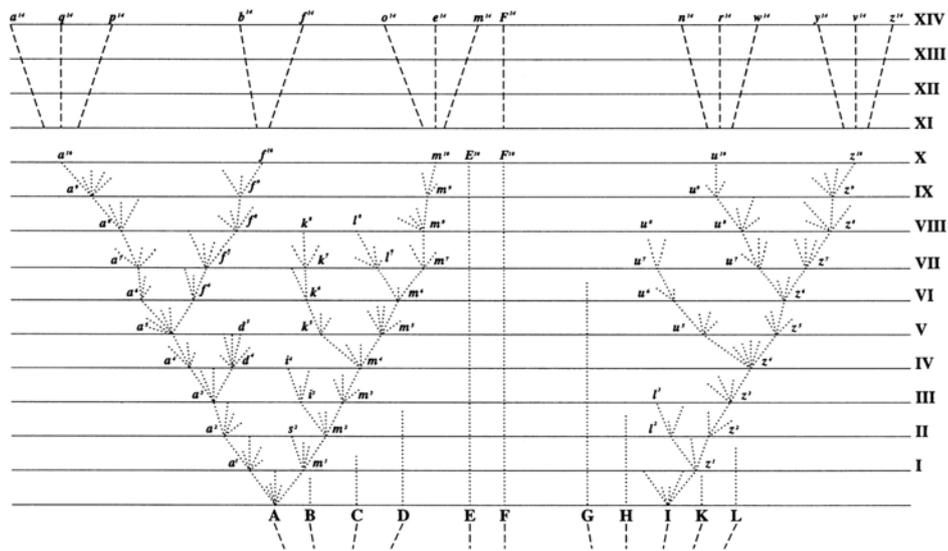




Stem and crown group dynamics: mapping the origins of modern diversity



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Abstract

“At which points in time did modern diversity arise?” is a long unanswered question in the field of evolutionary biology. A major reason why it has not yet been solved is the conceptual confusion stemming from the mystification of the Cambrian explosion and its implications on evolutionary theory. In this paper, these conceptual issues are addressed and phyla are defined as crown groups, which enables investigation into their origins. Constant birth-death-model simulations of evolution under varying speciation, extinction and diversification rates show that it is diversification rates that govern when crown groups emerge, and not absolute levels of speciation or extinction. The difficulties estimating true diversification rates are discussed and three directions for future research based on these findings are suggested.

Introduction

The structure of the tree of life is the result of millions of years of evolution. Its shape is the result of diverse influences that include ecological, climatologic and genetic factors. To study evolution is to investigate which factors affect the evolutionary pathways of organisms and how they do so.

Perhaps one of the most basic factors affecting the patterns of evolution is the frequency with which organisms speciate and go extinct. Speciation and extinction have both been studied continually and intensively since the dawn of evolutionary biology. Darwin himself remarked upon the apparently varying rates of speciation across different genera and presumably time (Darwin, 1859), a reflection later repeated in the form of the theory of punctuated equilibrium (Gould and Eldredge, 1972). The study of the nature of mass extinction events (*e.g.* Raup and Sepkoski, 1982) is almost a field in itself and speciation has always appeared to biologists and paleontologists as a core component of evolution and has consequently been extensively studied (*e.g.* Mayr, 1942). Modern work has included considering the relationships between speciation rates, key innovations and niche occupancy (Purvis *et al.*, 2011) and putative correlations between carbon emission and extinction rates (Ruhl *et al.*, 2011).

Modern diversity

An obvious point of inquiry relating to speciation and extinction rates is how these affect modern diversity. Identifying points in time at which modern diversity arose, and why, is of great importance in seeking to understand the processes and mechanisms governing evolution. When did the extant clades emerge and under which circumstances did they do so?

The phyla are the largest grouping of animals in the animal kingdom and necessarily represent diversity in its entirety. Consequently, the origins of the phyla have become the subject of investigation when considering the origin of modern diversity. The common understanding of these origins is that all or almost all of them occur in the Cambrian. The Cambrian explosion is frequently credited with providing us with all extant phyla during a compressed event of exceedingly high rates of evolution (*e.g.* Valentine *et al.*, 1999).

This view of the origin of modern diversity is perhaps best known from the book *A Wonderful Life* (Gould, 1989) in which the author posits that the rate with which evolution occurred was greatly accelerated during the Cambrian, resulting in a diversity equal to, if not greater than, that which we observe today. The causes, or frequently the cause, of this accelerated event have since become a central point of research (*e.g.* Saltzman *et al.*, 2011 and Marshall, 2006). The event is likely to have begun earlier, *i.e.* having roots in the Ediacaran (*e.g.* Fortey *et al.*, 1996 and Fortey *et al.*, 1997) or earlier (Erwin *et al.*, 2011).

What is a phylum?

The Cambrian certainly exhibits a remarkable and perhaps unsurpassed burst of morphological evolution and a seemingly sudden appearance of fossilizable hard parts. But to what extent it is useful to regard the Cambrian explosion as the point of emergence of all

modern phyla is questionable, particularly as a consensus on the definition of a phylum has not been forthcoming. The lack of a clear and objective definition of a phylum testifies to the difficulties with prior approaches to this problem and hints that there may be some underlying conceptual issues that need addressing.

The definition of a phylum risks tending towards the circular if it comes to rely on their early origin or a product thereof, *i.e.* phyla will be defined as emerging in the Cambrian because they emerge in the Cambrian, as pointed out by Fitch and Sudhaus (2002) along with a number of other difficulties concerning the arbitrary nature of the current understanding of phyla. Scholtz (2004) termed this understanding “strongly characterized by typological thinking”. It is imperative, therefore, for the field to reach an agreement on how to objectively define what a phylum is. It was to this end, in an attempt to resolve confusion on the topic, that a definition based on body plans, *i.e.* shared characters of its members, was suggested (Budd and Jensen, 2000).

In this view, phyla consist of extant taxa sharing a body plan of characters which is put together piecemeal along the stem group as it approaches the basal node of the crown (Fig. 1).

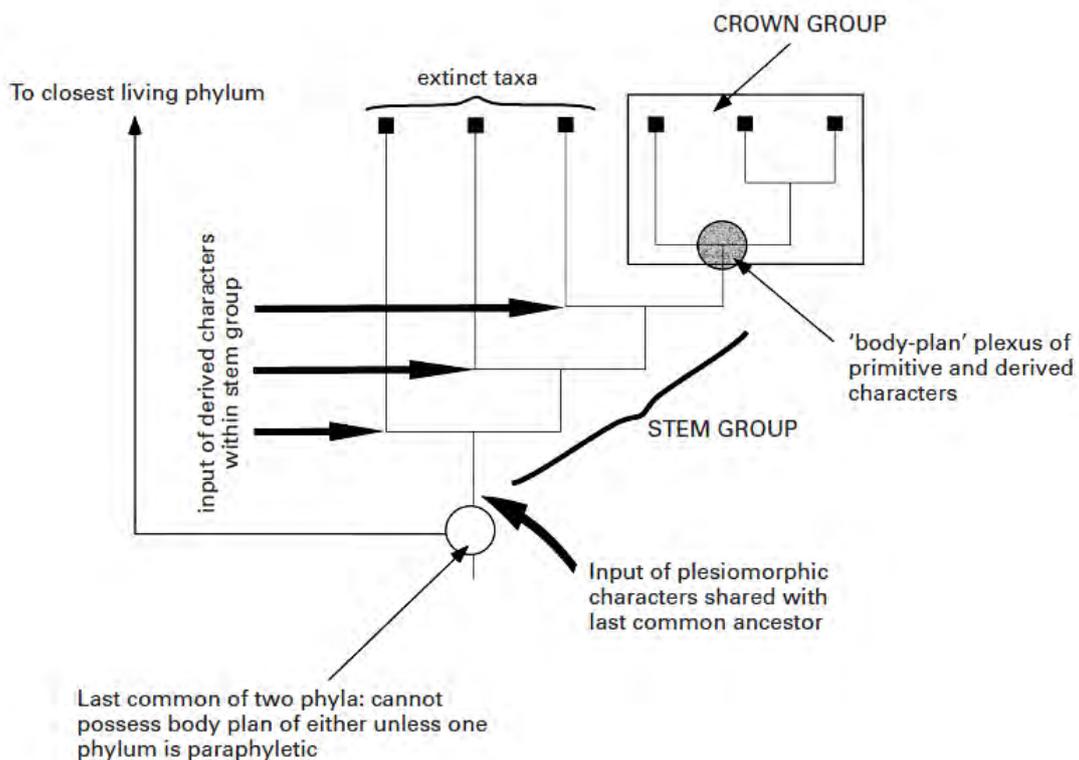


Fig. 1: Budd and Jensen’s illustration of the body plan based definition of phyla. Phyla are defined as crown groups with the suite of characters of the most recent common ancestor to all living taxa defining the body plan for the clade. From Budd and Jensen (2000).

This definition has been resisted on the grounds of a number of complications it raises, *e.g.* how then to relate to secondarily lost characters (Briggs and Fortey, 2005). The field as a whole has been somewhat reluctant to embrace this new terminology, preferring to stand by the notion of the phyla emerging in the Cambrian (*e.g.* Gould, 2002).

Budd (2001) uses the example of birds and crocodiles to illustrate the concept. He considers what the most recent common ancestor of the two groups would have looked like. We know that the most recent common ancestor of birds was in all respects a bird itself and that the most recent common ancestor of crocodiles was a thoroughly crocodile-like creature as well, but what of the most recent common ancestor of these groups? It cannot have been both a bird as well as thoroughly crocodile-like. Consequently, there must be an evolutionary space between both living clades. It is this evolutionary space that is defined as the stem group.

In this light, a phylum *sensu* Budd and Jensen is an extant clade including all taxa going back to their most recent common ancestor uniting the group with its set of characters. Stem group taxa become the animals exhibiting stepwise addition of new characters heading up to the most basal node of the crown group. This is an immensely useful way of looking at fossils as it provides an excellent framework for cladistic analyses of morphological evolution, which is, after all, the primary type of information that fossils offer us. However, the fact that some fossil taxa then do not belong to any phyla has been given as a source of distress (Briggs and Fortey, 2005).

However, I argue that the delimitation of phyla to extant groups only should not be considered a revision of terminology. Rather, it provides us with a useful definition for large clades of organisms, which has previously been unavailable. Donoghue (2005) writes of the crown and stem group concept that we should “adopt new concepts rather than adapting existing ones and thus diminishing their utility”; a sentiment with which I fully agree. When considered within the correct framework, the fossil record may provide us with information not yet discovered due to conceptual failings of the past, and we may see that events such as the Cambrian explosion are “rapid, but nevertheless resolvable and orderly” (Budd, 2003).

Modeling the origins of modern diversity

When phyla are considered as crown groups, and related extinct taxa relegated to the status of stem groups rather than phyla proper, the question “when did the extant clades emerge?” becomes even more central as it seeks to identify the origins of modern diversity. In this paper, I will explore how the emergence times of crown groups are affected by varying speciation and extinction rates in a birth-death-model of evolution.

A birth-death-model begins with a lineage splitting in two and from then on allows that speciation occurs at a certain rate and extinction at another. So, in each time step of a simulation, there is a certain likelihood of a lineage speciating and a certain likelihood of it going extinct. Changing these rates alters the structure of the generated trees in different ways. For example, high speciation rates obviously generate denser trees.

Most studies of this sort of tree dynamics focuses on diversification rates, which is the extinction rate subtracted from the speciation rate (*e.g.* Silvestro *et al.*, 2011 and Ricklefs, 2007). Ricklefs also identifies biases of which one should be aware when estimating diversification rates based on phylogenetic reconstructions, the common method of estimating historic diversification rates employed today.

Raup (1983) showed that major animal clades inevitably appear early in radiation events as “an artifact of the geometry of the evolutionary tree”. While this is likely to be the case, it does not tell us anything about the origin of the phyla, *i.e.* the crown groups of those major clades.

Aims

I will investigate how the time of emergence of crown groups is affected by varying speciation, extinction and diversification rates. Using a constant birth-death-model I will generate random trees under varying parameters and compile data on the time of crown group emergence. The following scenarios will be examined:

- (1) Increasing equal speciation and extinctions rates (diversification rate = 0)
- (2) Increasing rates of speciation for a given extinction rate
- (3) Increasing diversification rates

Methods

For all simulations, the R package *TreeSim* (Stadler, 2010) was used with the R software, version 2.13.2. See Hartmann et al. (2010) for algorithms utilized in this package. All graphs were generated in Microsoft Excel, version 14.0.4734.1000.

To investigate the scenarios of equal rates of speciation and extinction, 50 trees of 114 time steps were generated with equal extinction (E) and speciation (S) rates 0.1, 0.3, 0.5, 0.7 and 0.9. Sets of 100 trees were generated with each set of parameters. Trees that went extinct before present were discarded. The crown group emergence times of the first 50 trees surviving to the present were saved.

Due to software limitations, trees generated where S exceeded E could not be longer than 15 time steps. The diversification rate (D) is $S - E$. Consequently, to investigate the other scenarios, E was set to 0.1, 0.3, 0.5, 0.7 and 0.9. For each E, 50 trees each were simulated for D values of 0, 0.2, 0.4 and 0.6. When $D = 0,8$, i.e. with $S = 0,9$ and $E = 0,1$, the simulations could not be run due to computational difficulties. In those instances where $S > 0,9$, trees were not generated.

Sets of 100 trees were generated with each set of parameters. Again, the trees that did not survive to the present were discarded and the crown group emergence time of the first 50 surviving trees was saved.

Results

The absolute values of S and E do not affect the timing of crown group emergence (Fig. 4); as long as the diversification rate of the tree remains 0, the crown group emerges halfway through the simulation, *i.e.* at 0,5 of the simulation's full time. This appears to be a fractal feature of the resulting trees generated; at any point chosen in the tree as the origin of the total group, the crown group will emerge on average half-way between that point and the present.

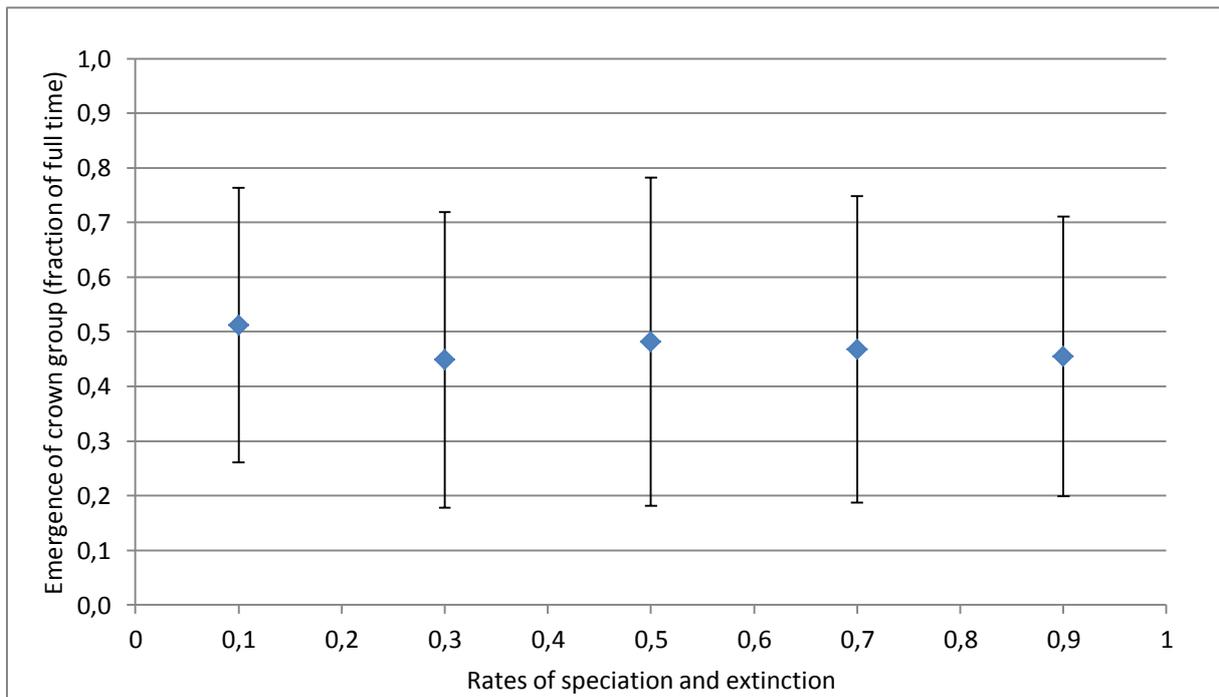


Fig. 4: The effect of equal absolute values of S and E , given along the x-axis, on the time of emergence of crown groups.

With increasing diversification rates, *i.e.* increasing S relative E, the emergence point of the crown group moves further back in time (Fig. 5). The values in each line are parallel with regards to diversification rates, *i.e.* the same excess of S over E has the same effect on crown group emergence times regardless of the absolute values of either.

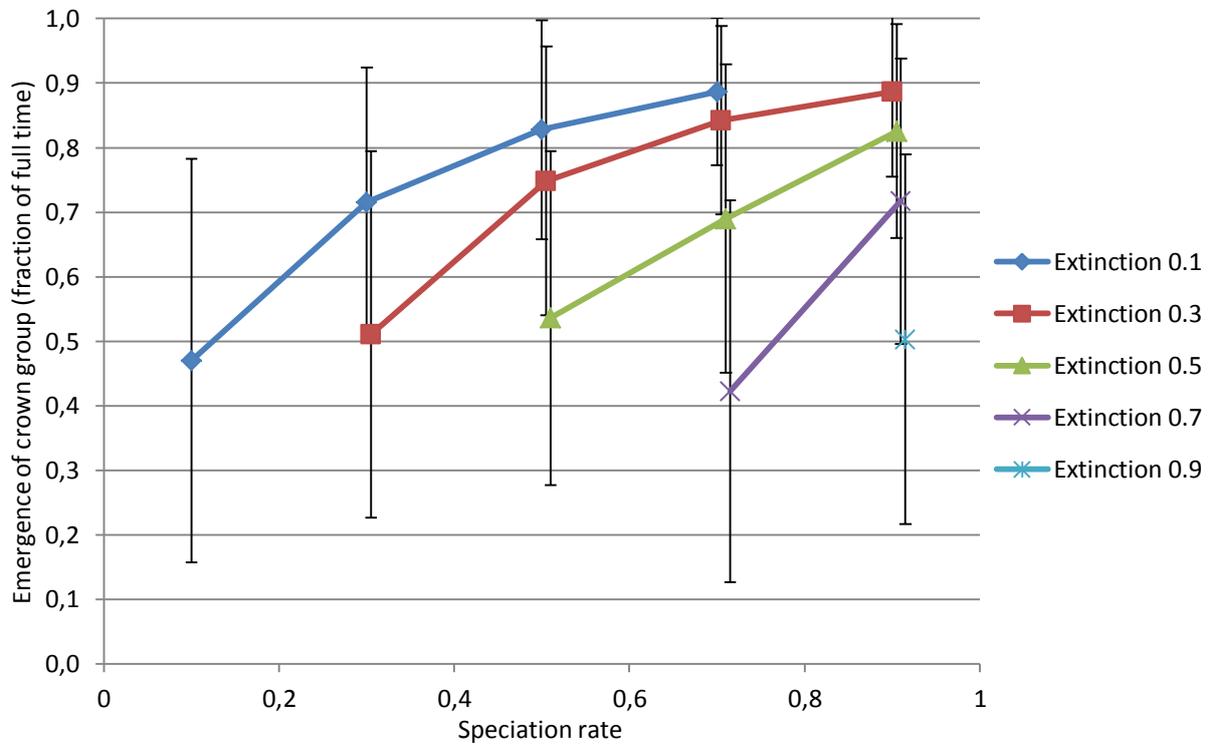


Fig. 5: The effect of increasing speciation relative extinction rates on the time of emergence of crown groups. Each line represents an extinction rate with the x-axis providing the corresponding speciation rate. Note that some values are slightly offset their x-value to avoid blurring of error bars; the only real positions on the x-axis are 0,1, 0,3, 0,5, 0,7 and 0,9.

Increasing diversification rates (Fig. 6) move the emergence of the crown group back in time, and with increasing E relative S, the emergence of the crown group moves forward in time. The curve extrapolated from the data points in Figure 6 is asymptotic. In other words, when extinction is non-existent, the origin of the total group will be the same as the origin of the crown group and consequently the crown group emergence time will be 1,0.

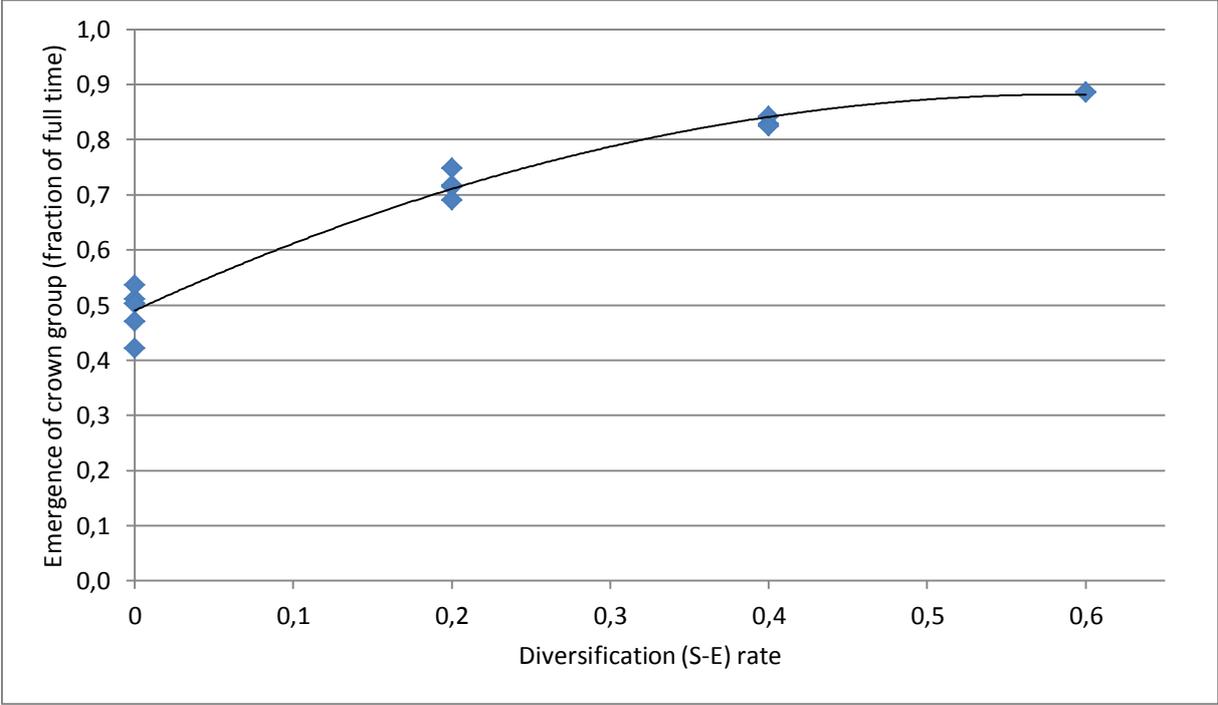


Fig. 6: The effect of increasing diversification rates, x-axis, on the emergence time of crown groups. The data points used here are the values from Fig. 5.

Discussion

Diversification rates

The results of the simulations demonstrate that the absolute rates of speciation and extinction do not in themselves determine the time of origin of crown groups (Fig.4). Rather it is the diversification rate (Fig. 6), a result of the interplay between the two, that affects crown group emergence. Consequently, it is possible to estimate historic diversification rates given the time points of total and crown group emergence. Conversely, it is possible to estimate the timing of crown group emergence from known, or estimated, diversification rates. These results show the significance of defining phyla as crown groups, and hints at the unexplored utility of the stem and crown group concept.

However, the implicit assumption that diversification rates are stable through time is obviously incorrect and does not reflect our current understanding of historic patterns (*e.g.* Alroy, 2008), which includes mass extinction and radiation events. Accommodating scenarios where $E > S$ is very difficult with a constant birth-death-model, as simulations in which extinction occurs more often than speciation will tend towards producing trees that go extinct before the present. Future research in the field should therefore attempt to develop tools capable of producing sliding rate birth-death-models that can test the effect of mass extinction events. Such tools could also be used to test estimates of historic patterns in diversification rates (*e.g.* Alroy, 2008) and investigate whether these are consistent with our present understanding of crown group emergence times.

Other work with sliding rates models should investigate whether high diversification rates must remain high in order to generate the observed pattern of crown group emergence (Fig. 6) or if an early burst of diversification is sufficient to establish this pattern. Strathmann and Slatkin (1983) found with regards to the total group that if “speciation rates exceed extinction rates at the initial radiation of the clade, but before the clade becomes large, speciation rates come to equal extinction rates and both are low, persistence from before the Ordovician up to the present becomes likely.” Whether or not this pattern is mirrored in crown group dynamics represents a potential research interest.

McInnes *et al.* (2011) postulate that extinction “eventually draw[s] a veil over past dynamics, suggesting that some questions are beyond the limits of inference”. The approximation of historic rates of diversification is indeed complex as it is affected by its two fluctuating components; speciation and extinction, which in turn are influenced by a wide range of factors (Stadler, 2011). Rates of speciation are typically estimated from the appearance of new fossil forms, obviously rendered difficult by the incompleteness of the fossil record. The rate of extinction, then, is perhaps even more difficult to estimate.

Extinction rates

Despite constant birth-death-models being the norm, the issue of how to accommodate the fluctuating nature of extinction rates into evolutionary simulations has long tested

evolutionary biologists. It has even been suggested that it may be “useful to think of the diversification of species as a random process of speciation without extinction” (Hey, 1992).

Van Valen (1985) famously suggested that extinction rates were constant through time. A view supported by the findings of Gilinsky and Bambach (1987) who concluded that “the normal course of diversity change in higher taxa is controlled principally by the changing pace of origination and only secondarily by the process of extinction”. However, this view has recently been challenged by McPeck and Brown (2007), who argue that diversification rates are far less correlated to diversity than simply clade age.

However, in terms of implications for the birth-death-model, modeling constant extinction rates punctuated by mass extinction events may prove an interesting opportunity, as suggested earlier. Indeed Foote (1994) finds that extinction rates tend to vary in unison in a way that speciation rates do not. This is presumably related to the fact that mass extinction events affect multiple organisms while speciation events, by definition, affect only one.

Exactly how extinction and speciation rates are related to environmental factors remains to be fully understood (Stadler, 2011). Exploring this relationship would yield the understanding necessary to generate accurate evolutionary simulations with real life patterns of diversification.

Diversity and disparity

The relationship between diversification rates and morphological evolution is theoretically complex (Foote, 1997). Establishing the nature of this relationship would of course add value to the ability of estimating divergence rates from the time of crown group emergence. The development of statistical methods to achieve this is ongoing (*e.g.* FitzJohn, 2010 and Erwin, 2007).

Why it should be the case that so much morphological innovation is exhibited during the Cambrian is puzzling. Erwin (1994) presents a number of hypotheses that have been forwarded to explain this phenomenon. For example, the developmental hypothesis posits that morphological innovation becomes less frequent due to the inherent genetic canalization of morphological change, while the ecospace hypothesis states that morphological innovation is only possible when empty ecospace is available. Mapping the relationship between the rate of morphological evolution and the rate of diversification could be used to test these hypotheses.

Imagine, for instance, that it is found that the rate of diversification is strongly connected to the rate of morphological evolution. This finding would not lend support directly to either of the above outlined hypotheses, but it would only be compatible with the ecospace hypothesis, seeing as we know that diversity continues to increase despite the accumulated morphological change of the ages.

Palaeobiogeography

It is important to remember that crown groups need not necessarily be phyla and can, of course, be clades of any size. Bearing this in mind, a potential application of the results

published here is the mapping of local rates of diversification. The geographical distribution of organisms may correspond to e.g. migration events, environmental changes or niche competition. Mapping the emergence time of geographically delimited crown groups could produce local maps of diversification rates, which can then be considered in a biogeographical framework. Powerful tools for this type of work are available in the form of geographical software systems such as GIS.

Conclusions and future directions

The research questions explored in this paper have only been available owing to the conceptual framework of the crown group phylum concept. Abandoning the synonymy of the Cambrian explosion and the origins of modern diversity is necessary in order to approach this topic meaningfully.

Constant birth-death-model simulations of evolution reveal that diversification rates, *i.e.* the interplay between speciation and extinction, determine the timing of crown group emergence and not the absolute values of speciation or extinction themselves. Consequently, it is possible to estimate diversification rates of the phyla, or any other crown group, from the time of their emergence relative the time of their total group emergence.

Future research on this topic should work towards three goals:

- (1) Creating birth-death-models with sliding rates to test:
 - a. The effects of stable extinction rates punctuated by mass extinctions.
 - b. True estimates of historic diversification rates (Alroy, 2008)
 - c. Whether or not an initial burst of diversification, followed by a period of equal speciation and extinction, is sufficient to establish a crown group early on that survives to the present (Strathmann and Slatkin, 1983).
- (2) Investigating the relationship between the rates of morphological evolution and diversification, hopefully shedding light on putative evolutionary mechanisms governing morphological innovation.
- (3) Creating palaeobiogeographical maps of estimated diversification rates, with an aim to recognizing key biogeographical events.

Budd and Jensen (2000) write that the conception of early origins of modern diversity is “partly inevitable, partly illusory”. Given that phyla, when considered in a sound conceptual framework, can emerge at any point and that the cause of much of the confusion regarding the origin of the phyla is through mistakenly classifying stem group animals as crown, I argue that this conception is simply wholly illusory.

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