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EVOLUTIONARY DIVERSIFICATION OF REEF CORALS: A COMPARISON OF THE MOLECULAR AND FOSSIL RECORDS

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Understanding historical patterns of diversity dynamics is of paramount importance for many evolutionary questions. The fossil record has long been the only source of information on patterns of diversification, but the molecular record, derived from time-calibrated phylogenies, is becoming an important additional resource. Both fossil and molecular approaches have shortcomings and biases. These have been well studied for fossil data but much less so for molecular data and empirical comparisons between approaches are lacking. Here, we compare the patterns of diversification derived from fossil and molecular data in scleractinian reef coral species. We also assess the robustness of molecular diversification rates to poor taxon sampling. We find that the temporal pattern of molecular diversification rates is robust to incomplete sampling when rates are calculated per interval. The major obstacle of molecular methods is that rate estimates are distorted because diversification rates can never be negative, whereas the fossil record suffers from incomplete preservation and inconsistent taxonomy. Nevertheless, the molecular pattern of diversification is comparable to the pattern we observe in the fossil record, with the timing of major diversification pulses coinciding in each dataset. For example, both agree that the end-Triassic coral extinction was a catastrophic bottleneck in scleractinian evolution.

KEY WORDS: Diversification, extinction, fossils, molecular phylogenies, reef corals, speciation.

Although historical patterns of diversity dynamics are most commonly inferred from the fossil record, it is possible to infer at least diversification rate from the molecular record using time-calibrated molecular phylogenies. If the patterns of diversification estimated with molecular methods can be trusted, then macroevolutionary questions can be asked in groups with poor fossil records and, perhaps more usefully, diversification rates can be inferred independent from potential biases in the fossil record. But how reliable are molecularly derived estimates of diversification dynamics and how do they compare to estimates derived from the fossil record? Both of these questions have received little empirical investigation.

Even though the methods for estimating diversification rates from fossils or molecules are quite similar (Alroy 2009), there is a drastic difference in analytical protocols. In paleobiology, we accept that taxonomic turnover rates in fact vary substantially over time. The major goal of paleobiological research into taxonomic rates has been to develop methods for quantifying the historical pattern rates while minimizing bias (Foote 2000, 2001; Alroy 2008, 2010; Alroy et al. 2008). Taxonomic problems and

preservational biases continue to be a major pitfall in the use of fossil rates (Smith 2007). Diversification rates from molecular phylogenies often assume a specific model of diversification. Rates are assumed to be nearly constant over time and any temporal variation in rate is measured indirectly (Rabosky 2006; McPeek 2008; Phillimore and Price 2008; Venditti et al. 2009) or modeled (e.g., Rabosky et al. 2007; Rabosky and Lovette 2008). The most commonly used method to identify variation in rate over time is Pybus and Harvey's (2000) γ-statistic, which is based on the shape of the frequency distribution of branch lengths. Additionally, rate shift methods (e.g., Paradis 1997, 1998) can be used to find points in time when diversification rates change. The major question these methods have been developed to answer is if diversification rate is constrained.

Exploring causes of diversification and extinction, however, requires knowing the temporal patterns of diversification with confidence. Although it is possible to identify times where diversification changes and correlate them temporally with major environmental changes (e.g., Steeman et al. 2009) or to measure the net differences in diversification for binary or quantitative traits (Maddison et al. 2007; Alfaro et al. 2009; FitzJohn et al. 2009; Lynch 2009; FitzJohn 2010), the association between putative causes and rates can also be highly variable. What is needed is a time series of rates to identify general patterns of association between diversification and environmental changes (Kiessling and Simpson 2011) or biotic traits (Simpson and Harnik 2009; Simpson 2010). Estimating a temporally explicit pattern of diversification from molecular phylogenies is thus a major task.

Here we present a new approach to measuring the temporal pattern of diversification in molecular phylogenies. First, we do not rely on a single "best" tree but use tree-averaging to assess diversification pattern. We then derive a time series of diversification rates and compare this to the species-level rates estimated from the fossil record. Because diversification rate is simply speciation minus extinction rate, we can further infer the degree of concordance between fossil and phylogenetic rates by subtracting the molecularly derived diversification rate from fossil speciation and by adding the fossil extinction rates to the molecularly derived diversification rates. These operations allow us to quantify the degree to which the signal of underlying diversity dynamics is embedded in molecular phylogenies by incorporating a minimal amount of information from the fossil record. We use scleractinian reef corals because they have a rich fossil record of which we obtained an extensive species-level dataset that we can use as an independent check on the molecularly derived patterns. Corals are thought to be susceptible to environmental change (Carpenter et al. 2008) but we need to better understand the evolutionary consequences of such change.

Data and Methods

MOLECULAR DATA

For the molecular divergence estimate, we used a 144-taxon set of two mitochondrial genes, CO1 and Cytochrome B, which were downloaded from GenBank (see Table S1 for taxa and accession numbers), including 10 outgroup species. We sampled 120 of the ca. 780 extant zooxanthellate species (15%).

The sequences were realigned using the Clustal algorithm in Seaview 4.2 (Gouy et al. 2010), resulting in 1407 bp after concatenation. The divergence estimates were performed within a Bayesian framework using BEAST 1.5.2 (Drummond and Rambaut 2007). We applied the GTR + I + Gamma model (four rate categories) as determined by jMODELTEST (Posada 2008) and a relaxed molecular clock using the uncorrelated lognormal model (for fossil calibration choice see below). To ensure that the chain reached stationarity, eight separate analyses were run for 20 million steps and sampled every 1000 steps, with each of the first 10 million steps (i.e., 10,000 sampled generations) discarded as burnin. The post-burnin trees were then combined in LogCombiner 1.5.2 and analyzed in Tracer 1.4.1 (Rambaut and Drummond 2008). The effective sample size was >1000 for all parameters, suggesting our replicate analyses were adequately sampling the target joint distribution. See Figure S1 for the time-calibrated maximum clade credibility tree.

For each fossil calibration we used a maximum and minimum bound with uniform probability that the split could have occurred at any point during the selected time interval, as in our opinion the scleractinian fossil record is not sufficiently known to assign lognormal or exponential priors with decreasing probability toward older ages. The calibration for the root of the tree was determined to be between 271.0 and 245.0 Ma, based on the occurrence of the fossil scleractiniamorphs in the Middle Permian and the oldest record of the true scleractinians in the Anisian stage (Ezaki 1998; Stanley 2003). Because the phylogeny of scleractinian corals is poorly known, we ran a preliminary analysis in BEAST with only the root calibration applied and scleractinians constrained as monophyloetic relative to the outgroup taxon Corallimorpha; the phylogeny obtained was then used to select fossil calibrations for the ingroup. We chose the following 10 calibration priors, with the fossil information taken from the Paleobiology Database (PaleoDB, http://paleodb.org). The stratigraphically oldest fossil occurrences of genera were used as minimum bound, and the maximum bound was derived from 95% confidence intervals on this first appearance datum (Strauss and Sadler 1989): *Isopora–Acropora*, 15–5.3 million years ago (Ma); *Acropora–Montipora* 67.7–37.2 Ma; *Acropora–Stephanocoenia* 90.1–63.4; *Stephanocoenia–Siderastrea* 151–58.7 Ma; *Siderastrea–Goniopora* 151–91 Ma; *Lobophyllia–Symphyllia* 31.3–19 Ma; *Pocillopora–Seriatopora* 42.7–28.4 Ma;

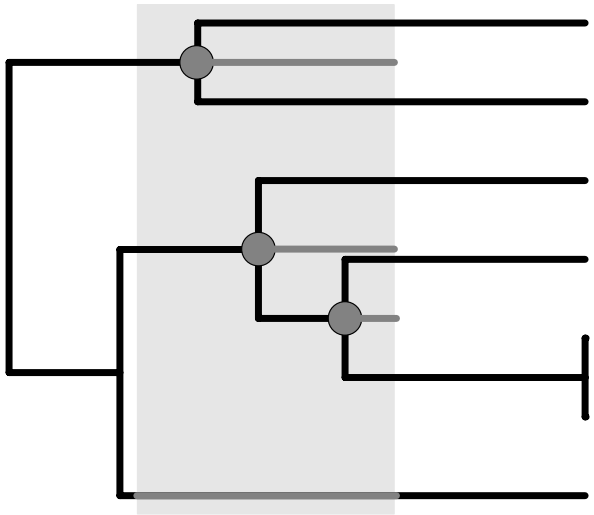

Figure 1. An illustration of the aspects of time-calibrated phylogenies that are used to calculate diversification rates within a time interval. The number of nodes and their distance from the top of the interval are used as are the lengths of branches that just range through without speciating. Diversification rate is estimated as the number of nodes divided by the sum of all branch lengths.

Stylocoeniella–Pocillopora 52–37.2 Ma; *Echinopora–Oulophyllia* 49.3–21.9 Ma; *Cladocora–Hydnophora* 183.3–100 Ma.

FOSSIL DATA

Fossil data were downloaded on 17 March 2011 from the PaleoDB after extensive taxonomic vetting and standardization by the authors (RBS and WK). The final data consisted of 17,924 occurrences from 4842 species. The data were downloaded with the max, min, and mean occurrence ages in millions of years checked, and species with uncertain affinities were excluded.

TIME SERIES OF DIVERSIFICATION RATES

Scleractinians have relatively uncertain phylogenetic relationships (Fukami et al. 2004, 2008; Kitahara et al. 2010). Therefore, we use a pool of time-calibrated molecular phylogenies derived from the Bayesian posterior distribution of our molecular clock analysis to estimate the temporal pattern of diversification rates by model averaging. For each of the 80,008 trees obtained, we fitted a separate truncated exponential distribution to number of branching events and branch lengths observed (Nee et al. 1992; Nee 2001) in each stage. The information that went into the diversification rate calculation is illustrated in Figure 1. There are n branching events per tree, and branching event i occurs at time t_i. The time span represented by each stage is denoted and youngest age of the stage is denoted t_s. The maximum likelihood estimate of the slope ($\hat{\delta}$) is a function of the number of nodes within a time interval (k_s) and the sum of all branch lengths within the interval (including branches that range through without speciating) is equal to

$$\hat{\delta} = k_s \Big/ \left[(n - k_s)\Delta t_s + \sum_{t=1}^{k_s} (t_i - t_s) \right]. \qquad (1)$$

The first term in the denominator tallies the number of branches that range through the interval without branching and multiplies them by the span of the window of observation. The second term sums the lengths of branches that first occur in the interval. Iterating equation (1) for each stage yields a time series of diversification rates. The final time series of rates was estimated using model averaging (Claeskens and Hjort 2008) by treating each tree in the posterior pool as a separate model, which is equal to the average per stage diversification rate for all trees. Equation (1) is easily implemented in R (R Development Core Team 2008) by iterating the yuleWindow function in LASER (Rabosky 2006) over a timescale.

SUBSAMPLING ANALYSIS OF DIVERSIFICATION RATES

Poor sampling of extant diversity can be particular detrimental to measuring accurate diversification rates. We tested the robustness to poor sampling by deteriorating simulated trees. We simulated a phylogeny using a time-homogeneous birth–death model, with birth and death rates set to produce about 750 extant species over 250 million years. After pruning out extinct species, we dropped an increasing proportion of random tips, down to 1%. We produced 100 replicate trees at every sampling intensity. From the resulting subsampled trees, we then estimate a time-series of diversification rates and measured the average correlation coefficient of between the changes in diversification rates in the full tree and the changes in rates in each subsampled tree.

We also use random subsampling to evaluate the robustness of diversification rate estimates in the empirical coral tree. Our full tree contains 144 tips. We started by dropping 10 tips leaving 134 random tips initially and repeated the analysis with 10 fewer tips until a minimum sampling of 14 tips is reached. After the random tips were dropped in each tree, we recalculated the time series of diversification rates on the reconstructed tree. At each sampling level, we replicated the analysis 100 times.

TIME OF SPECIATION AND EXTINCTION

We used the stratigraphically oldest fossil occurrence to date the time of speciation. We evaluate sampling completeness (P) by utilizing the occurrences-based data present in the PaleoDB. Sampling completeness (Alroy 2008) is a function of the number of species found in an interval and the two immediately adjacent ones, called three-timers (tht) and the number of species found in

adjacent intervals but not the focal one (part-timers, pt): $P = tht / (tht + pt)$.

TIME SERIES OF SPECIATION AND EXTINCTION RATES

Speciation and extinction rates were estimated from fossil occurrences recorded in the PaleoDB. Estimating per-stage boundary crosser rates (Foote 2000; Bambach et al. 2004; Alroy 2008; Alroy et al. 2008) involves tabulating the numbers of four fundamental types of taxa: (1) the number of taxa that both enter in and cross out of an interval, N_{bt}; (2) those that enter in and go extinct in the interval, N_{bL}; (3) those that originate in the interval and cross out of it, N_{Ft}; and (4) the taxa that are restricted to the interval, N_{FL}. Maximum likelihood origination rates ($\hat{p}$) are a function of the number of taxa that cross through an interval and the number originating there: $\hat{p} = -\ln [N_{bt}/(N_{Ft} + N_{bt})]$, whereas extinction rates ($\hat{q}$) are a function of the number of taxa crossing through an interval and entering into it: $\hat{q} = -\ln [N_{bt}/(N_{bL} + N_{bt})]$ (Foote, 2003; Kiessling and Aberhan, 2007).

Results and Discussion

PATTERNS OF DIVERSIFICATION

Our molecular estimates of the date of early divergence of modern reef corals fall consistently in the Early Triassic, circa 250 Ma, whereas we date the origin of Scleractinia as a whole as late Permian. Figure 2 shows the average age of each node estimated from the posterior distribution of trees. The slope of this curve is the diversification rate, such that increases in slope correspond to higher diversification rates. There is a large gap between the first two scleractinian nodes that, on average, ranges from the Early Triassic to the Late Jurassic. We know from the fossil record that scleractinians diversified dramatically during the Triassic but suffered a major mass extinction and reef crisis at the Triassic–Jurassic boundary (ca. 200 Ma; Flügel 2002; Kiessling et al. 2009; Kiessling and Simpson 2011). The pattern of molecular diversification supports the possibility that there was a complete turnover of scleractinians during the 50 million year interval of the Triassic so that the modern coral fauna diversified after the end-Triassic extinctions or even after the more modest Early Jurassic extinction event (Lathuilière and Marchal, 2009) such that Triassic reef corals are all stem group. After the Jurassic, the lineage-through-time plot steepens and suggests variable but similar rates over time. The fossil record of scleractinian species diversity (Fig. 3) shows considerable volatility over time with Late Jurassic and mid-Cretaceous diversity peaks and a decline in diversity until the mid Paleogene.

Molecular diversification rates measured from the branching times and branch lengths within each stage (Fig. 4A) can be compared directly to the species-level pattern of diversification rates estimated directly from the fossil record (Fig. 4B). One important difference is that molecular rates are always positive

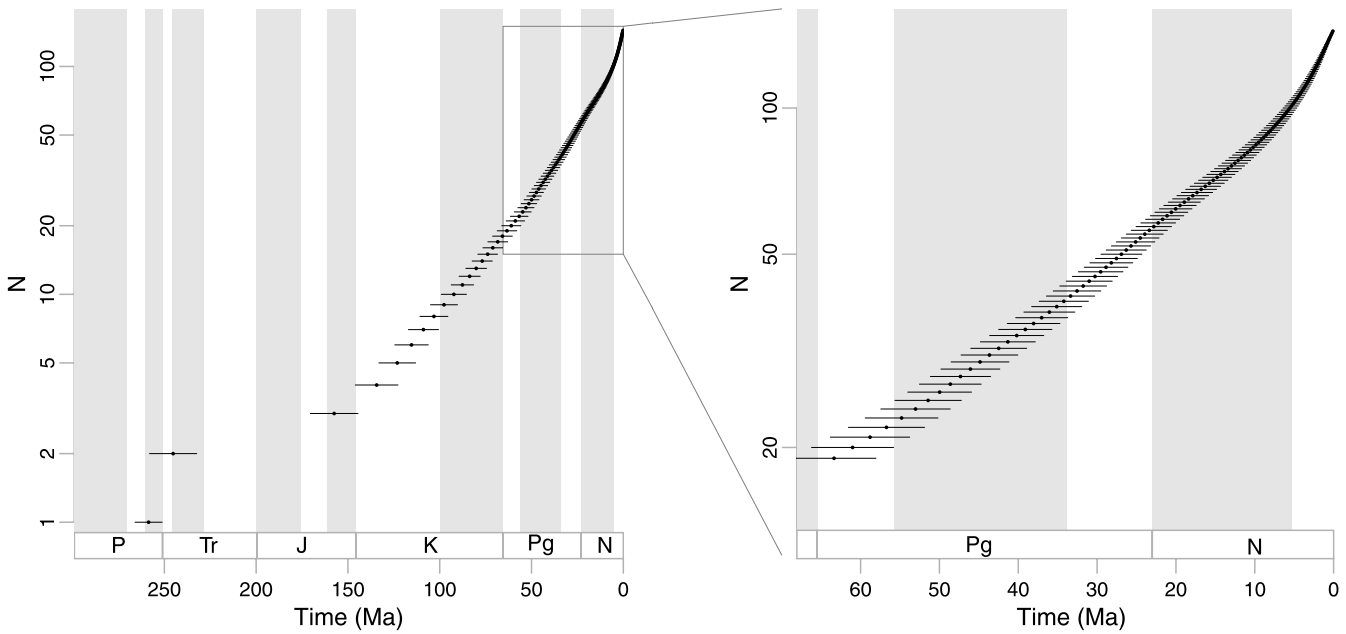

Figure 2. **Average accumulation of lineages over time based on the posterior distribution of time-calibrated molecular phylogenies. Error bars represent one standard deviation on the estimate of ages of each node among the posterior distribution of trees. The vertical gray bands in this and subsequent figures denote geologic epochs. Abbreviations in the timescale along the bottom of figures indicate the periods; P = Permian; Tr = Triassic; J = Jurassic; K = Cretaceous; Pg = Paleogene; N = Neogene.**

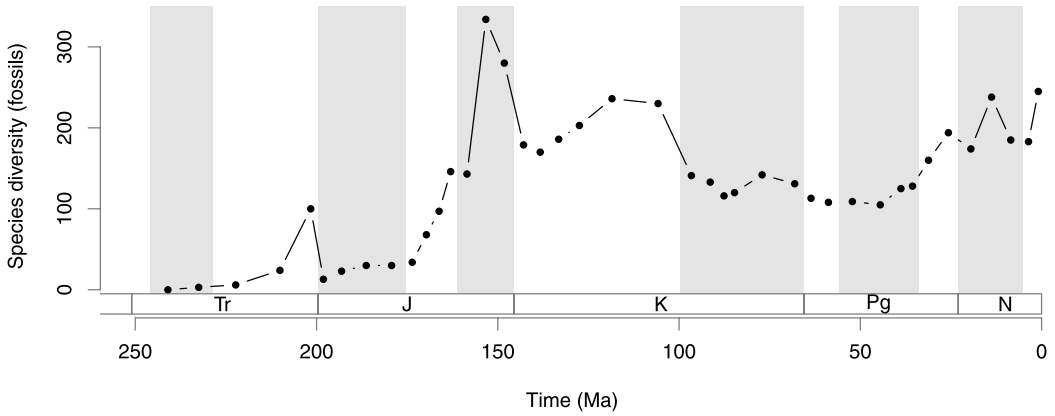

Figure 3. A species-level diversity curve of scleractinians derived from the fossil record. Diversity is measured as the number of boundary crossing species.

whereas fossil diversifications are commonly negative. Molecular rates are also lower in magnitude than fossil rates. However, there are striking similarities. Rates are high in the earliest Jurassic and drop in the later Early Jurassic. Peak diversification rates occur in the middle Jurassic, although not simultaneously in species-level curves (Fig. 4A, B). Two peaks in diversification rates occur in the lower Cretaceous, as does a peak in the upper Cretaceous. The fossil record shows volatile rates across the Paleogene and early Neogene that the molecular rates do not show. Both do exhibit an increase toward the Recent in the last three stages of the time series. We provide genus-level patterns of diversification rates also (Fig. 4C, D). Genus-level phylogenetic rates are calculated by dropping all but one random species in each genus (with the exception of the polyphyletic *Favia*). Genus-level paleontological rates are considerably less volatile with many details seen in the species-level pattern disappearing. The diversification peak in the middle Jurassic and a peak in the Barremian are the only details that match between these curves.

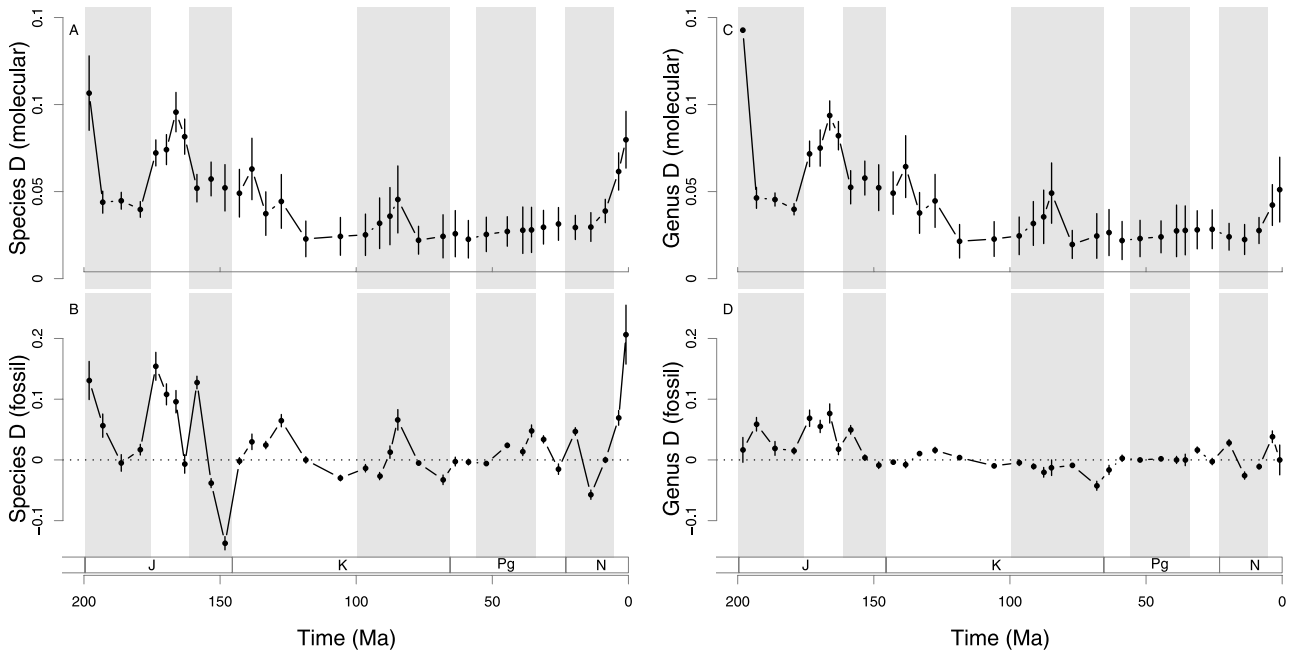

Figure 4. The patterns of diversification rates in scleractinian corals. Species-level diversification rates (A) are estimated from molecular phylogenies by model averaging across the pool of trees in the posterior distribution. Error bars denote one standard deviation. (C) Genus-level diversification rates estimated from molecular phylogenies with only one random species per genus kept. Rates are attained by model averaging across the pool of trees in the posterior distribution. (B) Species-level and genus-level (D) diversification rates estimated from the fossil record. Error bars denote one standard deviation calculated from 1000 bootstrap replicates.

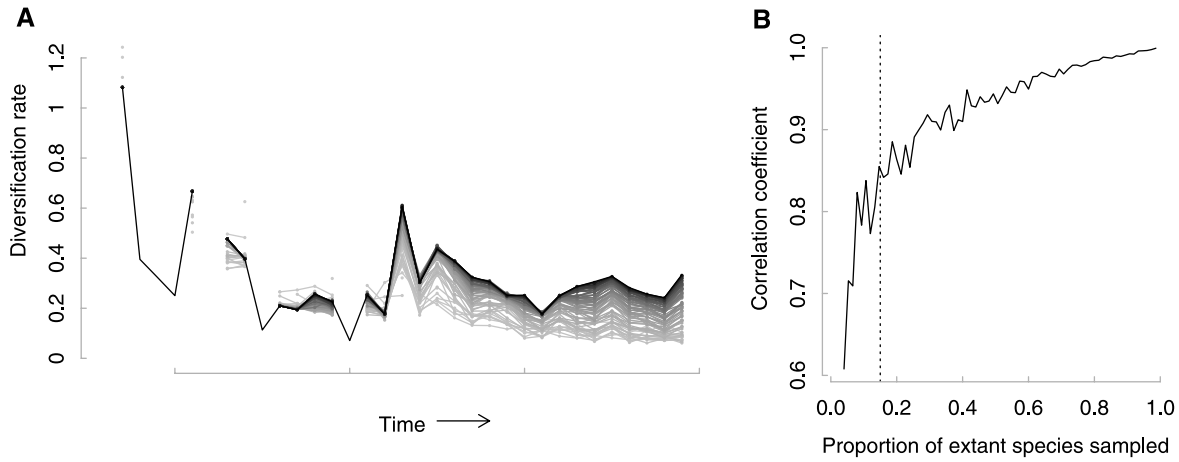

Figure 5. **The effects of incomplete sampling on estimates of the pattern and magnitude of diversification rates. A tree with 750 extant species was generated with a time-homogenous birth–death process. (A) Diversification rates from the full extant tree is shown in black, gray curves show diversification rates from subsampled trees, lighter shades of gray indicate sparser sampling. Time flows from left to right. (B) Correlation coefficients between full and subsampled diversification rates. Comparisons are made on the changes in diversification rates over time. The vertical dashed line shows 15% sampling, which is the sampling level of extant reef corals we have in our empirical tree.**

BIASES IN THE MOLECULAR RECORD

First and foremost, the per interval method we use here (as well as any other method) will not estimate true rates if diversifying subclades are not included within the tree. This is a general issue and affects the fossil record as well. Accurate rates must be measured on at least a representative subset of the diversifying lineages. Our phylogenetic data cover 16 of the 17 (94%) morphologically defined zooxanthellate families and 72 of the 110 genera (65%). Although our species coverage is small (15%), we are thus confident that we have directly sampled the major radiations of modern reef corals.

In the molecular lineage-through-time plot (Fig. 2) and in the time series of diversification rates (Fig. 4A) we observe an upswing in the diversification rate near the Recent. Although diversification rates might in fact increase near the Recent, this increase may be partially an artifact if there is low extinction and rates are constant. If there are no extinctions near the Recent, an upswing in rate is expected as the slope of the lineage-through-time plot shifts from measuring diversification (speciation minus extinction) to pure speciation rate (Nee et al. 1994; Nee 2006), and tossing out the branches leading directly to tips has been advocated (Phillimore and Price 2009) to avoid mixing rates. The fact that we observe this pattern is itself evidence that our phylogeny is fairly well sampled. Lineage-through-time plots derived from undersampled trees tend to flatten out near the recent because they oversample the deep nodes (Cuismano and Renner 2010). One of the benefits of our method is that the presence of branches leading to extant species without speciation (either due to overdispersed sampling or few recent extinctions) does not bias our estimate of diversification rate. These branch lengths are counted in the denominator of equation (1), so an excess of long ranging tips will lower the rate estimate, counteracting the bias.

Extinction and missing species both increase the branch lengths between inferred sister species (Slatkin and Hudson 1991; Nee et al. 1992; Nee 2001). These two types of missing species are expected to induce what we call the "Push of the Recent." The Push of the Recent, by systematically lengthening branches, has two consequences beyond the conflation of speciation and diversification rates discussed above: (1) diversification rates will tend to decline overall, and (2) any real changes in diversification rates will tend to smear backwards in time and therefore not be accurately dated. The distorting effect of the Push of the Recent is expected to increase as sampling declines. By artificially aggravating this effect with subsampling, we can assess what features in the diversification pattern maybe due to poor sampling. The apparent changes in diversification rates are expected to gradually disappear and smear back in time as sampling becomes increasingly poor. Any real change in rates should remain but may become dampened, as sampling gets worse. Our simulation confirms that the magnitudes of rates decline with sampling (Fig. 5A), but the details of the diversification trajectories estimated from the subsampled trees are the same in all time series. We find (Fig. 5B) that our method is highly robust to undersampling the Recent, with a correlation in excess of 0.8 when 15% of extant species are sampled (which is the level we have for corals).

Likewise, we subsampled the empirical phylogenies. As expected the lineage-through-time plots are sensitive to poor sampling (Fig. 6). Surprisingly though, poor sampling does not lead to lower rate estimates (Fig. 7). Only near the Recent (in the Neogene) do rates decline as sampling gets worse suggesting that

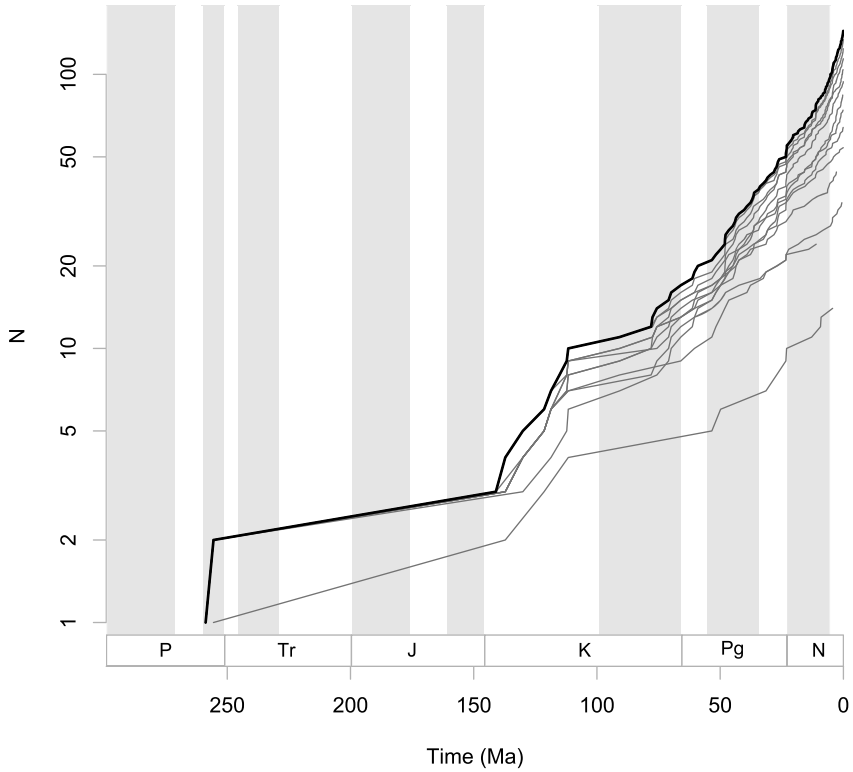

Figure 6. **The effects of poor sampling on lineage through time plots for a single exemplar scleractinian tree. Random tips are dropped and the lineage-through-time plots are derived from the subsampled phylogenies. We sample between 134 and 14 species, dropping by increments of 10 species.**

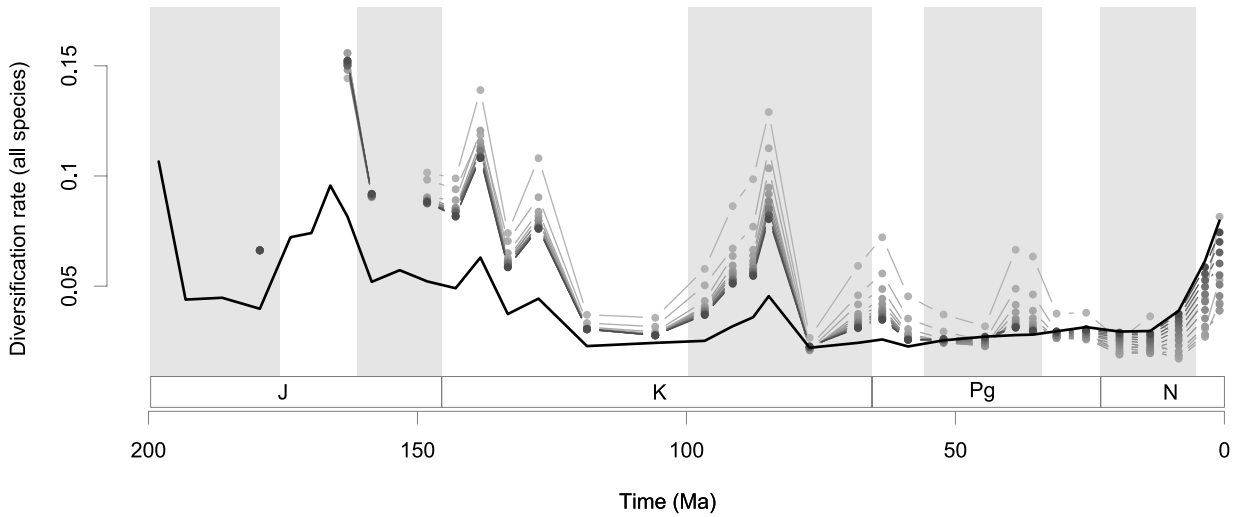

Figure 7. **Diversification rate trajectories derived from subsampled time-calibrated molecular phylogenies. Diversification rates are estimated from molecular phylogenies of 134 species by model averaging across the pool of trees in the posterior distribution. Diversification rates calculated from subsampled trees in the posterior distribution where subsampling was repeated 100 times for all 80,008 trees from the posterior distribution. We sample between 134 and 14 species, dropping by increments of 10 species. Sampling intensity is proportional to the shade of points; darker gray equals more sampling. The black line shows the rates estimated from the full tree.**

our undersampling of Recent diversity is biasing these rates most. Prior to the Oligocene (the last epoch of the Paleogene) however, rate estimates from subsampled trees are higher than for our full tree, counter to our expectations based on simulations. The increases in rates do not occur uniformly over time but are concentrated in times of higher diversification. Two times of diversification become highlighted, one in the earliest Paleogene and the other at the end of the Eocene, which are both seen in the fossil diversification also. The rarefaction curve that measures the relationship between the number of tips and the correlation between full and subsampled diversification rates remains high, even when phylogenies are reconstructed with only 10% of the species of our original pool (Fig. S2). Even though our phylogeny contains only 120 of the 776 extant reef coral species (Veron 2000; Cairns 2007), the effectively flat rarefaction curve suggests that our diversification pattern is robust.

What explains the discordance between the simulated and empirical patterns? Two possibilities could explain why the two effects of the Push of the Recent do not affect our time series of rates. The lack of backwards smearing could be due to the relatively large temporal span of geological stages but, more likely, the hierarchical structure of phylogenies makes the temporal pattern of diversification largely immune to backwards smearing. The hierarchical branching structure of phylogenies prevents the propagation of branch lengths (due to extinction or sampling) from extending past the proximal node. Because rates are estimated using only information contained within a single time interval, the tendency for all branches over the whole tree to lengthen with extinction does not influence our calculation. This is good news for estimating patterns of diversification but limits the extent to which extinction can impart a signal in a phylogeny.

That rates do not declining with subsampling is more surprising. In the simulations, trees were generated using a time-homogeneous birth–death model and so the loss of a random tip could remove a node at any depth independent of how many branches range through that interval. The net result is that there is a tendency for nodes to decline faster than branches, producing lower rates throughout. The fact that subsampled rates tend to become larger in times of truly high rates may provide a clue. If speciation is not time-homogeneous, but occurs in pulses, there will be intervals where there is a much larger proportion of nodes to branches ranging through the interval. Removing a random tip will of course also remove a node. But due to the large number of nodes that occur in a time of high diversification, dropping tips that originate then will have less of an effect than would dropping a tip that originated prior to that time. On average then, when there are pulses of diversification, the higher rates in subsampled trees is driven more by losing the early branches that range through an interval than tips that originate in that interval.

BIASES IN THE FOSSIL RECORD

Several different biases affect inferences of diversification dynamics in the fossil record. Taxonomic inconsistency may be prevalent in fossil corals due to homoplasy of skeletal characters. Also, the aragonitic skeletons of scleractinian corals are prone to dissolution such that older corals are much less well preserved than younger corals on average. Although our fossil data have been taxonomically standardized to minimize these biases, volatile sampling intensity is still an issue, but corals were also truly rare at times in the past (Kiessling 2009). There are, for example only 396 occurrences of corals in the Early Jurassic, but 4258 in the Late Jurassic, which has an even shorter duration. The preservation potential of each time interval can be directly estimated by measuring the sampling completeness (Fig. S3). These values are low in large part because species ranges are not typically longer than a couple of stages, but it highlights intervals where rate estimates will be most affected. Four intervals stand out, the Hettangian stage of the early Jurassic, the Berriasian stage of the early Cretaceous, the Coniacian of the late Cretaceous, and the middle Eocene. Of particular interest to us is the preservational depression in the earliest Cretaceous, which results in an exaggerated decline of diversification at the end of the Jurassic (Fig 4B).

DIVERSITY DYNAMICS FROM MOLECULAR PHYLOGENIES?

Diversification rate equals speciation minus extinction rate. As long as the rates derived from phylogenetic and paleontological data represent a similar set of species, we can use this fact to empirically combine estimates of speciation or extinction rates from the fossil record with the molecular estimate of diversification rate. We can estimate extinction in molecular data by simply subtracting molecular diversification rates from fossil speciation rates and we can estimate molecular speciation by adding molecular diversification rates to fossil extinction rates. Major extinctions can only reduce molecular diversification rates to zero rather than plunging to negative values as they would if the full extent of species loss was recorded. To sidestep this distortion, and focus on the pattern of rates, we mean center and scale diversification, speciation, and extinction rates prior to combining paleontological and phylogenetic rates. This exercise should be seen as a test for the presence of a signal of underlying diversification dynamics in molecular phylogenies rather than a method of estimating precise rates because the resulting pattern will doubtless be distorted. Most importantly we can ask whether background extinction has left a signal in the molecular record uniformly over time (e.g., Quental and Marshall 2009, 2010).

Although many details of the fossil rates are not in the inferred rates, we find that the large-scale pattern of rates is captured: volatile and high rates in the Jurassic, quiescence in the Cretaceous, and increasing rates toward the Recent (Fig. 8). The

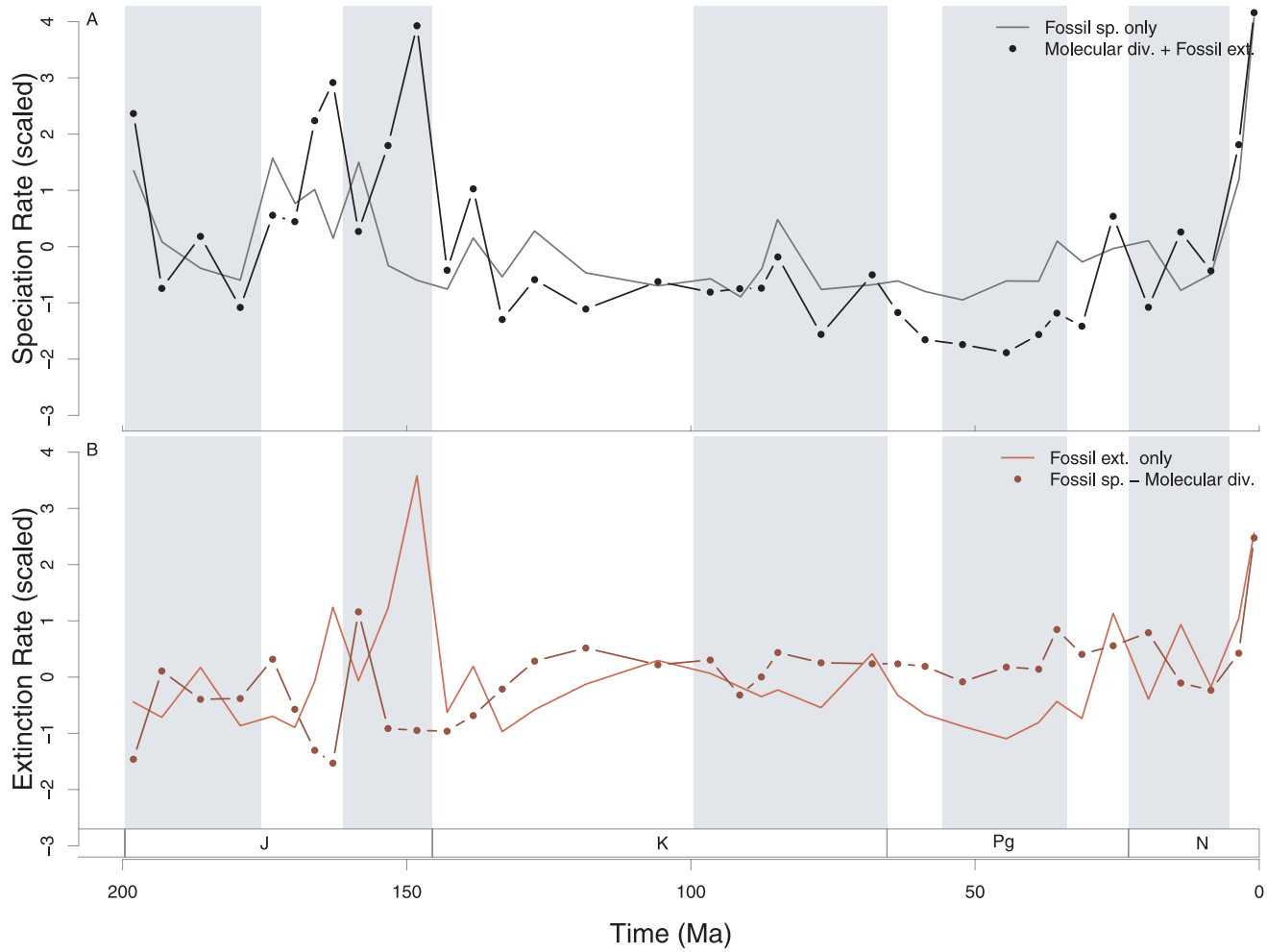

Figure 8. **Paleontological and phylogenetic diversification dynamics compared. (A) Phylogenetic speciation rates are inferred by adding fossil extinction rates to molecular diversification rates. (B) Extinction rates inferred by subtracting the molecularly derived diversification rate from speciation rates derived from the fossil record in each interval. Fossil and molecular rates are centered and scaled prior to addition and subtraction.**

correlation between changes in speciation rates (Spearman's $\rho = 0.295$, $p = 0.085$) is higher than the correlation between changes in extinction rates (Spearman's $\rho = -0.132$, $p = 0.449$). Thus the simplest way of combining fossil and phylogenetic rates fails to extract underlying speciation and extinction rates from the molecular data with high fidelity. More work is clearly needed to accurately derive these rates from phylogenies because we still cannot distinguish between times of low and negative diversification rates from the phylogenies.

Conclusions

Our comparison of the patterns of diversification derived from molecular phylogenetics and the fossil record of reef corals allows a number of empirical and methodological conclusions to be made:

- A long gap between first and second nodes in the molecular phylogeny is a signal of the end-Triassic extinction, which is well known from the fossil record. The modern reef coral fauna has a Jurassic origin.
- Inferences of net diversification rate are biased by the Push of the Recent but time-specific estimates within a window of observation are not as strongly affected. The timing of diversification events is well calibrated.
- Subsampling of time-calibrated phylogenies shows that coral diversification occurs in pulses and the timing of these pulses is well constrained and roughly matches observed diversification pulses in the fossil record.

Any direct comparisons between the patterns of raw diversification rates derived from the fossil and molecular records will be influenced by the deformation induced by the cumulative nature of the molecular record, but empirical rates during times of

high diversification are comparable between paleontological and phylogenetic data. Because the molecularly derived rates do show pulses in diversification rates in the same temporal pattern as the fossil record, we have a unique opportunity for cross-validation. The patterns of high diversification in the fossil record are also observed in independent molecular phylogenies.

Estimating extinction rates from molecular phylogenies remains a challenge. Based on the difference between fossil-derived speciation rates and molecular diversification rates, we tried to infer a time series of extinction, but its fidelity remains dubious owing to problems with both the fossil record and molecular rate reconstructions. The solution is obvious: We need more molecular data of extant corals and a more robust approach to fossil rates. A way forward might be to use a phylogenetic rather than the current taxic approach also to the estimates of fossil rates to separate true extinctions (the evolutionary end of lineage) from pseudo-extinctions (lineage split associated with name change). Unfortunately, the microstructural data needed for reliable cladistic analyses (Cuif 2010) are rarely preserved in fossil scleractinians.

Meanwhile we have shown here that the reconstruction of speciation and extinction rates from molecular phylogenies is possible in principle, if data from the fossil record are taken into account more fully than just providing calibration points.

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Supporting Information

The following supporting information is available for this article:

Figure S1. The time-calibrated maximum clade credibility tree.

Figure S2. A rarefaction curve showing the correlation coefficient between the diversification rate estimated from our phylogeny of 134 species and the diversification rate estimated from trees subsampled to include fewer species.

Figure S3. Preservation (sampling completeness) of reef coral species, assessed by the proportion of gaps in the record of species spanning at least three geologic stages.

Table S1. GenBank accession numbers for the species used in this analysis.

Supporting Information may be found in the online version of this article.