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Diversity dynamics: molecular phylogenies need the fossil record

Tiago B. Quental and Charles R. Marshall

Museum of Paleontology and Department of Integrative Biology, University of California at Berkeley, Berkeley, CA 94720, USA

Over the last two decades, new tools in the analysis of molecular phylogenies have enabled study of the diversification dynamics of living clades in the absence of information about extinct lineages. However, computer simulations and the fossil record show that the inability to access extinct lineages severely limits the inferences that can be drawn from molecular phylogenies. It appears that molecular phylogenies can tell us only when there have been changes in diversification rates, but are blind to the true diversity trajectories and rates of origination and extinction that have led to the species that are alive today. We need to embrace the fossil record if we want to fully understand the diversity dynamics of the living biota.

Molecular phylogenies and rates of diversification

Understanding the patterns and processes of diversification has long been of interest to paleontologists as we use the fossil record to document biodiversity change through time [1]. However, interest in diversity dynamics among biologists and the greater public has grown, particularly as we become aware of the impact of humans on the biosphere. Among biologists, the study of biodiversity dynamics was invigorated by the proposal that the rates and processes of diversification could be inferred from molecular phylogenies. This is particularly important given that many taxonomic groups have poor-to-non-existent fossil records [2]. In particular, the pioneering contributions of Nee et al. [3–5] and Harvey et al. [6] provided methods for detecting mass extinction events and for estimating speciation and extinction rates from molecular phylogenies despite the absence of the extinct species (but see [7] and [8]). This work was presaged by Thompson [9], and there were also parallel efforts by Hey [10] and Yang and Rannala [11]. In 2000, Pybus and Harvey [12] widened the scope of enquiry by shifting attention to the patterns and, through them, the processes of diversification. This line of research continues to be valued by biologists and new approaches continue to be developed [13,14]. In this contribution, we will discuss how our inferences about the pattern and processes of diversification change when we have direct access to extinct species.

Describing patterns and inferring processes from molecular phylogenies

To study patterns of diversification, Pybus and Harvey [12] introduced the γ statistic (Box 1). This is a simple tool for determining if a molecular phylogeny is consistent with a constant rate of diversification, or if there has been a decrease in the diversification rate (inferred when molecular phylogenies have significantly negative γ values). There is now a sizeable literature which indicates that many clades have decreasing diversification rates [12,15–17], in fact for about half of the 160 well-sampled phylogenies analyzed [15]. Considerable attention is now focused on exploring the implications of these findings for the evolutionary and ecological mechanisms responsible

Glossary

Boundary-crosser method: used to estimate the diversity at the boundary of adjacent geological time intervals by counting the number of taxa that must have crossed the boundary because they are known before and after it. This method has the desirable property of assuring the co-existence of taxa.
Chronogram: a phylogeny with branch lengths adjusted so that they are proportional to absolute time. Also known as a 'time tree'.
Crown group: a monophyletic clade that contains all extant members of the clade in addition to its last common ancestor and all of its descendants, both living and extinct.
Diversification rate: the rate of origination (speciation, λ) minus the rate of extinction (μ): ($\lambda - \mu$).
Diversity trajectory: a curve that portrays the number of species through time. It permits one to see if a given clade was diversifying or declining.
Equilibrium diversity: assuming diversity-dependent diversification, the expected number of taxa when the speciation and extinction rates are balanced, i.e. when the net diversification rate is zero.
Frequency ratio (FreqRat): statistical method used to measure the incompleteness of the fossil record by estimating the sampling probabilities per unit time (r) using the frequency of taxa that have stratigraphic ranges of one (f_1), two (f_2) or three (f_3) time intervals: $r = (f_2)^2/(f_1)(f_3)$.
γ statistic: a statistic that describes the center of mass for the nodes in a chronogram compared with the expected center of mass under a pure birth model. Nodes concentrated towards the base of a tree indicate a decrease in diversification rates, yielding negative γ values.
LiMe ratio: the ratio of the initial speciation rate (Lambda initial) and the extinction rate at equilibrium (Mu equilibrium). It assumes the existence of diversity equilibrium and, along with the size of the clade, and where the clade happens to be in its diversity trajectory, it plays a major part in determining the shape of the phylogeny.
Logistic growth: in the context of diversity dynamics describes the accumulation of species where the growth is initially exponential but as diversity accumulates the rate of species accumulation decreases, leading to a diversity plateau (the equilibrium diversity).
Net diversification rate: the average diversification rate needed to account for the diversity of a clade at any point in time. The actual diversification rates experienced by the clade might have been very different from this retrospective average rate.
Paleobiology Database: worldwide database of fossil collections. It provides taxonomic, geographic, stratigraphic, taphonomic, environmental, and collecting data, as well as providing analysis tools (http://paleodb.org).
Sampled in bin (SIB) method: method used to estimate diversity by counting the number of taxa within each geological time interval. Has the desirable property of being amenable to corrections of the incompleteness of the fossil record, but will typically overestimate the total diversity unless the time intervals are short with respect to the longevity of the taxa studied.
Stem group: Extinct taxa that lie phylogenetically between the last common ancestor of the living species of a clade (the crown group), and the nearest living relatives of that clade.

Corresponding author: Marshall, C.R. (crmarshall@berkeley.edu).

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Box 1. Detecting decreases in diversification rates

At the heart of most methods developed for extracting the diversity dynamics from molecular phylogenies is the conversion of the phylogeny to a chronogram (a time-calibrated phylogeny; see [36–38]) which can be visually represented by a Lineage Through Time (LTT) plot (Figure I). Once the chronogram has been constructed, a decrease in the net diversification rate can be assessed by determining if the nodes are concentrated deeper in the tree than expected by a pure birth process. This can be determined with the γ statistic [12], which measures how far the center of mass of the chronogram differs from the center of mass expected under a pure birth model. For a complete phylogeny (one where all the species have been included), the null hypothesis of a constant rate of diversification is rejected at a 5% level if γ is less than –1.645 [12]. This critical value must be adjusted if the sampling of the clade is incomplete [12]; incomplete sampling leads to more negative gamma values.

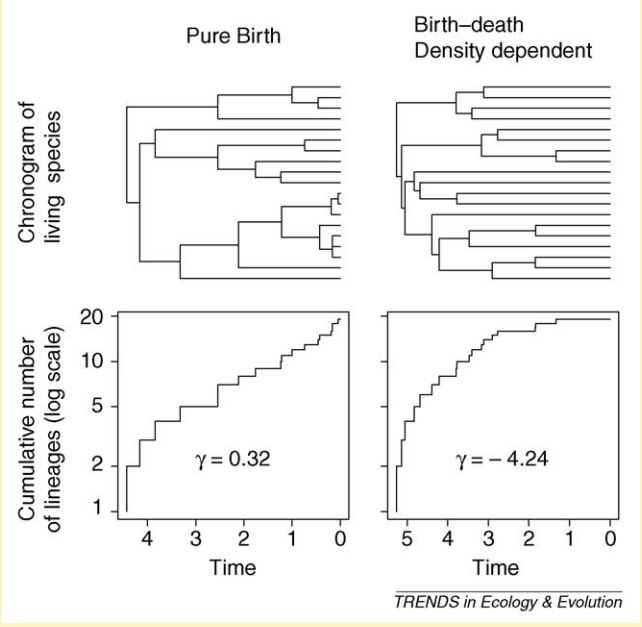

Figure I. Lineage through time (LTT) plots expected under different diversification models. The chronogram in the upper left was simulated using a pure birth model, whereas the one in the upper right was simulated with a diversity-dependent model of diversification in which speciation was diversity-dependent and extinction was constant. The corresponding LTT plots and their γ values are shown in the lower panels. The model of a constant rate of diversification is rejected for the diversification process shown in the upper right panel.

for the diversity of the living biota [2,15–21], although there is concern that methodological bias might account for some of the observed negative γ values [22,23].

Decreasing rates of diversification have been primarily modeled assuming diversity-dependent diversification (i.e. logistic growth) [16,17,21]. Under this framework, decreasing rates of diversification can be detected in a molecular phylogeny only if there is diversity-dependent speciation (Box 2 Figure Ia and c); diversity-dependent extinction (Box 2 Figure Ib) alone is insufficient to leave a signature of decreasing diversification on a phylogeny [17]. Initial modeling results suggested that extinction must also be zero to observe decreasing diversification rates in molecular phylogenies [17]. However, further computer simulations showed that the signal of

Box 2. Models of diversity-dependent diversification

Two fundamental models have been proposed to describe long-term diversity dynamics. The first class of models, the exponential models, suggest that diversity is not limited at all (e.g. [39],[40]) or, if it is, that the biosphere is so far from the equilibrium diversity that we can effectively ignore it. The second class of models (following McArthur and Wilson [41]) proposes the existence of a carrying capacity that caps the maximum diversity each portion of the biota can achieve [42–45], whereas variants of these models assess the impact of extinction on the extent to which the carrying capacity is realized [46]. At present, there is no consensus as to which model is best. At the heart of the logistic models is the notion of diversity-dependent diversification in which competition for limited resources retards diversification as species numbers increase. That is, species interactions have a negative feedback on diversification. Here we present three simple diversity-dependent models that have been used to simulate and describe the decrease in diversification rates seen in real clades.

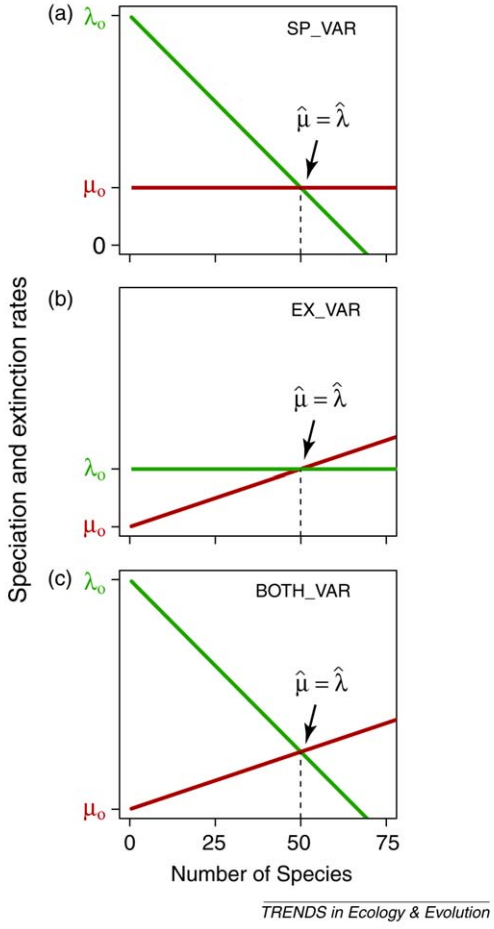

Figure I. Different models of diversity-dependent diversification. In the first model **(a)**, only the speciation rate decreases as a function of the number of species while the extinction rate is constant (SP_VAR). In the second model **(b)**, the speciation rate is constant but the extinction rate is diversity-dependent (EX_VAR). In the third model **(c)**, the speciation and extinction rates are diversity-dependent (BOTH_VAR). Initial speciation rate $= \lambda_o$; speciation rate at equilibrium $= \hat{\lambda}$; initial extinction rate $= \mu_o$; extinction rate at equilibrium $= \hat{\mu}$. Note that the diversification process enters a state of species turnover when the clade reaches the equilibrium diversity of 75 species. After this point, speciation and extinction rates are, on average, equal.

decreasing diversification rates can be preserved in molecular phylogenies if initial rates of speciation are high compared with the extinction rate (captured by the LiMe ratio) [21].

Can diversification dynamics be gleaned without fossils?

As pointed out by Ricklefs [2], a molecular phylogeny, by virtue of starting with the living biota, must show a pattern of increasing diversity with time regardless of the true diversity dynamics of the clade. This perceptual bias is reflected in the methods developed for inferring diversity dynamics from molecular phylogenies. These typically assume that the speciation rate is on average higher than, or occasionally equal to [10,19], the extinction rate. However, it is clear from the fossil record that this is often not the case. Paleontologically, our primary experience of biodiversity dynamics is one of the 'waxing and waning' of clades, with many clades showing complex diversity trajectories through time. Most clades (including many of the living clades) have had negative diversification rates at some point in their history.

The central question that must be answered is: do our views of the patterns and rates of diversification change when we have access to the extinct lineages? Here we argue that the answer is substantially 'yes'. If we cannot access the extinct lineages, we are blind to their extinction and the origination dynamics. Thus, not only do we lack data on the extinction dynamics of the clade, we also lack data on a portion of their origination dynamics. We support our conclusion with evidence drawn from computer simulations and the fossil record.

'Time-traveling' with computer simulation

As discussed above, if there is extinction, computer simulations show that diversity-dependent diversification can be detected in a molecular phylogeny only if the initial speciation rate is sufficiently high to ameliorate the erosive effect of the extinction. A metric that quantifies how high the initial speciation needs to be is the LiMe ratio (the ratio of the initial speciation rate to the equilibrium extinction rate) [21]. For example, if the speciation rate is linearly density-dependent and the extinction rate density-independent, then the LiMe ratio must be about $\geq$4 to give a 50% chance of seeing a decreasing rate of diversification in a molecular phylogeny using the γ statistic (with an equilibrium diversity of 100 species and when the computer simulations are stopped the first time the equilibrium diversity is reached [21]). When the computer simulations are re-run, keeping track of the γ statistic as the diversity-dependent diversification unfolds, we find that, even for large LiMe values (ones that should generate negative γ values), there is only a relatively narrow temporal window where one is likely to see a significantly negative γ value (Figure 1). At the initial phases of the radiation, the γ value is not yet significantly negative, reflecting the initial exponential phase of the radiation. Strikingly, after the radiation is complete, the γ value once again becomes non-negative but, rather than reflecting exponential growth, it reflects species turnover at a constant diversity [24]. The positive γ value seen in molecular phylogenies does not necessarily mean that the clades are diversifying [24–25].

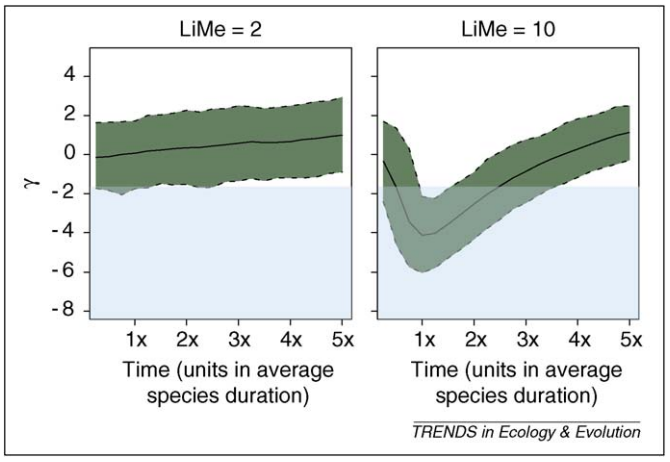

Figure 1. Expected behavior of the γ statistic, derived from computer simulations, as radiations with density-dependent diversification proceed. Each simulation assumed diversity-dependent speciation and constant extinction (Box 2), with an equilibrium diversity of 50 lineages. For each simulation, the γ values were calculated throughout the diversification process. Note that the time axis is measured in units of the expected species duration instead of absolute time. The solid line represents the average γ value for 1000 simulated trees and the dashed line the 95% confidence interval. The light-blue area represents γ values that significantly support a model of decreasing diversification rate (γ less than –1.645). When the LiMe ratio (the ratio of the initial speciation rate to the equilibrium extinction rate) is low (left panel), only seldom does the γ value indicate the decreasing diversification rate. When the LiMe ratio is high (right panel), the γ statistic only detects the decline in diversification for a short window of time that is (asymmetrically) centered about the time the clade first achieves the diversity equilibrium. Modified from Liow *et al.* [24].

Thus, a non-negative γ value might indicate: (i) true exponential growth (or even increasing rates of diversification); (ii) logistic growth in its earliest stages (which is effectively exponential); (iii) a wide range of diversity-dependent diversification processes; (iv) a clade that is maintaining a constant diversity and is simply experiencing species turnover (Table 1). With more imaginative computer simulations we may find additional scenarios that could lead to non-significantly negative γ values. We also note that for real molecular phylogenies (assuming that their dynamics were governed by diversity-dependent diversification), we do not have a simple way of determining where they are in their diversification trajectory (but see [21]). Interpreting the process of diversification for phylogenies with non-significantly negative γ values is fraught with difficulties.

Table 1. Range of diversity dynamics consistent with molecular phylogenies[a]

	γ less than –1.645	Ref	γ equal to or more than –1.645	Ref
Rate of diversification	Decreasing		Increasing; mildly decreasing; constant	
Possible diversity trajectories	1) Logistic growth	[17]	1) Exponential growth	
	2) Constant diversity through time with diversification pulse and heritable extinction within sub-clades	[19]	2) Early phases of logistic growth	[24]
			3) Logistic growth with a low LiMe ratio	[17,21]
			4) Species turnover at equilibrium diversity	[24]
	3) Declining diversity?	[current article]		

[a]We assume here that the γ value for a phylogeny reflects the true diversification of the clade, and is not an artifact of the inability to distinguish the most recently diverged species [23], or due to errors in the construction of the chronogram [22].

Is there too much evidence of diversity-dependent diversification?

The results from computer simulations described above suggest there are too many phylogenies that show decreasing rates of diversification for the process of density dependence to be ubiquitous. This counter-intuitive conclusion is readily explained. If diversity-dependent diversification was the rule for all clades, and if extinction is pervasive (as suggested by the fossil record), we would expect to see evidence of density dependence only in the subset of clades that had large LiMe values (i.e. that had high initial speciation rates compared with their extinction rates), and only for the subset of those that also happen to be close to the time they first reached (or will reach) their equilibrium diversity. The fact that about half of all phylogenies tested show significantly negative γ values suggests one of two things: (i) we are in an unusual time where most clades have high LiMe values and also happen to be relatively close to the time of first reaching their equilibrium diversity, or (ii) another diversification process is (also) operating (Table 1). However, it is also possible that the decelerating diversification rates (and hence the negative γ values) are simply the result of our inability to detect splitting events toward the present [23] or our inability to appropriately construct chronograms [22].

Do decreasing rates of diversification indicate clades in decline?

Pybus and Harvey [12] recognized that a failure to sample all the species in a clade will result in more negative γ values than would otherwise be measured. To date, the literature has considered under-sampling only in the context of species that we know are extant, but that we have failed to sample. However, if several taxa have recently become extinct, there is also a failure to sample a subset of taxa. In this case there is no remedy for the under-sampling; the missing taxa are beyond reach. Thus, even though negative γ values might reflect diversity-dependent diversification, they can also be achieved if a clade is in significant decline, regardless of how the clade reached its peak diversity. However, as discussed above, the methods for analyzing molecular phylogenies [3–5] do not permit clades to have negative diversification rates even though the fossil record repeatedly shows clades in decline [26]. In fact, at most times in the geologic past (except for example after mass extinctions) about half the extant clades are diversifying, while the other half are in decline. Thus, another potential explanation for the approximately equal proportions of phylogenies we see with significantly negative γ values is that about half the living clades have negative diversification rates, i.e. half are in decline. If this is true, in the absence of the fossil record we will be unable to determine if the initial diversification is logistic. Inferring the process of diversification from molecular phylogenies with negative γ values is also fraught with difficulties.

Accessing the past through the fossil record

Computer simulation shows that there are many ways to generate similarly shaped phylogenies. At present, the only reliable way to discriminate among the various possibilities is to directly access the past, i.e. through the fossil record. To illustrate the power of using the fossil record to discriminate between various diversification scenarios, we consider just one example: the diversification of the Cetacea. The rich and well-understood fossil record of the Cetacea shows a very different diversity trajectory and indicates very different origination and extinction rates than those inferred from the molecular phylogeny.

Cetacean diversity dynamics: the molecular phylogenetic perspective

Analysis of molecular phylogenetic data for 87 of the 89 currently recognized species of the Cetacea indicates a non-significantly negative γ value [27] (Figure 2a), and numerical analysis of the phylogeny suggests the clade has undergone three specific increases in diversification rate. Thus, the molecular phylogeny suggests exponential growth. Ignoring human impacts, this implies that, in terms of diversification, this is the best of all possible times to be a cetacean. Finally, numerical analysis of the molecular phylogeny indicates that the extinction rate for the group is zero, and that there was a lull in the rate of origination between the late Oligocene and the mid-Miocene [27].

Cetacean diversity dynamics: the paleontological perspective

The fossil record of cetaceans is relatively complete, has been recently re-evaluated [28–30], and is readily accessed through the Paleobiology Database. Nonetheless, the incomplete preservation typical of most fossils makes distinguishing closely related species difficult. For this reason, the analysis of the cetacean fossil record is based on fossil genera (as is commonly the case in paleontological studies) [31]. In the analysis below, we assume that there is no substantial difference in the way that the living and fossil cetacean genera are recognized and defined.

Analysis of the rich fossil record of the Cetacea provides a completely different picture of the diversity trajectory from the one inferred from the molecular phylogeny. First, even if we take the most conservative reading of the fossil record (using the boundary-crosser method) and assume that the fossil record has faithfully recorded the complete history of cetacean diversity, we find that the diversity of genera has remained approximately constant over the last ~12 million years. There is no evidence to support the molecular phylogeny-derived hypothesis of unbridled exponential increase (Figure 2b). In fact, at the mid-Miocene–late Miocene boundary, there were at least 49 genera present compared with the 41 living genera. If we assume that fossil genera had a similar average number of species as the living genera (at 2.2 species/genus), the fossil record indicates that, rather than experiencing exponential growth throughout their history, the Cetacea have (at best) only just maintained a steady diversity over the last ~12 million years (Figure 2b).

However, the fossil record is incomplete, so the true diversity of cetaceans in the past was probably much higher than that indicated by this literal reading of the fossil record. As an estimate of the incompleteness of the cetacean generic fossil record, we note that ~22–24 of the 41 living genera have a fossil record, i.e. the genus fossil

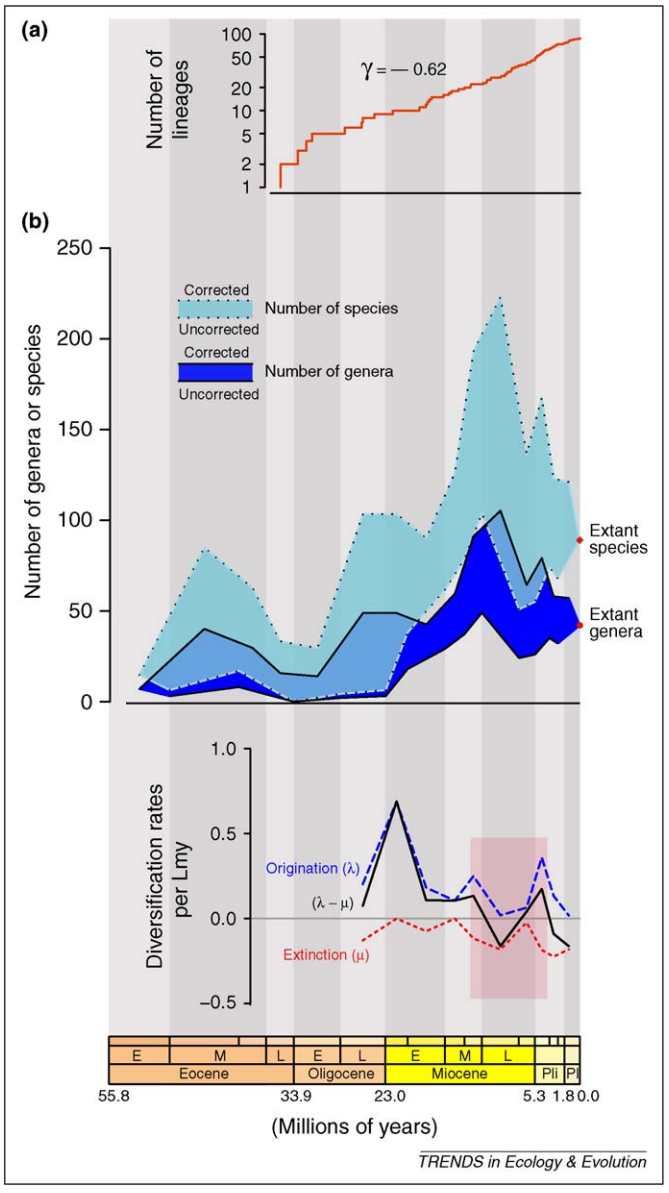

Figure 2. Cetacean diversification viewed through the eyes of a molecular phylogeny and the fossil record. (a) The lineage through time (LTT) plot is based on the most recently published Cetacean molecular phylogeny published by Steeman *et al.* [27]. The γ value is consistent with a model of constant diversification rate. (b) Fossil-based diversity curve at the genus and species levels. The lower boundaries of the envelopes represent the most conservative estimate of cetacean diversity, which uses the boundary-crosser method of counting taxa and assumes that the fossil record is complete. The upper boundary of the estimated diversity curve uses the sampled in bin (SIB) method of counting diversity, and includes a correction for the incompleteness of the fossil record and assumes that all taxa in an interval co-existed (Box 3). The raw data used were the number of fossil genera; the number of species was estimated by applying the species/genus ratio of the living taxa (2.2) to the fossil genus diversity curve. (c) Fossil-based diversification rate plot at the genus level calculated using the boundary-crosser rate method [57]. There are insufficient data to estimate rates prior to the late Oligocene. Steeman *et al.* [27] suggest increases in the net diversification rate during times of ocean restructuring, the most important of which is shown by the red box. The fossil record shows that cetacean diversity has probably been dropping since the mid-Miocene and that the current net diversification rate is negative. Fossil data are from Uhen and Pyenson [28] and were analyzed through the Paleobiology Database. All three panels share the same timescale. The stratigraphic intervals sampled are indicated by the small unnamed boxes at the top of the timescale.

record is ~54–59% complete. Similarly, the FreqRat method of Foote and Raup [32] (which uses only fossil data) indicates that the fossil record of genera is ~52% complete at the stage level. It would appear that the real diversity in the past was almost twice the observed fossil diversity.

A more refined estimate of the true diversity of cetaceans over time can be made. The boundary-crosser method is conservative because it takes the fossil record literally, and because it ignores taxa found in only one stratigraphic interval [33]. The true diversity was probably much higher. To put an upper limit on how much higher, we counted the number of taxa present in each stratigraphic interval (the sampled in bin method), and then corrected that number by an estimate of the preservation potential of each interval (see Box 3), which ranged from 0.22 to 0.85. When the observed diversity in the fossil record is corrected using this approach (Figure 2b, upper diversity curves), it would appear that the Cetacea had an all-time high diversity in the late Miocene, and that there has been a long-term trend of decrease in diversity ever since. In the late Miocene (Tortonian), there are 67 named fossil cetacean genera. Once we compensate for the incompleteness of the fossil record, it appears that there may have been as many as ~130 genera, compared with the 41 today. If we assume there were 2.2 species/genus as there are today, there may have been ~270 species in the late Miocene compared with 89 today. Even if the fossil genera were all monospecific, it appears that there were more species in the late-Miocene (~130) than there are species alive today (the 89 described species).

However, these estimates probably overestimate the true cetacean diversity because the sampled in bin method assumes that all taxa in an interval co-existed, whereas it is likely that at least some of the taxa last seen in an interval had become extinct before some of those first seen in the interval had originated (a motivation for the boundary-crosser method was to circumvent this problem). Given this *caveat*, a measured reading of the fossil record indicates that cetacean diversity has been at least slightly declining (and perhaps plummeting) over the last ~12 million years.

Box 3. Estimating true diversities from the fossil record

Compensating for the incompleteness of the fossil record is not a trivial task, in part because fossil preservation varies with time and space [47]. However, the development of analytical tools [48–53] has greatly improved our ability to compensate for the incompleteness of the fossil record. The most commonly used approach for accommodating non-homogeneous sampling in the fossil record is the use of sub-sampling methods (e.g., [48–50]). However, sub-sampling discards data and therefore is not useful if one is interested in absolute diversity trajectories. An alternative approach is to try to directly quantify the incompleteness of the fossil record. This can be done by first calculating the preservation potential for each stratigraphic interval, i.e. the probability of finding a taxon in the interval. This is estimated by first counting the number of taxa that range through the interval, i.e. that are known before and after the interval. The preservation potential is simply the proportion of range through taxa present in the interval [54,55]. The total diversity in an interval is then estimated by dividing the number of taxa actually sampled in the interval by its preservation potential. However, this may overestimate the total standing diversity because not all taxa found in an interval may have co-existed (some may have become extinct before others had originated). More sophisticated methods exist for estimating preservation potentials of stratigraphic intervals, for example see Alroy [56], but they are more demanding of the data and were not used here.

Origination rates and extinction rates can also be estimated directly from the fossil record [33]. Here again the fossil record indicates completely different origination rates and extinction rates compared with those inferred from the molecular phylogeny. First, there is substantial extinction (Figure 2c). This is unsurprising given that, compared with the 41 living genera, there are 226 extinct genera (with perhaps twice that number once we take into account the incompleteness of the fossil record). The notion that the extinction rate has been zero is completely unsustainable. Encouragingly, biologists are beginning to recognize that estimating extinction rates from molecular phylogenies is unreliable [8]. Similarly, the origination rates derived from the fossil record are much higher than those estimated from the living taxa alone. The peak genus origination rate (which should be smaller than the species origination rate) in the fossil record is ~4.5-times higher than the peak species origination rate inferred from the molecular phylogeny. Moreover, whereas the analysis of the molecular phylogeny suggests a lull in origination between 25 and 20 million years ago, the fossil record indicates a burst of speciation at that time. Omission of the fossil taxa greatly distorts the patterns and magnitudes of the estimated rates. Finally, the fossil-based rates of genus origination and extinction provide quantification of the decline in the net diversification rate since the late Miocene (Figure 2c), with the average genus net diversification rate of –0.04 per lineage per million years over the last ~12 million years (myr), and –0.13 per lineage per million years over the last ~3 myr. It appears that, rather than this being the best of times to be a cetacean (as suggested by molecular phylogenies), it is in fact one of the worst of times (ignoring the added insult of human impacts).

Why is there conflict between molecular phylogenies and the fossil record?

The reason why the patterns seen in the fossil record and those inferred from molecular phylogenies can be so different is simple. The diversity we see at present is a consequence of the long-term balance between origination and extinction, but this long-term net rate of diversification inferred from a molecular phylogeny need bear no relationship to the current or any past rate of diversification. The cetacean data demonstrate this well. In this case, the net rate of diversification over the history of the crown group is consistent with steady growth, but the fossil record shows a dramatic radiation during the late Oligocene to mid Miocene, followed by a decline from this high diversity over the last ~12 million years. The average rate of diversification needed to account for the living diversity may have nothing to do with the actual diversity trajectory that led to the living diversity.

Thus, while both molecular and paleontological approaches give good estimates as long as their assumptions hold, the important difference is that the molecular assumptions are unrealistic (uniform rates in time and on the tree), and the methods are not robust to their violation (e.g. [8]). The paleontological assumptions are more modest (correct taxonomy and stratigraphy, within-stage homogeneity) and the analysis of the fossil record still give sensible results even if assumptions such as rate homogeneity across taxa are violated.

Finally, we note that the fossil record and molecular estimates of diversities and rates need not be comparable if the fossil record includes large numbers of stem-group taxa (taxa that predate the last common ancestor of the living species). However, in the case of the cetaceans, most Oligocene and all Miocene and younger taxa belong to the crown group. Therefore this is not the reason for the discrepancies between the molecular and paleontological estimates of the speciation and extinction rates for the cetaceans.

Dealing with complex temporal trajectories

Many molecular phylogenies have patterns of lineage accumulation that are too complex to be adequately characterized by the relatively simple γ statistic or even by more complex tools (e.g. [34]). For example, a phylogeny of Australian and southern African legumes [35] shows an initial diversification followed by a long plateau with essentially no lineage accumulation, followed by a steady and relatively rapid rate of accumulation of lineages to the present. Simple diversification models cannot generate lineage accumulation plots with this shape. Aided by computer simulation, Crisp and Cook [35] interpreted this pattern to be the result of an exponential diversification, interrupted by a large extinction event. However, as with the simpler lineage accumulation patterns discussed above, there are usually several alternative processes that can account for any given pattern. For example, in the case of the legume data, there might have been an initial phase of diversity-dependent diversification that resulted in a low diversity plateau followed by a more recent radiation. It is exceedingly hard to reach firm conclusions about the rates and processes of diversification from molecular phylogenies, regardless of the analytical tools, without input from the fossil record (Table 1). The absence of information on extinct species is a severe limitation.

Conclusions

Much has been claimed about the rates and patterns of diversification of the living biota from the analysis of molecular phylogenies, but we feel that only a subset is reliable. The most reliable statements concern the identification of clades with changes in their rates of diversification [12]. If one is willing to accept that decreasing rates of diversification are due to diversity-dependent diversification, then it appears that the only way to explain an observed decrease in diversification rate is through a change in the speciation rate [17,21]. However, we suspect that there are other models, specifically those that allow substantially negative diversification rates, which might account for the observed decreases in diversification. The computer simulation studies and the analysis of the cetacean diversity dynamics discussed above indicate that a wide range of processes can give similarly shaped molecular phylogenies (Table 1). Further, in the absence of direct data on the extinct taxa, the rates of average diversification inferred from molecular phylogenies need bear little or no relationship to the true rates of diversification. We will

have to dig much deeper to extract meaningful information about the rates and processes of diversification from molecular phylogenies. We need the fossil record if we are to understand all but the simplest features of the biodiversity dynamics that have led to the living biota.

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