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Five palaeobiological laws needed to understand the evolution of the living biota

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The foundations of several disciplines can be expressed as simple quantitative laws, for example, Newton's laws or the laws of thermodynamics. Here I present five laws derived from fossil data that describe the relationships among species extinction and longevity, species richness, origination rates, extinction rates and diversification. These statements of our palaeobiological knowledge constitute a dimension largely hidden from view when studying the living biota, which are nonetheless crucial to the study of evolution and ecology even for groups with poor or non-existent fossil records. These laws encapsulate: the critical fact of extinction; that species are typically geologically short-lived, and thus that the number of extinct species typically dwarfs the number of living species; that extinction and origination rates typically have similar magnitudes; and, that significant extinction makes it difficult to infer much about a clade's early history or its current diversity dynamics from the living biota alone. Although important strides are being made to integrate these core palaeontological findings into our analysis of the living biota, this knowledge needs to be incorporated more widely if we are to understand their evolutionary dynamics.

One of the cornerstones of evolutionary theory is the idea of differential survival. The fact of death, the termination of the lives of individuals, is central to evolutionary change. For biologists working on the timescales of generations, the importance of differential survival has been well understood and well studied since Darwin. On longer timescales, however, although it is well recognized that there has been extensive termination of unique morphologies and lineages, study of the living biota alone offers relatively little when trying to determine the importance of these extinctions, given that among the living we only have direct data on the survivors. This presents significant challenges when trying to elucidate the evolutionary process that produced the living biota.

Fortunately, the fossil record provides unique and invaluable data on the nature of extinction, including its selectivity, recurrence times, magnitudes and causes. While there has been a dramatic increase in the number of integrated palaeontological and neontological studies^{1–4}, from a palaeobiological perspective, the field of biology has not yet fully assimilated the fundamental findings from the fossil record. Here I summarize these findings in the context of their relevance to our understanding of the living biota. I express this knowledge in the form of simple laws (Box 1), in the hope of facilitating the incorporation of the longstanding and fundamental discoveries of palaeontology into the foundations of thinking in evolutionary biology and ecology, something that has yet to be fully realized.

The first law of palaeobiology

Lineages become extinct. While the notion of immortality at the level of individuals has been rejected for millennia, it was not until around 1800 that the idea that species could become extinct was established through the discovery of fossils that could not be ascribed to any living species⁵. More formally, the first law can be expressed in terms of the probability that clade will ultimately go extinct, P_e :

$$P_e = 1, \text{ when } \lambda \leq \mu \quad (1)$$

$$P_e = (\mu/\lambda), \text{ when } \lambda > \mu \quad (2)$$

where λ and μ are the per taxon origination and extinction rates respectively, the expected number of origination or extinction events per lineage per unit time (see refs^{6,7}). Equation (2) assumes the clade began with one species. The first law indicates that lineages always have a non-zero probability of ultimately becoming extinct.

The second law of palaeobiology

The average species longevity is the reciprocal of the extinction rate. More formally, if the rate of extinction is constant with time and independent of species age, then the species durations are distributed exponentially and the mean species longevity (t_{mean}) is the reciprocal of the per taxon extinction rate (μ)⁷:

$$t_{\text{mean}} = 1/\mu \quad (3)$$

and the median longevity (t_{median}) is given by⁷:

$$t_{\text{median}} = \ln(2)/\mu = 0.693/\mu \quad (4)$$

Note that equation (1) forms the basis of Van Valen's law^{8,9}. Raup⁷ provided a broader range of equations relevant to cladogenic processes beyond equations (1)–(4), drawing on the statistical work of Kendall¹⁰ and Bailey⁶.

Application of the second law. The average taxon longevity can be used to estimate the number of extinctions that a clade has experienced during its history, even though the fossil record is incomplete. A particularly well studied group is the North American (north of Mexico) mammals, with a rich fossil record of at least 3,000 described fossil morphospecies^{11,12} compared with 350 living species (excluding marine and introduced species¹³). It has also been analysed with unusually high temporal resolution¹² (~1 million years, Myr). Cohort survivorship analysis reveals a remarkably constant rate of extinction throughout the Cenozoic^{11,14}, excluding the largely human-driven megafaunal extinctions of the late Quaternary. The extinction rate averaged over the entire group is 0.43 extinctions per lineage per Myr, determined by dynamic

Box 1 | Five palaeobiological laws needed to understand the evolution of the living biota and the reasons for their significance.

First law: lineages become extinct. The extinction of lineages, like the death of individuals, is an integral part of the evolutionary process, even though extinct lineages are hidden from view when only analysing living species.

Second law: species longevity = 1/extinction rate. (1) Species are geologically short-lived. (2) Thus, the living biota represents only a tiny subsample of all species that have existed (for example, the living mammal species represent ~4% of all post-Cretaceous mammal species).

Third law: the average origination rate \approx the average extinction rate. (1) Except perhaps for the youngest evolutionary radiations, molecular phylogenetic analyses that yield zero or low extinction rates compared with origination rates are almost certainly wrong. (2) Origination rates derived from molecular phylogenies are typically much too low, as they fail to take into account the origin of

extinct species. (3) Rates of origination and extinction measured in the fossil record are typically high.

Fourth law: species richness results from time varying origination and extinction rates. Evolutionary models, whether used directly or as priors, that treat evolution as a pure birth (Yule) process, or as one with fixed origination and extinction rates should be avoided if possible, unless it is demonstrated that their use does not lead to biased results.

Fifth law: extinction erases a clade's history. (1) Ancestral character states observed in the fossil record are sometimes completely unanticipated given the living biota. (2) Diversity trajectories (for example, LTT plots) derived from molecular phylogenies often bear little resemblance to diversity trajectories seen in the fossil record—they are of little use when trying to infer the history of a group.

survivorship analysis¹¹ after correcting for the incompleteness of the fossil record¹⁴. This translates into a mean longevity of 2.3 Myr (equation (1)) and a median longevity of 1.6 Myr (equation (2)). Thus, every 1.6 Myr about half the standing diversity became extinct. This is short compared with the duration of the Cenozoic, ~66 Myr, some 41 median longevities in duration, the timespan over which most major eutherian mammal groups have existed^{15,16}.

Implication of the second law: there is a vast number of extinct species. Assuming a similar average longevity for all mammals, the mean longevity of the North American species can be used to estimate the number of mammal species that have existed globally since the extinction of the non-avian dinosaurs, 66 Myr ago. Today, there are slightly fewer than 5,500 described living mammal species. If we assume the group dates back to ~66 Myr ago¹⁵, and that they diversified logistically to a carrying capacity of 5,500 (recognizing that the trajectories of individual subclades are typically not logistic), then there have been a staggering ~157,000 mammal species since the extinction of the dinosaurs (see Methods). If instead one assumes the rates of origination and extinction were equal and stochastically constant (that is, not diversity dependent), and that it took about a species duration (~2 Myr) to first reach 5,500 species after the end-Cretaceous mass extinction (see 'Caveat'), then the estimated total number of mammal species generated in the past 64 Myr is almost the same, 156,860 species (see Methods).

Thus, the living species represent only some 4% of all Cenozoic mammalian morphospecies that have ever lived—for every living mammal species there are ~27 extinct species. In fact, this is probably an underestimate because: (1) the peak species richness in the Cenozoic may well have been higher than today's richness, based on their Cenozoic diversity trajectory¹²; (2) it appears that the biome today that has the highest species richness (that is, the tropical moist forests¹⁷) has shrunk considerably in the past dozen Myr¹⁸, which further supports the idea that the diversity of mammals may have been higher in the early to mid Miocene¹² (15–23 Myr ago) than today.

Note that the short mean species longevity for North American mammals is not exceptional. For example, among the few groups where mean species durations have been estimated, largely marine invertebrates, late-Palaeozoic crinoids (echinoderms) (1.38–2.72 Myr depending on the clade and time interval analysed¹⁹), and extinct graptoloids (hemichordates) (0.65–1 Myr)²⁰ have similar durations. However, other groups have longer species lifetimes, for example, the extinct blastoids (echinoderms) (5.1 Myr)²¹, and

among protists, planktic foraminifera (5–10 Myr, depending on their morphology)²². There are relatively few data available for plants at the species level (although there are now excellent data at the genus level²³). However, older estimates for species of angiosperms²⁴ are relatively fast (~3 Myr) compared with Coniferales (just over 5 Myr), pteridophytes (~12 Myr), and cycads (~15 Myr). Note that the difficulty in developing reliable palaeontological taxonomies at the species level, given incomplete morphological preservation, has meant that there are more data on longevities and extinction rates at the genus level than at the species level.

The third law of palaeobiology

The average extinction rate approximately equals the average origination rate. If λ_{average} and μ_{average} are the per taxon origination and extinction rates averaged over the history of the clade then typically:

$$\lambda_{\text{average}} \approx \mu_{\text{average}} \quad (5)$$

If the clade is extinct, then $\lambda_{\text{average}} = \mu_{\text{average}}$, which can be formally demonstrated using the fourth law (see below). For clades that are still diversifying $\lambda_{\text{instantaneous}}$ will be greater than $\mu_{\text{instantaneous}}$, and when they are in decline $\lambda_{\text{instantaneous}}$ will be less than $\mu_{\text{instantaneous}}$. However, except perhaps for the earliest phases of rapid diversification, λ_{average} will nonetheless approximately equal μ_{average} over the history of clade.

Empirically, the third law has strong support from the fossil record, where it has long been noted that, even for living groups, measured long-term origination rates only slightly exceed long-term extinction rates, with the possibility that the true underlying rates might even be equal⁷.

There are at least two ways of understanding why this holds. The first is through Malthusian reasoning; unchecked exponential growth, when origination exceeds extinction, quickly runs afoul of limited resources, and so is unsustainable in the long term; that is, with limited resources the origination rate cannot exceed the extinction rate for very long, and even as new resources become available, exponential growth will quickly turn that new resource into a constraint on diversification, even if the resource pool is growing²⁵ (unless it is growing exponentially). Thus, as resource limitation is encountered, the instantaneous origination and extinction rates will quickly converge, leading to a convergence in the long-term averages. This is exactly analogous to birth and death rates for populations, where the average birth and death rates are approximately equal for most populations over extended periods of time.

The second way of understanding the third law is simply that when species durations are short compared with the longevity of a clade, there must be substantial extinction, and thus origination and extinction rates must be nearly equal. Analysis of the living mammals illustrates this. For this group the longevity of the clade is ~41 times the median longevity and for every living mammal there are some 27 extinct species (see ‘The second law of palaeobiology’). If mammal species richness has been more or less at equilibrium over the past 50 Myr, which seems to be the case¹², then the average origination and extinction rates must have been, and are observed to be¹², approximately equal over that time interval. Even if the current species richness of living mammals was the result of exponential growth, the high species turnover means that the origination rate would still have been similar in magnitude to the extinction rate; to generate 5,500 species over 66 Myr requires a net diversification rate of 0.13 ($\ln(5,500)/66$). Thus, with an extinction rate of 0.43 species per species per Myr (as described above), the origination rate would only have been 0.13 higher, at 0.56 species per species per Myr.

Note that the failure to take into account extinction compromises our ability to estimate origination rates; to estimate realistic origination rates one needs to take into account not just the living species, but also all those that have gone extinct²⁶. Thus, for the living eutherian mammals, if we believed the extinction rate was zero, then the inferred origination rate for the Yule process (that is, with no extinction) would be just 0.13 species per species per Myr. However, once species turnover is taken into account, assuming exponential growth, the origination rate is 4.3 times higher, at 0.56 species per species per Myr (see immediately above).

Relevance of the third law. The empirical observation of approximately equal origination and extinction rates from the fossil record is in stark contrast to over a decade now of reports of zero or low extinction rates for many clades, or subclades, derived from molecular phylogenies, even by methods that allow for time varying origination and extinction rates. A particular case in point is the analyses of the cetacean diversity dynamics. The fossil record is particularly good, with 54–59% of living genera found as fossils, and shows that over past ~12 Myr the average net genus diversification rate has been negative, with a higher average extinction rate than origination rate²⁶. However, the latest analysis of cetacean diversification rates derived from a molecular phylogeny shows a net positive rate over the same time period, with a rapid increase just when the fossil record shows the rate becoming negative²⁷. Furthermore, the extinction rate derived from the molecular phylogeny is much smaller than the origination rate, by almost an order of magnitude. Why such a profound discrepancy? It appears that about 12–15 Myr ago, as the world entered the long-term late Neogene cooling trend²⁸, the delphinids (dolphins and their relatives) began to radiate, which the molecular phylogeny picks up well, but at the expense of the much more diverse non-delphinid cetaceans, whose demise is largely invisible in the molecular phylogeny but clearly seen in the fossil record.

Having said this, an earlier analysis of the cetacean molecular phylogeny did recreate the diversity drop seen in the fossil record²⁹. However, that analysis yielded a zero extinction rate when applied to the entire phylogeny—diversity decline was only detected when the phylogeny was broken up into a series of monophyletic and paraphyletic groups, and even then the method returned zero extinction rate estimates for the monophyletic groups.

Nonetheless, some studies have led to inferences of roughly equal rates of origination and extinction, for example in the analysis of the Proteaceae³⁰, which offers hope for the ability to infer origination and extinction rates from the indirect temporal evidence captured in DNA sequence data. However, as the example of the cetaceans above indicates, it may be very difficult to ever know if these results will be accurate without a good fossil record.

Caveat. Having said this, on short timescales it is quite possible that clades in the early stages of evolutionary radiation may not have experienced much extinction. Thus, λ_{average} could be substantially larger than μ_{average} at the beginning of evolutionary radiations—but this has yet to be established. Note that in computer simulations of logistic diversification, the growth phase, when λ_{average} is significantly greater than μ_{average} , was found to be surprisingly short, in the order of just one mean species duration³¹. Thus it seems likely that the average extinction rate will typically converge on the average origination rate quite rapidly on geological/evolutionary timescales.

Conversely, for some living clades, the fossil record indicates that over the recent geologic past the average origination rate is lower than the average extinction rate, for example the cetaceans²⁶ and several terrestrial mammal groups including the elephantids, hyeanids, equids, camelids, rhinocerotids and antilocaprids³². The possibility that living clades have negative diversification rates, that is, that they have been in decline, over the past half dozen to dozen Myr (3–6 average mammal species durations) is seldom entertained in the absence of a fossil record, yet may be quite common. In support of this supposition, a new method that does require molecular phylogenies or the fossil record shows that many of the young endemic plant and animal clades on the Hawaiian islands are in evolutionary decline on all but the big island of Hawaii, despite their young age³³.

Recommendation. It is hard to overemphasize the importance of the third law—for most clades for most of their histories there has been almost as much extinction as origination. Thus, the preponderance of molecular analyses that yield zero extinction rates, or extinction rates that are a small fraction of the origination rate are almost certainly inaccurate, especially when one reflects on the fact that zero or low extinction translates into exponential growth, which is just as unlikely at the species level as it is at the population level. In light of the third law, we need to test the methods for deriving extinction rates from molecular phylogenies against rates measured in the fossil record, and continue developing methods that integrate molecular phylogenetic and fossil data in dating molecular phylogenies, such as the fossilized birth–death process³⁴ and total evidence dating³⁵, to provide better estimates of origination and extinction rates. Critically, we need to bear in mind the possibility that phylogenetic data from only living taxa might simply be insufficient to reliably infer past origination and extinction rates³⁶.

The fourth law of palaeobiology

Changes in species richness are driven by differences in origination and extinction rates that vary over time. More formally, the standing species richness, $S(t)$, at time t , assuming a single progenitor species, is given by:

$$S(t) = e^{[\lambda(t) - \mu(t)]dt} \quad (6)$$

where $\lambda(t)$ and $\mu(t)$ are the per species origination and extinction rates as a function of time (see ref. ¹⁰, equations 13 and 11). When the fossil record is good, it can be very informative in terms of providing data on how rates of origination, extinction and diversification vary as a function of time, and they are virtually never constant^{37–39}. Note that $\lambda(t)$ and $\mu(t)$ are instantaneous rates, whereas in the third law the origination and extinction rates are average rates.

Implications of the fourth law. Given the fourth law it is unsettling to see models of diversification, used directly or as priors in Bayesian analysis, where there is either no extinction term (that is, use of the Yule process), or when both ‘life’ and ‘death’ processes are included but where both are set at constant values. Importantly, the use of incorrectly formulated quantitative approaches can lead to misleading results. For example, substituting a constant birth (Yule process) prior with a constant birth–death prior in the calibrating of the divergence times of the living cycads leads to very different

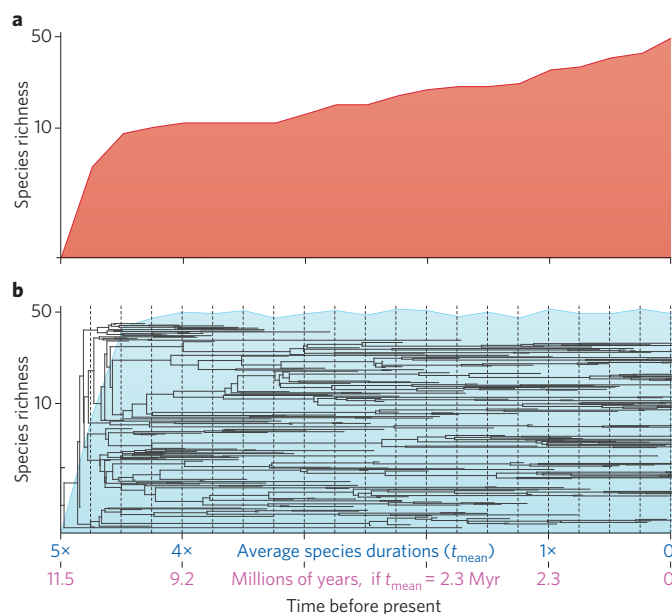


Figure 1 | The importance of taking into account extinction when making inferences from LTT plots. **a**, LTT plot for 49 hypothetical living species, which, after an initial burst of speciation, could be interpreted as showing constant, or even a slowly increasing rate of diversification towards the present (given the gently increasing slope with time). **b**, The LTT plot for the same clade once all the extinct taxa are added; the phylogeny used to make Fig. 1a was derived from a computer simulation of logistic growth (see Fig. 2 in ref. ³¹) with a fixed carrying capacity of 50 species—the underlying diversification rate was approximately zero for 80% of the history of the clade, despite the appearance of the constant, or even gently accelerating, rate of diversification when only the living species are analysed.

estimates of their divergence times⁴⁰. Note that without a fossil record, or some other independent way of testing inferred divergence times, it may be hard to know which prior gives the more accurate answer.

Fortunately, in the past few years there has been an increase in the development and use of methods that allow for time varying origination and extinction rates^{2,3}, but these methods still need more extensive testing with groups that have good fossil records to determine how well they are able to capture the trajectories and magnitudes of past origination and extinction rates. And as noted above, we also need to bear in mind the possibility that phylogenetic data from only living taxa might simply be insufficient to reliably infer past origination and extinction rates³⁶.

The fifth law of palaeobiology

Extinction erases a clade's history, making it difficult to infer ancestral character traits and its diversity dynamics from the living biota alone. One of the primary consequences of the ubiquity of extinction, and the fact that species are short lived (the first and second laws) is that most of the history of most clades has been erased. This makes it hard to determine ancestral character states without help from the fossil record^{1,41}. For example, in the absence of a fossil record we would not know that the first tetrapods were not fully terrestrial⁴², or that they had more than five digits per limb⁴³, that the first lungfish were marine^{41,44}, that fivefold symmetry is not ancestral for echinoderms⁴⁵, that many of the synapomorphies of living birds evolved before flight⁴⁶, nor could we have inferred the unexpected morphology of *Ardipithecus*, which lies close to the last common ancestor of humans and chimpanzees⁴⁷.

The difficulty in accurately determining ancestral character states is made particularly difficult when extinction is non-random

with respect to the trait being considered. Thus, for example, among caniform mammals (dogs, bears, weasels, raccoons, etc.) the ancestral body size seen directly in the fossil record is about an order of magnitude smaller than that inferred using the body sizes of the living species mapped onto a molecular phylogeny—there is evidence of directional selection towards increased body size in multiple caniform subclades, rendering inaccurate estimates of the ancestral body size in the absence of the fossil record¹.

The prevalence of extinction also makes it difficult to determine a clade's true diversity dynamics^{2,3,26}. For example, analysis of lineage through time (LTT) plots derived from molecular phylogenies are often used to conclude that living groups are in the midst of ongoing radiations, especially if they show steady or increasing rates of diversification (Fig. 1a), as has been hypothesized for birds⁴⁸ and cetaceans⁴⁹. However, there is a wide range of diversity trajectories, including long-term species loss⁵⁰, that can lead to very similar LTT plots^{26,31}, once the extinct species are removed. Thus, for example, the LTT plot shown in Fig. 1a was derived from a simulation of a logistic diversification process³¹; the true diversity trajectory is shown in Fig. 1b. While the LTT of the living taxa shows a positive and gently increasing diversification rate towards the present, the true diversity has been static for 80% of the clade's history, with the signature of logistic growth being erased in just 3 average species durations (data not shown)³¹. Moreover, the LTT plot significantly under-estimates the spectacular initial radiation of the clade. Thus, returning to the real world examples, the cetacean fossil record indicates the group as a whole has been in decline over the past dozen Myr²⁶ despite the apparent positive rate of diversification inferred from the molecular phylogeny^{27,49}. For birds the fossil record is not of sufficient quality to test the interpretation of the LTT plot, but given the wide range of underlying diversity dynamics that can yield LTT plots that look like the avian LTT plot²⁶, the conclusion that birds are still radiating is premature. In fact, given that forest biomes have decreased in area and productivity since the middle to late Cenozoic¹⁸ it is quite possible that the number of bird species has actually been in decline over that same period.

Finally, lack of appreciation of the extent to which the early history of a clade is erased by extinction has led some to infer that the absence of a change in slope in LTT plots associated with major events, such as mass extinctions, indicates that those events had no major impact on the clade. Thus, for example, the claim has been made that the end-Cretaceous mass extinction had little effect on the living mammal species, given the lack of perturbation in the mammal LTT plots across the Cretaceous/Palaeogene (K/Pg) boundary^{15,51}. However, for mammals, the fossil record clearly shows a burst of diversification and morphological innovation after the mass extinction^{51–53}, which laid the foundation for the subsequent Cenozoic radiation of mammals, even though these cannot be seen in molecular phylogenies.

Future prospects

We are seeing a much deeper appreciation for the magnitude of extinction, its role in shaping the living biota, and the development of tools for incorporating it into the analysis of molecular phylogenies^{2,3}. Nonetheless, the palaeontological insights encapsulated by the laws described above have not yet become part of the foundational thinking in evolutionary biology. We need better molecular phylogenetic tools, more comprehensive testing of these tools on groups with good fossil records, better methods for integrating palaeontological and neontological data^{1–3}, as well as better methods for using the fossil record to estimate origination and extinction rates^{54–57} if we are to understand the evolutionary dynamics of the living biota. For groups without a fossil record, we need to learn what statements can and cannot be made from the living species alone.

To ignore the central role of extinction in shaping modern biodiversity, even though it is hidden from view when we only analyse living species, is akin to ignoring the role of differential survival, that is, death, when trying to understand the evolutionary process.

Methods

Computing the number of mammal species since the K/Pg event. Two approaches were used to estimate the total number of Cenozoic mammal species. First, species richness was modelled by logistic growth with an equilibrium diversity of 5,500 species, an equilibrium extinction rate (and thus equilibrium origination rate) of 0.43 lineages per lineage Myr (see 'Application of the second law'), where the origination and extinction rates had the same strength of diversity dependence, with zero extinction at the inception of the crown group 66 Myr ago. Thus, the initial origination rate was twice the equilibrium value. The modelled diversification was repeated 10 times, starting with 1 progenitor species 66 Myr ago, with the density dependent origination and extinction rates updated every 0.1 Myr. The total number of species generated per simulation ranged from 147,200 to 161,644 with an average of 157,000 species.

The second approach assumed stochastically constant (that is, not diversity dependent) and equal rates of origination and extinction, with a beginning diversity (a) of 5,500 species 64 Myr ago, allowing 2 Myr (about an average species duration) for diversity to reach that 5,500 species from a single progenitor species. The total number of species generated is given by $a(1 + \lambda t)$ (see ref.¹⁰, equation in text immediately below eq. 48; and ref.⁷). Thus, the total mean estimated species number is $5,500(1 + 0.43 \times 64) = 156,860$.

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Competing interests

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