) diverges in the same limit. The fastest-decaying functional form for \( p(t) \) which gives a divergent integral is \( p(t) \sim 1/(t \log t) \). We can however eliminate the factor of \( \log t \) from this expression by appealing to only the grossest features of the fossil record, because if \( p(t) \sim 1/(t \log t) \), then Equation (4) implies that

\[
w_t(\tau) = \frac{\log t}{\log(t + \tau)}.
\]

(5)

\[\footnote{In fact, we can include a succession of factors of the form \( \log \log t \), \( \log \log \log t \) and so on in the denominator of the function and still get a divergent integral. However, these are very slowly varying terms and, since the available fossil data span less than two decades in \( t \), it is safe to ignore such possibilities.} \]
This is a very slowly decaying function of $\tau$, and not remotely similar to the approximately exponential survivorship curves seen in the fossil record. It is therefore fairly safe to say that $p(t)$ should decay no faster than $1/t$. Coupled with the results of Section 2.1 this means that $p(t)$ must lie somewhere between being constant in time and falling off as $1/t$. This in turn implies that the extinction rate $x(t)$ also lies between the same limits, and that the diversity $D(t)$ lies somewhere between being constant in time and growing as $t$. These are fairly stringent constraints on these quantities, and allow us to rule out many possible functional forms.

The origin of time $t = 0$ in these expressions is not fixed by the analysis, and may be varied in any way we desire to fit the fossil data, with the qualification that it must fall before the earliest time $t_0$ for which data are available.

Our limits on the form of $p(t)$ also place limits on the survivorship curve. The fastest decreasing form of $w(t)(\tau)$ corresponds to the case of $p(t)$ constant in time. In that case, we find that

$$w(t)(\tau) = \exp\left[-\frac{\tau}{\tau_w}\right],$$

(6)

with a constant mean taxon lifetime $\tau_w = 1/p(0)$, where $p(0)$ is the constant value of the extinction probability. This form however seems unlikely as far as the Phanerozoic fossil record is concerned, since a constant value of $p(t)$, although compatible with our theory, would imply that both the extinction rate $x(t)$ and the diversity $D(t)$ are also constant (see Equation (1)), which is not in very good agreement with the data. In fact, as Figure 2 shows, the best available data indicate that $p(t)$ is quite close to its lower limiting form

$$p(t) = \frac{C}{t},$$

(7)

for some constant $C$. This form corresponds to the slowest decaying form for the survivorship curve:

$$w(t)(\tau) = \left(\frac{t}{t + \tau}\right)^C.$$  

(8)

Interestingly, for $C = 1$, this is similar to the form postulated by Baumiller (1993) which we mentioned in Section 1, although it arises here through a completely different mechanism.
2.3 Origination rate

In order that the diversity $D(t)$ be a constant or increasing function of time, we require that the integrand in Equation (1) be non-negative. This in turn implies that the origination rate $y(t)$ must always be greater than or equal to the extinction rate $x(t)$. On the other hand, since, as we showed in the last section, the diversity can increase no faster than linearly in time $t$, the integrand must also be a constant or decreasing function of time. This implies that $y(t)$ must always be less than $x(t)$ plus some constant. In other words, the origination rate is constrained to lie in the range

$$x(t) \leq y(t) \leq x(t) + \epsilon,$$

where the constant $\epsilon$ is given by

$$\epsilon = y(t_0) - x(t_0).$$

If $\epsilon$ is very large compared with the typical values of $x(t)$ over our data set then this is not a very severe constraint on the origination rate, and $y(t)$ can still vary in almost any way it pleases. However, as we will show in Section 3 when we come to examine the fossil data in more detail, this is not the case. In fact the value of $\epsilon$ is quite small by comparison with $x(t)$ which means that the origination is obliged to follow the extinction rate closely.

2.4 Lifetime distribution

Finally, let $r_t(\tau)$ be the probability density that a species present at time $t$ lives on for an additional time $\tau$ and then dies. We have

$$r_t(\tau) = -\frac{dw_t}{d\tau} = w_t(\tau)p(t + \tau).$$

The lifetime distribution, averaged over our entire time interval, is then given by

$$R(\tau) = \frac{\int_{t_0}^{t_1-\tau} r_{t'}(\tau)y(t') \, dt'}{\int_{t_0}^{t_1-\tau} y(t') \, dt'}.$$
Since one usually has \( \tau \ll t_1 \), the \( \tau \)-dependence of the upper limit of the integrals can be safely ignored.

3 Implications for fossil data

In Section 1 we discussed a number of different conjectures which have been put forward about extinction and origination in the fossil record. We now consider the implications of each of these conjectures within the theoretical framework presented above.

3.1 Form of the decrease in the extinction probability

Sibani et al. (1995) have conjectured on the basis of fossil data that the extinction probability \( p(t) \) per unit time decreases according to a power law \( p(t) \sim t^{-\alpha} \) with \( 0 \leq \alpha \leq 1 \). As discussed in Section 1, our best estimate of the exponent \( \alpha \) is around 1 or a little less. This result is in good agreement with our theory.

3.2 Form of the decrease in extinction rate

Newman and Eble (1998) have conjectured that the extinction rate \( x(t) \) is also falling off with time as \( x(t) \sim 1/t \). This result is compatible with Equations (2) and (7), although it represents the extreme case in which diversity is not increasing. It may be that the actual extinction rate decreases more slowly than this, allowing diversity to increase as well.

3.3 Form of the origination rate

The inequality (9) places limits on the values that the origination rate can take, forcing it to follow the values of the extinction rate, within a margin set by the constant \( \epsilon \). The value of this constant is given by Equation (10), but is rather hard to calculate since the average extinction and origination rates \( x(t_0) \) and \( y(t_0) \) at the beginning of the data set are poorly defined. A better way to estimate \( \epsilon \) is to note that it is also equal to the slope of the diversity curve as a function of time (Figure 2) at the point \( t = t_0 \). In the case of the
marine families in the Sepkoski database, for example, this gives a value of $\epsilon = 1.4 \pm 0.1$ families per My. The average extinction rate for the same data set is 6.1 families per My. Thus, the origination rate must follow the extinction rate quite closely at all times and can on average exceed the extinction rate by at most about 25%. This in turn implies that if the extinction rate is falling off over time (as it appears to be) then the origination rate must, at least on average, fall off as well, and by a similar amount and in a similar fashion. The results are even more pronounced in the case of genera, where $\epsilon = 3.7 \pm 0.4$ genera per My while the mean extinction rate is 52.3 genera per My.

3.4 Form of the increase in diversity

Benton (1995) has suggested that the standing diversity $D(t)$ increases exponentially with time. This is clearly at odds with our result that $D(t)$ can at most increase linearly in time. However, as Figure 2 shows, the data on diversity are sufficiently poor as to be compatible with a linear fit to within the available accuracy.

3.5 Form of the survivorship curve

Van Valen (1973) suggested that survivorship curves follow an exponential decay law $w_t(\tau) \sim \exp[-\tau/t_w(t)]$ within individual orders or phyla and, as we showed in Section 1, a similar form seems to hold for survivorship curves for larger groups of taxa as well. The results of Section 2.2 show that the survivorship curve can take precisely this form, with a constant mean taxon lifetime $t_w$, if the percentage extinction rate $p(t)$ is a constant in time. However, as we pointed out, the fossil data indicate that $p(t)$ is not constant in time, but rather is close to its lower limiting form of $p(t) = C/t$ (Equation (7)). This gives the form (8) for the survivorship curve, rather than the exponential form postulated by Van Valen. This discrepancy is less serious than it may appear to be, however. Van Valen postulated his law on the basis of a large number of plots of survivorship curves similar to Figure 3, which appear straight on semi-logarithmic scales. If we take the logarithm of Equation (8), we find that

$$\log w_t(\tau) = -C \log(1 + \tau/t) \simeq -C \frac{\tau}{t}, \quad (13)$$

when $\tau \ll t$. If the typical lifetimes $\tau$ of species are significantly less than $t_0$, which will always be the case provided the origin of time is well before the
beginning of our data set $t_0$, then this inequality is always satisfied and we will indeed see survivorship curves which appear as straight lines on a semi-logarithmic plot. Thus, Van Valen’s law appears to be compatible with our theory.

Equation (13) implies that the mean lifetime $\tau_w(t)$ which appears in Van Valen’s law should increase according to

$$\tau_w(t) = \frac{t}{C}. \quad (14)$$

Although this particular form has not to our knowledge been conjectured previously, there is evidence that lifetimes increase, on average, during the Phanerozoic. Raup (1988) for instance has analysed the survivorship curves of groups of fossil marine genera drawn from the Sepkoski database and shown that mean lifetimes approximately double from the Cambrian to the Recent.

3.6 Form of the lifetime distribution

As discussed in Section 1, the lifetimes of taxa in the fossil record have a highly left-skewed distribution which, as Sneppen et al. (1995) have suggested, may be a power law with an exponent $\beta$ in the range from $\frac{3}{2}$ to 2. The data are also compatible with forms which decrease faster than a power law. We now show that both of these hypotheses are compatible with the current theoretical framework, depending on whether the typical values of $t$ are larger or smaller than the typical taxon lifetimes.

The overall distribution of taxon lifetimes is given by Equation (12). If we assume the form (7) for $p(t)$, which seems to be implied by our theory and the fossil data, then $w(t,\tau)$ takes the form of Equation (8) and $R(\tau)$ is

$$R(\tau) \sim \int_{t_0}^{t_1} y(t) \left( \frac{t}{t + \tau} \right)^C \frac{1}{t + \tau} \, dt, \quad (15)$$

where we have neglected the normalizing factor in the denominator of Equation (12) and the $\tau$-dependence of the upper limit of the integral. If $y(t)$ decays sufficiently fast and $\tau \gg t$ in the region where $y(t)$ is significantly greater than
zero, then this expression becomes

$$R(\tau) \sim \tau^{-(C+1)} \int_{t_0}^{t_1} y(t)t^{C+1} \, dt. \quad (16)$$

The constant $C$ must be greater than zero, but can otherwise take any value we please, and hence $R(\tau)$ varies as $\tau^{-\beta}$ with an exponent $\beta > 1$. The assumption $\tau \gg t$ is not a realistic one however. In Section 3.2 we made the opposite and much more plausible assumption that $\tau \ll t$ for all values of $t$. In this case Equation (15) becomes

$$R(\tau) \sim \int_{t_0}^{t_1} y(t)\left[1 - (C + 1)\frac{\tau}{t}\right] \, dt = A - B\tau, \quad (17)$$

where $A$ and $B$ are positive constants whose exact value depends on the form of $y(t)$. On the logarithmic scales of Figure 3, this distribution is a highly convex function—the fossil lifetime distribution is less convex than this. For the case where $\tau$ is neither very much less than nor very much greater than $t$, the distribution of lifetimes can be expected to lie somewhere in between the two extremes derived here. We have confirmed this expectation by numerical integration of Equation (15) for a variety of different choices of $y(t)$. Our best guess is that the fossil data lie somewhere in this intermediate regime. This in turn implies that the correct origin of time for our theory is earlier than the beginning of the Phanerozoic, but not enormously so.

4 Conclusions

Many authors have noted that, although the fossil record shows evidence of events such as mass extinctions which are surely the result of unique and specific causes, there also appear to be clear trends in the pattern of origination and extinction. Examples are the apparent decrease in the rate of extinction and increase in the standing diversity over time. Also survivorship curves and the distribution of the lifetimes of taxa seem to follow quite well-defined forms. Several attempts have been made to explain these results, many based on detailed assumptions about possible evolutionary or ecological mechanisms underlying the processes of extinction and origination. In this paper we have taken the opposite approach and explored instead the simplest possible theoretical framework. We have shown that, by making only two basic assumptions
about the fossil extinction record, it is possible to place quite stringent limits on the way in which extinction and origination can take place. Our principal results are as follows.

(1) The fractional (or percentage) extinction rate at should decline over time at all taxonomic levels, but it cannot decline faster than $1/t$. This prediction is in good agreement with fossil record, which shows a decline close to this limiting form, within the statistical errors on the data.

(2) The total extinction rate also can decline no faster than $1/t$, and empirically it too appears to be close to this limiting form.

(3) The total origination rate must follow the extinction rate closely. For families, for example, the two can differ by no more than about 1 family per My.

(4) Survivorship curves should fall off with taxon lifetime $\tau$ at least as fast as a power of $t/(t + \tau)$ and at most exponentially. This result also is in good agreement with fossil data, and in particular with the empirical result known as Van Valen’s law.

(5) The diversity of taxa can increase at most linearly in time. This is at odds with the conjecture of Benton (1995) which states that diversity increases exponentially. However, the data for diversity are sufficiently noise-ridden that a linear fit is perfectly acceptable.

(6) The distribution of lifetimes of taxa must fall off as a power-law or faster. This too appears to be consistent with fossil data, although the data in this case are rather poor.

Our theory leaves many things unexplained. Although we have been able to place limits on the way in which various quantities may vary in time, we have not been able to pin any of them down completely. Furthermore, we have offered no explanation of the assumptions of our theory, that extinction declines on average, diversity increases, and no species lives forever. These issues cannot be resolved solely by mathematical analysis of the kind presented here. Only by exploiting real biological and palaeontological insight can we hope to find a solution to these long-standing problems.

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