

# Evolution: No extinction? No way!

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**The fossil record reveals rampant extinction. However, analyses of time-calibrated molecular phylogenies often find no extinction at all. A new paper shows that estimates of zero extinction are entirely incorrect and are caused by limitations of analysing phylogenies that sample only living species.**

Even the most cursory glance at the natural world shows us that the evolution of life on Earth has led to vastly divergent fates for different groups of organisms: some are extraordinarily diverse, while others are represented by scant few species; for instance, for every species of mammal, there are about 1000 insect species<sup>1</sup>. Almost half of this enormous diversity of insects is accounted for by beetles (Coleoptera) alone<sup>2</sup>. In fact, insects are so diverse that we have described less than a quarter of their estimated diversity and they vastly outnumber their close relatives (Figure 1). If we want to understand the origin of these patterns of diversity in different clades, we need to unravel the processes that generated this imbalance. What happened in the past that has resulted in the natural world's inordinate fondness for beetles?

The number of extant species at a given time is the consequence of the interplay between speciation events (lineage births) and extinction events (lineage deaths) that happened in the past. The interplay of these events results in diversity increases (or decreases) through time. Are megadiverse clades, such as insects, the consequence of elevated speciation, decreased extinction or perhaps both? Accurately estimating how speciation and extinction rates have varied is also vital if we want to understand how biotic (e.g. competition) and abiotic (e.g. major environmental change) factors have regulated the diversity of different lineages through time<sup>3</sup>.

Extinction and speciation rates are now frequently estimated in macroevolutionary analyses using so-called 'birth–death models'<sup>4</sup>. These models have been hugely influential, particularly for our understanding of how random processes can leave apparent

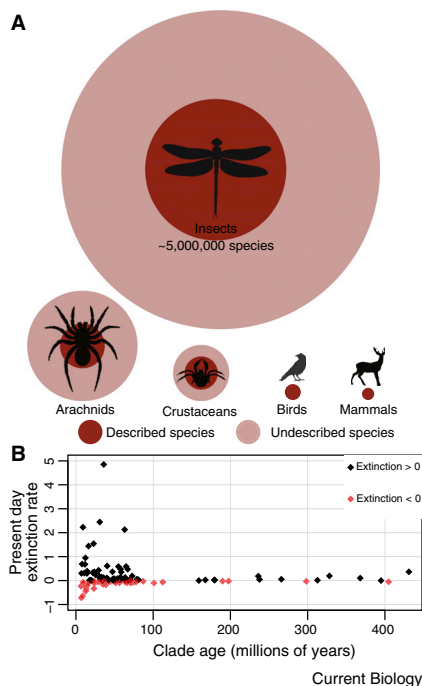
patterns in the fossil record<sup>5</sup>. They are now an integral component of our macroevolutionary toolkit, having become key component parts of routine analyses, such as time-scaling the tree of life<sup>6,7</sup>. They have proliferated in recent years, with new approaches devised to infer time-dependence (i.e. shifts in speciation or extinction rates<sup>8</sup>) or diversity dependent rates<sup>9</sup>, where speciation rates slow and extinction rates increase as diversity increases. These analyses are frequently carried out using only time calibrated phylogenies of extant taxa ('extant timetrees'), and therefore do not explicitly incorporate the fossil record to estimate past extinction rates<sup>10</sup>.

One curious outcome of many of these analyses is that the estimated extinction rates are much smaller than one would expect, and that many analyses have recovered extinction rates of zero<sup>11</sup>. To a paleontologist, this notion is outlandish, especially as the fossil record suggests that 'background' extinction rates are roughly stable through long periods of geological time and are punctuated by devastating mass extinctions<sup>12</sup>. This conflict between extinction rates calculated from extant timetrees and from observations from the fossil record has been difficult to explain. Nevertheless, these zero extinction estimates have previously been interpreted as reflecting the real processes that operated in the past, such as no, or minimal, extinction of *Anolis* lizards during their radiation on Caribbean islands<sup>13</sup>. In a new paper<sup>14</sup> in this issue of *Current Biology*, Stilianos Louca and Matthew Pennell show that not only are these estimates of no extinction unequivocally incorrect, but they result from the same quirk of the estimation process that has recently called into question if extinction rates can be estimated from extant timetrees at all<sup>15</sup>.

A recent landmark paper<sup>15</sup> by the same authors demonstrated that many combinations of speciation and extinction rates (the "congruence class") can produce the same time calibrated phylogeny and that these scenarios cannot be distinguished based on this phylogeny alone. Instead, estimates of speciation and extinction rates will converge on some 'congruent' scenario that is indistinguishable from the true scenario. Clearly though, this cannot be the whole story. If dated molecular phylogenies really lack the ability to distinguish between alternate combinations of extinction and speciation rate, why is zero extinction so often estimated rather than some random positive value?

By definition, extinction rates must have positive values: –1 lineages going extinct per lineage per million years is obviously nonsensical. Analyses concerned with diversification dynamics therefore naturally fix extinction rates to have positive values. Louca and Pennell<sup>14</sup> used a series of simulations and analyses of empirical datasets to explore why estimates of the present-day extinction rate from extant timetrees are frequently zero. In these analyses, they relaxed the assumption of positive extinction rates, finding that the congruent diversification scenario recovered by maximum likelihood analysis often has negative extinction rates. When this is not permitted by the analysis, the estimate is instead pulled towards the boundary condition of zero extinction, even though the congruence class contains an inordinate number of diversification scenarios with positive extinction rates. Previous explanations for erroneous estimates of extinction from molecular phylogenies have typically involved model inadequacy of some kind (e.g. not modelling rate variation among different





**Figure 1. Biodiversity imbalances in animals and zero extinction throughout geological time.**

(A) The great imbalance in diversity in living animals (data from<sup>1</sup>; modified from a graphic by Russell Garwood). (B) When allowed by analyses, biologically meaningless negative present-day extinction is estimated for clades of all ages. Data are from the ‘unconstrained’ analyses from Louca and Pennell<sup>15</sup>, where negative extinction rates were permitted.

lineages<sup>11</sup>). However, even when the same homogenous birth–death process (i.e. no variation in rates through time or across lineages) is used to simulate the data and estimate the present-day extinction rate, still no extinction is inferred.

In order to check just how pervasive this issue might be for empirical data, Louca and Pennell<sup>15</sup> analysed empirical timetrees from across the eukaryote tree of life and found an estimate of zero present day extinction for roughly a third of these datasets. Furthermore, when extinction rates were allowed to have biologically meaningless negative values, that’s exactly what was estimated for all cases where no extinction was recovered by a homogenous birth–death model. This suggests that this issue impacts real-world datasets and not just in the realm of simulations. The ‘zero extinction problem’ has been associated with species level phylogenies with relatively young divergences<sup>11</sup> but the empirical trees include clades from a large range of

ages, sampling young clades that are less than ten million years old all the way to ancient groups rooted in the Palaeozoic (Figure 1B).

The implications of these findings are stark. Not only is estimating extinction rates using only phylogenies of extant taxa potentially ill-advised<sup>15</sup>, Louca and Pennell<sup>14</sup> now show that they can be wholly misleading. These papers add to a roster of evolutionary phenomena for which analyses of extant taxa alone may offer limited, uncertain or totally incorrect inferences<sup>16,17</sup>. Where, then, can we go from here? One option is abandoning estimating extinction rates from extant timetrees altogether<sup>11,14</sup> and instead estimating diversification parameters that can be inferred directly from molecular phylogenies, i.e. the pulled speciation rate<sup>12</sup>. This may be our only option for much of the tree of life, especially given that the majority of clades have left little or no fossil evidence. Our other option is integrating additional evidence. Such additional evidence could come from population genetics<sup>14</sup>, but this leaves very ancient processes (such as those that generated the imbalances in Figure 1A) completely out of reach. The other (and perhaps most obvious) source is the fossil record.

Adding fossil data to macroevolutionary analyses when it is available has numerous benefits to the quality of our inferences, improving the accuracy of ancestral state reconstruction<sup>16</sup>, allowing differing modes of evolution of continuous traits (e.g. body size) to be distinguished<sup>18</sup> and also improving our understanding of the shape of the tree of life<sup>17</sup>. The fossil record is our best evidence that an inordinate number of species have become extinct (anthropogenic extinctions aside) and it seems only natural that integrating the fossil record directly with the rapidly expanding phylogenies of living species will be beneficial. Methodological advances now allow morphological data from extinct and extant species, molecular data and fossil ages to be combined in unifying Bayesian phylogenetic analyses, where extinction and speciation rates are co-estimated with a time-calibrated phylogeny<sup>7</sup>. Although these methods were initially developed with recovering evolutionary timescales in mind, they have already been shown to benefit other

aspects of macroevolutionary analysis, especially concerning the palaeontological record. This includes recovering more accurate phylogenetic trees for palaeontological datasets based on simulations<sup>17</sup> and therefore these total-evidence analyses may hold the key to unlocking the unique insights offered by the study of the fossil record. However, a natural and rather troubling concern is that the problem of ‘model congruencies’ is more pervasive than we may realise and could also impact this model-based approach<sup>14</sup>. These recent papers<sup>14,15</sup> offer a cautionary tale about the reliability of our estimates of the parameters of these models.

This potential pitfall aside, integrating fossil evidence in this way will not be an easy task, especially given the challenging and time-consuming nature of coding morphological characters for taxonomically inclusive datasets of living and extinct species<sup>19</sup>. Integrating the results from a number of analyses in a ‘metatree’ approach may be the best way of overcoming this time hurdle<sup>19</sup>, although current approaches may not fully incorporate the phylogenetic uncertainty associated with most datasets that incorporate fossils<sup>19,20</sup> and likewise may not fully benefit from the advantages of co-estimating phylogenetic trees and timescales from a mixture of data from extinct and extant taxa<sup>7,17</sup>.

The revelation that we cannot infer historical extinction rates for many clades need not be nihilistic. The new studies of Louca and Pennell<sup>14,15</sup> will lead to necessary skepticism about inferences that are most likely incorrect and any renewed efforts to integrate the rich sources of data available from living and extinct species are arguably only positive<sup>7,16–19</sup>. Who knows what else we might learn along the way?

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## Vision: Space and colour meet in the fly optic lobes

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Colour vision involves colour-opponent cells, which are excited and inhibited by different wavelengths. Synaptic interconnections between *Drosophila* Dm8 cells are required for forming spatio-chromatic receptive fields with a center and surround of opposing polarity which can invert, depending on the stimulus.

Can a fruit fly like *Drosophila melanogaster* distinguish a green from a red apple, simply based on vision alone? What most of us might find a trivial question is actually quite hard to answer. In fact, we don’t know. At least the fly’s ‘hardware’ for seeing colours is not bad — six rhodopsins with different wavelength sensitivities from the UV to the green ranges of the spectrum are expressed in different groups of photoreceptors<sup>1</sup>. Even more strikingly, these rhodopsins are organized in stochastically distributed subtypes of unit eyes (or ommatidia), called pale and yellow<sup>1</sup> (Figure 1A). Due to the resemblance to the arrangement of cones in the human retina, the fly retinal mosaic hence seems perfectly suited to process colour information<sup>2</sup>. While

behaviour experiments confirmed the fly’s ability to distinguish colours, as well as the retinal mosaic’s importance for doing so<sup>3–5</sup>, little is known about the physiological properties of underlying cells<sup>6–8</sup>. Very recently, amacrine-like Dm8 cells in the *Drosophila* optic lobe were shown to receive colour-opponent inputs from pathways previously believed to be ‘chromatic’ versus ‘achromatic’<sup>8</sup>. But how are these inputs processed by individual pale or yellow Dm8 cells, as well as on a population level? In this issue of *Current Biology*, Li and colleagues report wavelength-specific differences in Dm8 cell responses with pale versus yellow inputs, and using sophisticated genetic dissections they show (for the first time in any insect species) that these inputs are

organized into center/surround receptive fields<sup>9</sup>.

Colour vision across animals includes the ability to distinguish two stimuli (like a red and a green apple) purely based on their spectral content, independent of intensity. In all cases, this involves different classes of photoreceptor cells containing different rhodopsins, like the vertebrate S, M, and L cones (named after short, mid-, or long wavelength sensitivity). Much work in vertebrates (and less so in insects) has focused on the underlying circuit mechanisms, both by performing behavior experiments, as well as through the characterization of the physiological properties of colour-sensitive interneurons<sup>10</sup>. These studies revealed spectral antagonism, i.e. the fact

