The Jurassic/Cretaceous boundary: a mass extinction in tetrapods?

# Summary

This thesis will explore the macroevolutionary dynamics of tetrapod vertebrates across the Jurassic/Cretaceous (J/K) boundary, investigating the time period spanning 164 to 100 million years ago. This particular time interval has been targeted due to its interesting research history. Initially, this boundary was considered to represent a mass extinction, but was subsequently downgraded, either to a relatively minor event or to representing fairly normal levels of background extinction. However, recent studies accounting for biases in fossil record sampling have indicated severe declines in a number of tetrapod groups crossing this boundary, although the timing, cause and pervasiveness of these patterns within all tetrapods is currently unclear. As such, the J/K boundary appears to represent a significant time interval for patterns of life on Earth, yet remains a largely neglected time interval. The primary target of this thesis is to assess the impact of various sampling biases on the trajectories of tetrapod biodiversity, and then construct a series of ‘corrected’ biodiversity curves throughout the Late Jurassic and Early Cretaceous. The secondary aim is to reveal the selectivity patterns and processes that corresponded to extinction or survival across this time interval. A case study, focusing on one group J/K boundary crossing tetrapods, the atoposaurid crocodylomorphs, will enable the resolution of finer scale macroevolutionary patterns. Such studies are becoming increasingly relevant in providing data that can be fed into predictive models for threatened analogous modern organisms with the onset of global climatic disruption, and understanding what factors have shaped past life on Earth. The main questions that will be addressed here are: (1) what are the diversity dynamics during the Late Jurassic and Early Cretaceous for tetrapods? (2) How are these patterns influenced by the way in which we have sampled the fossil record? (3) Can we find any correlation between genuine biodiversity signals and biotic or abiotic factors that reveal the macroevolutionary history of these groups? Each one of these questions is inter-related, and play host to a number of secondary, but no less significant, questions about mass extinctions, tetrapod evolution, and our understanding of biodiversity patterns and processes in deep geological history.

# Introduction

One of the greatest questions of our time is whether we are in the midst of a biodiversity crisis. Some statistics indicate that we are indeed about to tip over the brink into the 6th major mass extinction of the last 500 million years, on occasion highlighting the value of palaeontological data in constructing a holistic conservation biology framework (Barnosky, et al., 2011). The key driver of this current crisis is purportedly driven by external, or non-biological, environmental and climatic factors, due to the onset of anthropogenic climatic disruption (Warren, et al., 2013). Humans have a continuous, direct impact on the environment, as well as indirect impacts on biodiversity. This ranges from increasing the atmospheric and oceanic uptake of carbon dioxide, to affecting local biogeochemical cycles through pollution. This undoubtedly will continue to leave its fingerprint on ecosystems and their biodiversity, but through ways in which we cannot currently predict, although some estimate the ecological rebalance and restructuring might take around 10 million years at current rates (Alroy, 2008). The patterns and processes involved in organismal extinction in the past are, and should continue to be, of substantial interest for conservation biology if we are to understand future dynamics and mitigate irreversible biodiversity loss. Many studies are now geared towards binding historical and palaeontological records of extinction to guide our understanding of future responses, for example in New Zealand avifauna (Bromham, et al., 2012), and mammals (Cardillo, et al., 2004) (Carrasco, 2013).

## Macro-extinctions and macroevolution

Extinction is an intrinsic part of the evolution of life on this planet. Species originate, their populations expand, contract, and then go extinct - it is the dominant theme for this Earth-wide play. If it were not for extinction, it is highly unlikely that any of the species we know, including ourselves, would be present today. Species need to go extinct to pave the way for new types, new experiments. This is one of the underlying concepts of natural selection, and is no new phenomenon to palaeontology. On occasion, however, extinction rates are elevated beyond the usual to such a degree that entire ecosystems, taxonomic groups, and extremely high percentages of organisms all suffer a ‘grand dying’, i.e., a mass extinction. Extinction is just one of many factors, such as integration, invasion, competition, and evolutionary adaptation (via ‘key innovations’) that contribute to the history of life.

A mass extinction is loosely defined as having occurred when a significant number of species from a broad biotic and geographic range go extinct over a relatively short period of geological time, approximately 1 million years according to Wignall (2001). These biological crises can also be a product of reduced speciation rates, whilst extinction rates actually remain consistent throughout the crisis interval, but which nonetheless manifests itself as a decline in net biodiversity. Likewise, a mass extinction can be taxonomically restricted, with some groups declining while others diversify, producing no negative net impact on global biodiversity. Five elevated extinction intervals are largely accepted and heralded as the ‘big five’ mass extinctions during the Phanerozoic: the mid-Devonian at the end-Ordovician (450-440 million years ago, Ma), Frasnian-Farmennian boundary (375-360Ma), end-Permian (251Ma), end-Triassic (200Ma), and end-Cretaceous (66Ma). This has been the consensus for some time now, but new methods are challenging some of the long-held views of the trajectory and patterns of biodiversity in deep geological time.

In the latter half of the 20th century, many studies reviewed and substantially re-evaluated the fossil record and assessed the ecological, evolutionary and geological significance of past mass extinctions (see (Benton, 1994) and (Jablonski, 1994) for reviews). This was ignited by an overview of Phanerozoic mass extinctions by Newell in the mid-20th Century (Newell, 1952) (Newell, 1963) (Newell, 1967) (Hallam, 1998), which was then developed in a quantitative mode using a compilation of fossil marine genera and families (Raup & Sepkoski, 1982) (Sepkoski, 1982) (Sepkoski, 1992). Mass extinctions were variably defined during this series of research and in subsequent publications, but commonly statistically identified as outliers that were outside the 95% confidence intervals for the otherwise ‘background’ trends of counts of raw taxa through time. The patterns that Raup and Sepkoski identified were largely considered the status quo for large-scale diversity patterns during the Phanerozoic for a substantial length of time, and were used as the basis for the investigation of external controls on biodiversity patterns, particularly with mass extinctions. A classic example of this is (Alvarez, et al., 1980) who was the first to bind a great extinction event, the end-Cretaceous, with stratigraphic evidence for a dramatic extra-terrestrial impact event. This paved the way for a series of increasingly popular investigations into mass extinctions and macroevolutionary patterns and processes.

These spear-heading studies of the late 20th century have largely been superseded in a number of theoretical and empirical ways in a current and growing body of research. Raw counts of the fossil record have been demonstrated to be poor indicators of biodiversity, due to the variable influence of anthropogenic and geological megabiases and the impact of incomplete sampling (Alroy, et al., 2008) (Alroy, 2010) (Benson, et al., 2010) (Benton, et al., 2011). The information we can use to analyse past biodiversity has been substantially enhanced by large data sets such as that curated by the Paleobiology Database (PaleoDB). Geological megabiases are those in which biodiversity is influenced by temporally heterogeneous amounts of rock available for sampling, or macrostratigraphic variation, and anthropogenic factors are those in which humans have variably sampled and assessed the available fossil record. Concurrent with these developments has been the development of new statistical procedures to investigate the patterns and processes which these large data sets can reveal to us, along with advances in our ability to analyse the evolutionary relationships of organisms, fuelled by an exponential increase in computational power.

One issue with these early studies, and that has crept through into many recent ones, is the unit of assessment for biodiversity at a given time. Taxonomy, by its very nature, is largely an arbitrary construct, designed for nothing more than the hierarchical arrangement of organisms within the tree of life. There exists no biologically meaningful unit above the level of species in this hierarchy, and links between species biodiversity and higher level taxonomic diversity are tenuous (Sepkoski, 1986). Many earlier studies analysed patterns of extinction in family-level taxa, so therefore do not necessarily translate into anything biologically significant (i.e., results are products of arbitrary taxonomic ranking schemes). Therefore, it is somewhat perplexing when studies attempt to draw biotic conclusions conducted on diversity studies at the genus or family-level, as has been historically common practice (Benton, 1985). Some groups, such as dinosaurs, have very few polyspecific genera, and therefore the genus level may be of use (Mannion, et al., 2011). The issue here is that these ranks are assigned to nodes or groups arbitrarily (even regarding generic names for taxa), and will each contain different diversities of species, evolutionary trajectories, macroevolutionary patterns within groups, and are therefore not comparable in any meaningful way (Robeck, et al., 2000). Arguments against reproducing species-level curves due to scaling issues or incompleteness (e.g., (Benton, 2001)) matter little when a total assessment of complete biodiversity is not the target, and only patterns of relative diversity are. It is for these reasons, that when analysing macroevolutionary dynamics, the only valid way of assessment is at the level of species.

Some authors are right to point out that supraspecific proxies of genera and families can be used, if there is perfect correspondence between all taxonomic levels (e.g., (Raup & Boyajian, 1988)). Several studies, particularly on marine invertebrates, have however demonstrated that genera may be suitable candidates for biodiversity in certain cases, by elucidating the impact of geographic range on extinction intensity (Raup, 1982) (Flessa & Jablonski, 1995). The nature of taxonomy is also a concern: one can speculate that as species are lumped or split through the inherently subjective nature of taxonomists (Sheehan, 1977), they effectively cancel each other out leaving a net imbalance of zero. If supraspecific taxa are to be used, the operational correspondence between them and the species level must be made clear *a priori* to any analyses, and subsequently accounted for in that they are abstractions or parallelisms to the genuine biological underpinning of diversity.

## The drivers of macroevolution

The drivers of extinction and origination can be broadly defined into two groups: extrinsic and intrinsic factors. Both of these correspond to determinations of selectivity patterns, and are what we see reflected in the patterns of the fossil record. Somewhat paradoxically, the precise nature of selectivity processes in the fossil record have received relatively little attention compared to simply understanding the nature of biodiversity patterns, given the implications such studies may have on our understanding of the processes governing current and future biodiversity. This is not quite the same as looking at large-scale correspondence between, for example, impact events and mass extinctions, but investigating the direct kill mechanisms.

The broader mechanics of extinction are, nonetheless, reasonably well understood on a theoretical basis. It may be that in many cases of mass extinction, there is no one singular cause, but more a ‘perfect storm’ of synergistic events that push life to its limits (Arens & West, 2008). It may even be that singularly, extreme events such as bolide impact events, ocean anoxia, or mass volcanism do not have the capacity to inflate extinction levels beyond normal background rates, and only when they act in concert do we see a rate shift beyond this (Arens & West, 2008). Determining the processes behind selectivity patterns is important in determining the scope of potential drivers behind macroevolutionary trends, and of critical importance in differentiating how different impact mechanisms will impact future biodiversity.

### Extrinsic factors

Environmental correlates to mass extinctions have a long history of research. Numerous causative correlates have been suggested, including ocean acidification, relative sea-level change (particularly at lowstand), extreme volcanism, ocean anoxia, bolide impacts, climate change, and chemical cycle shifts (Hallam & Wignall, 1997) (Hallam & Wignall, 1999) (Peters & Foote, 2002) (Veron, 2008) (Alroy, 2010) (Steinthorsdottir, et al., 2011). Extrinsic aspects of macroevolution are those which exist beyond organisms. This can be difficult to define in mutually exclusive terms, as many organisms act to change their surrounding environments as ‘ecosystem engineers’; for example, beavers. Organisms form part of the environment on a functional level, for example through dietary interactions, resource or mate competition, or migration patterns. It can be difficult to define these independently from physical factors within the environment, such as geochemical cycles, altitude, or temperature. Considering all of these factors together provides a holistic image of a dynamic system.

#### Relative sea level

Many studies have assessed the causative effects of sea-level change on biodiversity trends (Newell, 1967) (Jablonski, 1984) (Hallam, 1989) (MacLeod, 1998) (Hallam & Wignall, 1999) (Butler, et al., 2011) (Mannion, et al., 2011). Early studies assumed a simple correlation between global sea-level, biodiversity and extinction, although the picture has since been demonstrated to be more complex than this, with variations in taxonomic diversity instead having a temporal fidelity (Hannisdal & Peters, 2011). For example, there may be a common-cause hypothesis whereby sea level drives both diversity and sampling, or the rise of sea-level may lead to the more widespread distribution of harmful environments, such as anoxic zones into epicontinental seas (associated with the early phases of transgressions) or alter the chemical or biological stratification of the hydrosphere, each with their own set of feedbacks. Extensive periods of transgression may also reduce oceanic sediment flux, limiting the amount of marine rock available for fossil sampling during these times (MacLeod & Keller, 1991). The relationship between extinction periods and the transgression-regression cycle appears to be randomly distributed (Hallam & Wignall, 1999).

In the terrestrial realm, perceptions of biodiversity can still be impacted by changes in sea-level. These can be taphonomic, such as controlling the preservation potential or probability of an organism being transported to an area where it can be preserved. Coastal environments may also have a higher probability of being preserved during transgressive phases (Mannion, et al., 2011), which again highlights the importance of understanding sequence stratigraphic architecture when considering geological biases. The implication of this is that higher relative sea-level should correlate to peaks in apparent biodiversity. The inverse is that during periods of higher sea-level, there is relatively less terrestrial sedimentation due to decreased land surface area, so terrestrial fossilisation probability actually declines (Markwick, 1998) (Mannion, et al., 2011). Sea-level may also have a secondary geographic influence by controlling biogeographical vicariance, allopatric speciation, hybridisation, and population mixing as sea-levels rise and fall and bisect or recombine existing populations. The dividing aspect of this, for example during relatively high sea-levels, increases the possibility of speciation, and thus increased biodiversity, whereas relatively low sea-levels can lead to competitive replacement and extinction as new species interactions occur as barriers are removed to migration. However, increasing sea-level can also lead to range-size contraction, which can often be a precursor to population-level extinction (Upchurch & Barrett, 2005). As such, sea level will be compared with biodiversity in an attempt to detect these putative correlations.

#### Earth systems and geochemical cycles

The association between geochemical cycles, environmental factors and biological patterns in deep time has received considerable inquiry in the past due to the importance of unravelling the co-evolution of Earth and its biota. Geochemical data are now widely available in large isotopic or fossil-chemical databases, and can be used by geochemists and palaeoecologists to analyse supposed correspondence between ancient chemical cycles and patterns of biodiversity (Prokoph, et al., 2008). Unlocking potential environmental drivers behind macroevolutionary patterns is important, again, given the way in which humans are rapidly shifting the chemical balances on Earth, which may be having an impact on its biota. Geochemical signatures that will be considered in this thesis include the oxygen isotope fractionation record, the carbon dioxide record, strontium isotopes, and the carbon isotopic record. Each of these has purported links with external drivers of biodiversity patterns.

Temperature is often cited as a potential correlate with historical biodiversity patterns. In a time when the average global temperature on Earth is increasing, understanding the physical and biological impacts of temperature variations backwards in time is fundamental to our understanding of how to respond to and mitigate future impacts. At the J/K boundary, data from Gondwana suggest that there was an average global drop in temperature of about 10° Celsius leading up to the boundary (from the Oxfordian-Tithonian), followed by an equally abrupt warming of the same magnitude. This led to a rapid transition from an ‘ice house’ to a ‘green house’ world, with a general period of cooling over the boundary (Anderson, et al., 1999) (Scotese, et al., 1999). The Late Jurassic also began with a period of severe global cooling (Dromart, et al., 2003). The extent of this trend is questionable, however, as sea-surface temperatures indicate a general warming trend in the southern oceans throughout the Late Jurassic, followed by cooling from the Hauterivian-Aptian (140-125Ma). This data indicates that throughout this period, the southern hemisphere was experiencing a sub-tropical to tropical climate, pervading into high latitudes, and which may have persisted on until the Late Cretaceous (Bice, et al., 2003) (Jenkyns, et al., 2011). These relationships warrant further investigation.

#### Geographical range and the latitudinal diversity gradient

Geographic range size in a temporal context has received much due attention in the palaeontological literature (Carrasco, 2013). This is in part due to palaeobiogeography, which places speciation into two models (vicariance and dispersal), and also due to the effects of the species-area affect. The importance of determining the geographic susceptibility to extinction is about scale, as it can reveal whether extinction episodes were truly global, and the relative severity of local and regional events. The dissection of biodiversity data into different levels of geographic province is, therefore, crucial for unravelling the spatial patterns of macroevolution.

One of the most striking components of global biodiversity over the last 500 million or so years is the latitudinal diversity gradient (LDG). Often considered to have a first-order control on biodiversity patterns, the LDG describes the pattern of greater biodiversity in the tropics, gradually declining towards the polar regions. It exists for the majority of extant groups, both in the marine and terrestrial realms, and has gained much attention in the fossil record as if it can be tracked then it is strong evidence of a large-scale extrinsic control on biodiversity patterns through time (Jablonski, et al., 2006) (Mittlebach, et al., 2007) (Valentine, et al., 2008).

In Mesozoic tetrapods, results so far suggest that, at least in terrestrial forms, they did not conform to the LDG. Using a sampling-corrected diversity curve for Mesozoic dinosaurs (Mannion, et al., 2011) found that, conversely, dinosaur diversity peaked at temperate palaeolatitudes, which corresponds strongly to reconstructed estimates of land area. This strongly suggests that, at least in the group of study, climate may not have had as strong an influence on biodiversity distribution patterns in terrestrial faunas, and that instead continental fragmentation and vicariance may have been dominant in controlling diversity fluctuations. During the Jurassic, floral diversity and productivity were highest at middle latitudes, due to the migration of productivity concentrations through greenhouse episodes (Rees, et al., 2000). This may have important implications for the tetrapod LDG throughout this period.

#### Volcanism

Volcanic emissions have the potential to transmit large volumes of toxic or otherwise deleterious material into the atmosphere, such as sulphur dioxide or carbon dioxide. This can have a four-fold effect: lowering air-temperatures through direct insolation from ash and sulphate aerosols, increasing atmospheric toxicity and poisoning, causing of acid rain, and increasing atmospheric temperatures through release of greenhouse gases. As such, it is more the secondary effects of volcanism that are likely to have a beyond-local impact; it is entirely plausible that extinctions of local populations can be directly caused by volcanic events. There have been periods in Earth’s history where volcanism has been particularly geographical and temporally widespread; for example, with the Deccan Traps coinciding with the end-Cretaceous (Vogt, 1972) or the Siberian Traps and the end-Permian mass extinctions, but the correlation between these episodes does not appear to be consistent at a superficial reading of the raw records (Hallam, 1989).

Although there is little large-scale volcanism (either through large igneous provinces or continental flood basal provinces) during the Late Jurassic, the Early Cretaceous saw several episodes coinciding with the continuous break-up and rifting of Gondwana (Wignall, 2001). The Paraná flood basalts of South America and the Etendeka Traps of Namibia were jointly emplaced during this rifting phase during the Valanginian and Hauterivian, and are now divided by the South Atlantic (Harry & Sawyer, 1992) (Jerram, et al., 1999). In the Barremian, the single largest volcanic province on Earth was emplaced in the southwest Pacific, the Ontong Java Plateau. This is concurrent, and plausibly a driver of, anoxic environments and deposition throughout the late Barremian to Aptian (Bralower, et al., 1994) (Wignall, 2001).

#### Bolide impacts

Bolide impacts are notoriously known for their partial responsibility in the evisceration of non-avian dinosaurs at the Cretaceous/Palaeogene boundary some 66ma (Alvarez, et al., 1980). Their pervasive effect on other groups of organisms in terms of extinction intensity, however, is still a hot point of debate (Raup, 1992) (MacLeod, 1998). There are actually three bolide impacts known that are contemporaneous with the J/K boundary: the 70 kilometre diameter Morokweng impact crater in the Kalahari Desert, South Africa, dated at 145 million years old (end-Tithonian; (Corner, et al., 1997) (Hart, et al., 1997) (Reimold, et al., 2002)); the 40 kilometre wide Mjolnir crater in Norway from 142 million years ago (Tithonian, (Dypvik, et al., 1996)); and the 22 kilometre wide crater at Gooses Bluff, Northern Territory in Australia, dated at 142.5 million years old (Tithonian, (Milton, et al., 1972) (Milton & Sutter, 1987)). Interestingly, no correlation between these impacts and a purported 3-phase extinction event during the Tithonian has ever been thoroughly investigated (Walliser, 1996) (Bambach, 2006).

### Intrinsic factors

Within the palaeontological community, relative little has been explored in terms of biological factors that can lead to elevated extinction rates compared to extrinsic environmental components, based on advanced modern techniques (Friedman, 2009) (Sookias, et al., 2012). Biological parameters that lead to ecomorphological selectivity of extinction should, in theory, differ from environmental drivers through taxonomic selectivity. External pressure is expected to distribute extinction pressure more homogeneously in different organisms, or on different scales. Biological components, such as diet, are expected to impact upon different groups in different manners. This is known as the ‘chop’ or ‘trim’ dichotomy.

Intrinsic factors that may correspond to biodiversity patterns are those that are morphological or physiological, and functionally interactive with the environment, including other sympatric contemporary species. This form of interaction is partially covered by the ‘Red Queen’ model, whereby it is the interaction among species that drives their evolutionary dynamics, not abiotic factors (the ‘Court Jester’). As a process, it can be detected if environmental variables are in stasis, but morphological adaptation still occurs. If this process is dominant as a macroevolutionary force, then diversification rates will decrease as diversity increases (Ezard, et al., 2011).

#### Body size

Body size has received considerable attention in the palaeontological literature as a macroevolutionary-coupled functional ‘trait’, or aspect of functional ecology (e.g., (Sookias, et al., 2012) (Codron, et al., 2012)). As an aspect of organismal biology, it is perhaps one of the easiest things to measure for palaeontologists, and the development of proxies for body size has been a cornerstone of tetrapod evolutionary analyses in the past. The reasons for the use of body mass as a functional aspect of ecology are due to its apparent macroevolutionary trends manifest in such things as Cope’s Rule (a within-lineage directional trend of body mass increase) (Brown & Maurer, 1986) (Alroy, 1998) (Hone & Benton, 2005), and intrinsic aspects of biology such as range size, digestive strategy, thermal physiology, metabolic rate, and fecundity (Roy, 2008) (Cooper & Purvis, 2010) (Sookias, et al., 2012).

Body size is a continuous variable, and one measurable in many forms for all organisms on this planet. However, to have any heuristic value, it is generally considered as a series of distinct groups along a continuum. This has the possibility of being problematic, as when groups are demarcated, they must have a logical and evidence-based reason for assigning boundaries between groups. This is not always the case in past studies, where numbers are seemingly picked at random (e.g., (Fara & Benton, 2000) (Codron, et al., 2012)). Body size in all tetrapod groups will be investigated within a comparative phylogenetics framework, using various proxies to estimate total body size.

#### Morphology

Morphological disparity is a measure of the range of morphologies that a taxon or group of taxa can represent. It is a quantifiable metric, and can be used as a proxy for ecospace or morphospace occupation, and provides a comparative metric to diversity. What it represents is how rapidly a non-parameterised and presumably infinite form of functional space can be occupied as taxa diversify in terms of species richness and associated morphological radiation. Whether or not different scales of disparity equally represent functional or ecological behaviour has not been tested, and it should not be assumed that modular aspects of disparity (e.g., lower jaw outlines, cranial morphometrics) are parallel to total assessments based on data matrices (i.e., per-taxon lists of variable character states), which may or may not include data on the functional diversity of operational taxonomic units.

An advantage of disparity analysis is that they are largely independent of sampling biases, and thus are adequate representations of completely sampled morphological diversity (Brusatte, et al., 2012) (Butler, et al., 2012). Previous assessments of tetrapod morphological disparity have neglected to analyse it within a strict phylogenetic framework (Brusatte, et al., 2012). The issue here is that closely-related species are explicitly more morphologically similar, so likely to exhibited a contracted range of morphological disparity. It is possible to correct for this by using a proxy for phylogenetic distance (e.g., stratophenetic distance, or branch lengths), which removes the portion of morphological similarity that is purely due to phylogenetic relationships.

#### Diet

Dietary preferences at the ecosystem level can provide information on the food web interaction of organisms (Lang, et al., 2013). The simplest categorisation of tetrapod diets is into herbivores and carnivores. Relatively little has been conducted in the evolution of dietary shifts, particularly in non-archosaurian lineages (Sookias, et al., 2012).

## Geological megabiases and incomplete sampling in the fossil record

In an ideal world, analysis of historical trends of biodiversity would simply be a matter of making exact counts of all the species that ever existed through geological time. However, it has long been recognised that the fossil record is not a perfect curator of the history of all life on Earth (Gregory, 1955) (Newell, 1959) (Durham, 1967) (Raup, 1972) (Raup, 1976) (Sheehan, 1977) (Koch, 1978) (Signor III, 1978) (Kidwell & Holland, 2002). This issue was first placed in a quantitative context in terms of taxa-specific and temporal sampling issues, recognising that this had implications for how we compare fossil and extant datasets (Jablonski, 1994). This can, in part, be overcome by looking at patterns of relative diversity in fossils, which is essentially interpreting the temporal association of peaks, troughs, plateaus, and periods of stability estimated from the fossil record. There is a strong case that we do not need a perfect fossil record, and in fact many of the macroevolutionary aspects we want to study, such as clade replacement, correspondence between diversity and morphological disparity, spatial segregation and biogeography, and the trajectory of biodiversity through time are all quantifiable and comparable within a relative framework (Alroy, 2003).

The relationships between palaeobiodiversity and the structure of the fossil record have gained an increased interest in the last ten to fifteen years. This has been fuelled by the apparent association between the structure of the geological record and sampled biodiversity patterns through time, known as geological megabias. The geological record, in this manner, has been attempted to be quantified in a series of proxies such as fossil-bearing formations, raw formation counts, lithofacies diversity, numbers of sedimentary packages, or rock outcrop area (Smith & Benson, 2012) (Wall, et al., 2011) (Lloyd, et al., 2012) (Lloyd, et al., 2011). These are thought to be representative of the stratigraphic architecture of the preserved rock record and represent a false superficial reading of the raw fossil record. The second major mode of bias inflicted upon the fossil record is anthropogenic, or the way in which we have directly sampled the fossil record as it is. Neither of these issues are by no means intractable, and numerous devices now exist to compensate for their occluding effect. Unlocking the effect of these biases has profoundly altered the way in which we interpret the fossil record and our understanding of historical biodiversity patterns.

This apparent relationship between biology and geology is known as the species-area effect when rock area represents habitable area, and represents a strong first-order pattern in fossil record biodiversity. However, what it represents further is that our understanding of biodiversity patterns may be, in fact, driven by the nature of the geological record, and the mode in which it has been historically sampled. As such, there are three non-independent hypotheses that seek to explain this apparent interaction of geology and palaeobiodiversity. The first is simply that the species-area effect is a sampling artefact, where the coupling of rock availability (using one of the proxies mentioned above) drives the availability of fossils to sample, and thus artificially inflates diversity (Raup, 1976) (Smith, 2001). The second seeks to explain this association through invocation of a ‘common cause’ hypothesis, first investigated by Peters (Peters, 2005), and developed subsequently in empirical models. This hypothesis seeks to explain the association between apparent diversity and rock availability through a secondary mutual driver, such as tectonics or eustacy. The third is a recently-developed hypothesis describing the correspondence in terms of ‘redundancy’, which is the equivalent to reverse causality in which the diversity of species actually drives the number of fossil-bearing localities (Benton, et al., 2011). The issue remains to assess how interwoven these three factors are, the degree to which they independently operate on different scales, and how to account for them to render a more faithful representation of the biological record.

There are significant problems with these approaches to assessing and correcting for extinction patterns. Firstly, to what degree is last occurrence a reasonable proxy for lineage termination? To equate the two is to fall into the trap of absence of evidence is evidence of absence. There are probabilistic methods of statistically extending the temporal ranges of organisms by looking at frequency density distributions through their known stratigraphic ranges, but this is exceptionally problematic for tetrapods, in which much of the time species are only known from single individual fossil occurrences. Secondly, there is the issue of ‘pseudoextinction’, in which our perception of the fossil record indicates that a lineage has terminated, when in fact the species (or populations that represent that species) have evolved into new species, which is not a ‘true’ extinction as there has not been a reduction in net diversity, but it has remained constant. This is known as the ‘Signor-Lipps’ effect, or “artificial range truncation” (Signor III & Lipps, 1982, p. 295), and it’s opposite, pertaining the post-dating of origination events, is the ‘Sppil-Rongis’ effect. The Signor-Lipps effect can be produced when post-mortem factors such as sample size, relative abundance, and diagenetic heterogeneity combine to complicate the final appearance of taxa in the fossil record, and remove an indeterminate portion of the lineage duration. The potential effect this has, leading up to a mass extinction, is a change in the rate of extinction, which could manifest itself as a gradual shift as extinction intensity increases through time when in fact the reality would have been more instantaneous.

The problem of data quality must be addressed here. Given the nature of the stratigraphic and fossil records, we will never be able to perfectly track biodiversity trends through time. There are differences between the marine and terrestrial records that need to be overcome, or at least accounted for in some manner. The question, however, is are the data of high enough quality, and sufficient enough to accurately reflect the nature of the biological record and unravel macroevolutionary pattern and process. As the saying goes, “all models are wrong, some are just better than others”; therefore it is a case that when we use global databases, we recognise their limitations, but also that they are the best we have, and that they are sufficient to assess what we, as palaeontologists, need them for. This adequacy has been tested rigorously in some groups such as dinosaurs (Wills, et al., 2008), but less so in the other tetrapod groups that will be analysed here.

Because of this, understanding and unmasking the impact of structural biases in the fossil record has received considerable interest in the recent literature, revealing much about the co-variation of geological, taxonomic, and biological patterns. These biases exist in both the marine and terrestrial realms, with differential sedimentation, sequence architecture histories and patterns for each acting in concert to occlude the true nature of the biological record (Padian & Clemens, 1985) (Behrensmeyer, et al., 2000) (Smith, 2001) (Kalmar & Currie, 2010). Evidence that compensation for these biases is an effective measure of analysing ‘true’ biodiversity comes from the fact that diversity curves change, often dramatically, as biases are accounted for, and can often converge on similar signals using different statistical approaches.

Many methods exist currently to correct raw biodiversity curves to account for these sampling biases. Raup was the first to draw the link between apparent Phanerozoic marine diversity and amount of sedimentary rock available to be sampled (Raup, 1972). Since then, a host of studies have attempted to tease apart this relationship to test the adequacy of diversity patterns recovered from the fossil record. Tested geological proxies to date include estimates of total rock volume (Kalmar & Currie, 2010) (Raup, 1972), the number of sedimentary fossiliferous formations through time (Fountaine, et al., 2005) (Wang & Dodson, 2006) (Barrett, et al., 2009) (Butler, et al., 2009), rock outcrop area (Smith, 2001) (Smith & McGowan, 2007) (Wall, et al., 2011) (Mannion & Upchurch, 2011), or the use of global sea-level curves which are intimately tied to sedimentation rates (Butler, et al., 2011) (Mannion & Upchurch, 2010).

### Influence of the geological record

The number of geological formations is commonly used as a proxy for the amount of rock in a given temporal interval, and has been found to correspond to rock outcrop area, at least on a continental level (Peters & Foote, 2001). Their use is based on the assertion that formations accurately represent the variation in both facies and rock type through time. An extension of this is the number of fossil-bearing formations, which represents an aspect of the geology in where fossils have definitively been sampled from, as opposed to other proxies (e.g., outcrop area), where regions recorded may be entirely devoid of fossils. For example, for dinosaurs, the number of dinosaur-bearing formations would be used as a proxy for the dinosaur-bearing geological record. Whether or not the total number of sedimentary formations (or fossil-bearing formations) accurately reflects rock volume, and therefore can act as adequate proxies for available rock to sample, has not been rigorously tested on scales larger than local (Dunhill, 2011) or regional (Dunhill, 2012). There has been much debate over the adequacy of this proxy in the literature recently, given its relatively widespread application but seemingly lack of rigorous testing as to its fundamental value as a proxy (e.g., (Benton, et al., 2011) (Dunhill, 2012) (Benson & Butler, 2012) (Upchurch, et al., 2012). This debate largely revolves around the use of formations as a largely arbitrary construct, which while they may represent lithological or facies-related heterogeneities, may not be a valid proxy for the actual amount of rock available to sample. Using number of formations (i.e., arbitrarily named and bound rock packages, essentially a taxonomic construct) may therefore not appropriate due to their subjective and nature. This fact remains in spite of the discovery that rock outcrop area and number of geological formations appears to be closely correlated (Peters & Foote, 2001). What this means is that formation counts are subjective, and although carry geological meaning internally, may not be useful in comparative analyses due to the lack of a consistent definition or quantitative definition framework.

Rock outcrop area has been used as a proxy for rock record completeness in many studies to observe potential controlling factors behind biological signals in the fossil record (Crampton, et al., 2003) (Peters & Heim, 2010) (Wall, et al., 2011) (Smith & McGowan, 2011) (Mannion, et al., 2011). Map area is presumed to be an adequate proxy for rock accessibility, or exposure, due to the presumption that greater landscape coverage equates to greater exposed rock for opportunistic sampling (Peters & Foote, 2001) (Smith & McGowan, 2005) (Mannion, et al., 2011) (Hannisdal & Peters, 2011) (Smith & Benson, 2012). There are two methods currently used to measure the extent of sedimentary rock availability in this context. The first uses geological maps from repositories such as the British Geological Survey which express the areal extent of individual formations (e.g., (Peters & Heim, 2010) (Wall, et al., 2011)); the second uses an equal-grid sampling protocol, where map area is divided into a polygonal grid and the number of grids in which a particular rock type is present at outcrop over a particular time interval are summed (Smith, 2001) (Smith & McGowan, 2005) (Smith & McGowan, 2007). This latter method is often used in conjunction with historical accounts of the lithology and fossiliferous information, so therefore does include a crude estimation of fossiliferous exposure.

Outcrop area for a given formation (mapable rock unit) is map surface area estimated from the extent and geometry of the surface exposures of that formation. It is the interaction of the three-dimensional architecture of a rock body with the landscape topography, but is not linearly correlated to rock volume due to the intrinsic and prevalent geometric anisotropy (through folds, faults, lateral variations) of rock units. Therefore, map area may not reflect any genuine geological underpinning such as exposure area (that which you can physically touch and directly sample), or rock volume, or lithofacies variety, and the theory that it may represent a proxy for opportunity to sample fossil-bearing rocks or rock record itself is limited based on this extrapolation. Several studies have demonstrated the correlation between measured exposure area and estimated outcrop area, with varying results (Dunhill, 2011) (Dunhill, 2012). In New York State, England and Wales, a positive correlation between rock outcrop area and exposure does not exist. However, in California and Australia there is a positive correspondence between accessible rock and outcrop area. At a very crude level, it is possible to suggest that this distinction may have something to do with historical land use – California and Australia are both largely vast desert, and New York state and the United Kingdom are industrial, densely occupied, and largely covered by arable habitats, with fossil collecting largely being opportunistic events as superficial cover is stripped (e.g. historically for mining) or along coast lines.

That it might be correlated in some way to observed biodiversity, then, may not represent anything geologically significant, if all outcrop area represents is the areal representation of an anisotropic rock body. Geologically it certainly should not, in theory, have any meaningful control on biological signal. Therefore, its continued use should be cautioned based on the lack of a deterministic and rigorous basis for being a proxy for either the geological record or the number of opportunities to observe fossils, as many studies have used in the past. This caution is compounded in the current study based on the uncertainty in global-scale sedimentation patterns through the Jurassic/Cretaceous interval, and poor understanding of the correlation of global eustatic curves (Zorina, et al., 2008). A potential global sedimentation break associated with this, with evidence from regional unconformities, means that outcrop area may be an unsuitable proxy throughout this interval due to a general lack of sedimentary deposition and remaining exposed sedimentary rock.

Some studies (e.g., (Wall, et al., 2011)) maintain that, in spite of counter-arguments against rock outcrop area by (Benton, et al., 2011) and (Dunhill, 2012), when scaled to a resolution of which data from the PaleoDB is applicable, this discrepancy does not maintain an influence on diversity data. This is only partially justified, however, in the subjective assertion that “while outcrop maps may not perfectly reflect the areal extent of exposure, they certainly capture information on its spatial distribution” (Wall, et al., 2011, p. 55), without further empirical validation. The additional assumption that (Wall, et al., 2011) make is also invalid, in which they assume that outcrop area is a reflection of some sort (the relationship is not described) of rock volume. This assumption completely ignores the fundamental laws of geology, in that structural complexity at the exposure level reflects itself in the anisotropic distribution of subsurface rock volume, and is often not correlated in a linear fashion. Exposure is also not a historically constant metric, and is subject to change as superficial deposits are gained and lost, land use changes, and with erosion, particularly in coastal regions. The question remains, then, as to whether surface area is an adequate proxy for fossil-bearing exposure.

Conditions where outcrop area could satisfactorily act as a proxy for rock volume, and hence sampling, would be if the number of taxa collected had reached an azimuth and was becoming asymptotic through time, representing that additional sampling would not have any effect on net biodiversity in the formation. Alternatively, and in agreement with (Dunhill, 2012), rock outcrop area should consistently correlate with fossil-bearing exposure over different temporal and spatial scales, which will provide an unbiased and rigorous proxy for amount of rock available for sampling. Progress is being made in this field, with the demonstration of exposure-scale mapping using remote sensing through LiDAR (Light Detection and Ranging) and Geographic Information Systems on a local and regional scale (Dunhill, 2011) (Dunhill, 2012). Such proof of concept studies convey that quantification of the geological record is possible, in terms of exposed and available rock, and add a new dimension to the analysis of biodiversity, fossil record bias and heterogeneity, and species-area affects. However, these analyses are on local to regional scales, and may not be sufficient in altering or contributing to larger-scale macroevolutionary patterns such as radiations or mass extinctions. Dunhill also recognises the limitations in not being able to record the vertical component of exposure, and not being able to account for historical variations in exposure (Dunhill, 2012). Global studies, such as that of (Barrett, et al., 2009) could certainly benefit from integrating such studies to a degree, but with the awareness that the two are not in parallel in terms of seeking the same answers to the same questions. Future work should focus on the development of a suite of records, as in (Dunhill, 2012), and concatenate them to produce a ‘global’ series of events that could be used as a more realistic rock record proxy. The integration of facies-related data with this would greatly improve the strength of such records.

The question comes down to sufficiency. How sufficient are both rock outcrop and the number of formations, fossil-bearing or otherwise, at reflecting a geological sampling bias, and how do they integrate with the concept of redundancy (i.e., convergence on the same signal through common representation of the same signal)? Taking a historical stance, outcrop area may be adequate if one considers outcrop area to be a representation of the total pool of rock that has been available for differential sampling as society has developed, and rocks have become exposed and covered as road cuttings and quarries evolve through time. The caution here is then that rock outcrop becomes a measure of probability, and not a linear and direct measure of total rock availability through time. The issue of redundancy is potentially higher with respect to a formation-based proxy. The concept here is that with natural fluctuations in diversity, the probability of preservation of a particular taxon increases or decreases and therefore so does the probability of the stratigraphic unit being a taxon-bearing formation. This important problem can be accounted for by scaling up the formation proxy, for example from sauropods to dinosaurs, or dinosaurs to tetrapods, so that taxon-specific redundancy trends are avoided and genuine biodiversity signals are instead captured, independent of the preservation-per formation probability.

Both of the above methods at attempting to quantify the amount of rock available for sampling are, in conclusion, subject to potential error. They are, however, both methods that can be used as the basis for attempting to remove geological bias from diversity curves, based on the hypothesis that the more rock available to sample, the more fossils can be obtained and the greater alpha taxonomy reconstituted. What is undoubtedly required in the future is development of measures of the actual historically exposed fossil-bearing rock area, which would be a theoretically sound proxy for the correspondence between geology and biology, or a metric for the total volume of a formation, which could represent the total quantity of rock that is hypothetically available to be sampled (Crampton, et al., 2003). These logical extensions would, if possible to create, represent more faithful proxies for the geological record. In sum, what this signifies is that there are currently theoretical and methodological difficulties in developing a global correction scheme for systematic removal of geological sampling biases. In spite of these limitations, rock outcrop area and the number of fossil-bearing formations, when considered carefully in terms what they mean in different contexts and at different scales, may still provide meaningful corrections for removing the impact of sampling bias on the fossil record.

In the context of this current study, regional sedimentation rates over the Jurassic/Cretaceous boundary may have varied substantially. Regionally concentrated unconformities from the Tithonian through to the lower Valanginian (about 152 to 138Ma) are strongly diachronous, resulting from sea-level regression and eustatic lowstand (Haq, et al., 1987), that may relate to the emplacement of mantle plumes (Zorina, et al., 2008). A global eustatic drop may also be responsible, and the diachronous nature of the unconformities due to the variation in tectonic stability; i.e., tectonic uplift causing earlier unconformities compared to regions of subsidence. This would have caused low sedimentation rates, followed by a general increase in sedimentation as relative sea-level increased again following the J/K boundary, which is a pattern found on both a global and regional level (Grabowski, et al., 2013) (Haq, et al., 1987). Despite this consistent trend, the implications for the use of outcrop area as a proxy for the geological record throughout this period are concerning, due to the heterogeneity of sedimentary packages, the lack of a single plausible driving factor, and difficulties in assigning the sedimentary packages to a specific geological time.

### Anthropogenic influences on sampling effort

Humans also have a part to play in inflicting biases on fossil collecting effort, and therefore our understanding of the factors controlling their distribution (Alroy, et al., 2008) (Peters, 2008) (Benton, 1985). Such biases are more to do with how we have collected from the geological record, including, for example, humans sampling only the biggest or best-looking fossils, or only being able sample from particular horizons due to geomorphological, time, or exposure constraints. These issues, however, can be compensated for to provide a more transparent understanding of the fossil record. Additional human-induced factors include the issue of worker effort, or knowledge accumulation through time, and how this changes our historical understanding of macroevolutionary patterns (Bernard, et al., 2010) (Ksepka & Boyd, 2012).

Additional artefacts include the monographic effect, where groups that have received more detailed attention, particularly with respect to taxonomy, may be inflated taxonomically, or simply are more diverse as more effort has gone into describing new species. Similar issues arise for particular periods in time, as some may be more intensely sampled than others due to locality issues, or even political constraints. Proxies for worker effect can be represented by the number of dinosaur-bearing collections, defined for the PaleoDB as an irreducible, independent and discrete location where fossils have been collected from a specific stratigraphic horizon (Mannion, et al., 2011).

A second method of observing the impact of worker effort is to construct collector curves. These are essentially plots of the number of named species through time, based on publication records. By plotting a cumulative frequency curve against the date of naming and description, the rate of taxonomic diversity increase of particular groups can be observed through time. When this curve begins to reach its zenith and flatten off (i.e., the rate of increase of species’ erection falls markedly), then it’s a reasonable indication that the species’ diversity of that particular group is becoming taxonomically saturated (Benton, 1998). The assumption behind this, of course, is that the fossil record represents an accurate depiction of the biological record, in that all that could have been preserved has been collected, so has no way of compensating for animals that were potentially present but not preserved.

### Phylogenetic diversity

The role of phylogeny in governing macroevolutionary patterns is well-understood from a fossil record perspective (Norell & Novacek, 1992) (Weishampel & Jianu, 2000) (Upchurch & Barrett, 2005) (Benton, 2010) (Benton, 2012). Phylogenetic diversity is a second way, along with taxic diversity, in assessing biodiversity patterns in the fossil record. It requires knowledge of the temporal association of a species and that species’ evolutionary relationships, and is effectively a method of mapping phylogeny on to stratigraphy. The main advantage though relies on the concept of sister species. Reciprocal sister species must have an identical origin in time and space from where the node splits into the two respective branches, following the bifurcation model of speciation. This allows one to extrapolate the first occurrence times of associated sister taxa based on the geometry of the tree, to create ‘ghost lineages’ using minimal implied basal stratigraphic ranges. These reflect missing species’ occurrences in the fossil record, and are compensated by our knowledge of what we know must have been present in a given time given a phylogenetic hypothesis (Norell, 1992) (Barrett, et al., 2009).

## The Jurassic/Cretaceous boundary

Early research into mass extinctions recognised that there was some sort of aberration from background extinction rates across the Jurassic/Cretaceous (J/K) interval, but that it was geographically and taxonomically constrained to a degree that did not warrant its identification as a mass extinction, *sensu stricto* (Benton, 1986) (Hallam, 1986) (Hallam & Wignall, 1997). Sepkoski and Raup (Raup & Sepkoski, 1982) identified a mass extinction in marine invertebrates at the boundary, at the taxonomic level of Family, and comparable in magnitude to the well-known Triassic/Jurassic extinction event. Similar results were recovered by several studies subsequently (Raup & Sepkoski, 1984) (Sepkoski, 1984) (Sepkoski, 1993) (Benton, 2001) (Alroy, et al., 2008). Hallam corroborated this pattern, identifying the boundary as a “possible mass extinction” (Hallam, 1998), but suggested that this pattern may be the product of a bias towards European fossils in their database. This suggestion is somewhat validated by regional studies of the western Tethys and western Europe, with a cooling episode in the late Tithonian followed by a temperature and humidity increase during the Berriasian (Grabowski, et al., 2013).

Currently, the state of understanding of the J/K interval is relatively poor compared to other more ‘exotic’ crisis periods. This is in part due to the lack of a robust global chronostratigraphic framework, and also due to difficulties in distinguishing between local, regional, and global events, especially in marine environments (Sellwood & Valdes, 2006) (Tremolada, et al., 2006). Only one of these studies too uses any form of sampling standardisation (Alroy, et al., 2008) to account for inherent megabias. Accordingly, revision of this important interval is needed in light of new theoretical underpinning of macroevolution, methodological refinement of accounting for sampling biases, and a more refined understanding of the nature of the fossil record. In terms of biodiversity patterns over the Jurassic/Cretaceous interval, there has been relatively little research compared to the more ‘dramatic’ Mesozoic extinctions. Studies have varied from local scale taxon-specific (Nishida, et al., 2013) (Ruban, 2011) (Gasparini, et al., 1999) to larger tetrapod-scale (Benton, 1989) (Benson, et al., 2010) (Benson & Butler, 2012) (Benson & Druckenmiller, 2013), or as parts of larger global-scale studies of marine invertebrates (Sepkoski, 1984) (Alroy, 2008) (Alroy, et al., 2008) or dinosaurs (Barrett, et al., 2009) (Mannion, et al., 2011) (Upchurch, et al., 2012). According to (Bambach, 2006), many groups still suffered elevated extinctions over the interval (at a raw reading of the fossil record), including scleractinian corals, rhynchonellid brachiopods, some groups of bivalves and ammonites, and marine reptiles. Such taxonomic selectivity is an indicator that a genuine biological signal is being found, albeit scrappily, surrounding the Jurassic/Cretaceous, and that a secondary artefact that equally impacts all groups is not a primary driver of recovered patterns.

Only one study to date has specifically focussed on tetrapods over this interval, and only published in abstract form to date (Orcutt, et al., 2007). This analysis focussed on temporally constrained local faunas over the boundary, and preliminary results suggest that the J/K interval represents a mass extinction in tetrapods, particularly in theropod dinosaurs and mammals, while other groups such as crocodiles and turtles were largely unaffected. The study also finds that ornithischian dinosaurs increase in relative diversity compared to sauropods, suggesting some form of within-community ecological partitioning. This thesis will expand considerably upon this study, which does not appear to have reached fruition since abstract publication in 2007.

Other studies on tetrapods have considered the Jurassic/Cretaceous boundary as part of Mesozoic-scale studies on tetrapods. It has previously been found that at a raw species count, dinosaurs increase in biodiversity during the Late Jurassic, peaking in the Oxfordian-Kimmeridgian before declining into the latest Jurassic (Tithonian) (Dodson, 1990) (Sereno, 1999). These accounts, although similar to more recent analyses involving supertree-based diversity (Lloyd, et al., 2008), do not explicitly address how sampling biases and phylogenetic reconstruction impact our understanding of biodiversity trajectories through time. Aspects of this pattern have been corroborated by other studies, for example a substantial trough in sauropodomorph biodiversity leading up to the Jurassic/Cretaceous (Oxfordian) when various sampling artefacts are accounted for (Mannion, et al., 2011), although this is followed by an equally aberrant peak during the Kimmeridgian-Tithonian. However, a portion of this result may be attributable to uncertainty in the dating of Upper Jurassic terrestrial rocks. A similar signal in sauropodomorphs was recovered by (Barrett, et al., 2009), but with the diversity crash occurring in the Berriasian, and only a moderate decline in sauropodomorph diversity leading up the interval. Theropods and ornithischians seem largely unaffected, with only moderate drops in taxic diversity. Using residuals, (Wall, et al., 2011) found a peak in terrestrial diversity in the Upper Jurassic, followed by a significant trough in the Lower Cretaceous.

At the Family level (Fara & Benton, 2000) found that between the Tithonian and Berriasian, there was an almost halving in the completeness of the tetrapod record and distributed evenly among animals of all body sizes, in alignment with an increase in terrestrial tetrapod provincialisation as Pangaea continued to fragment from the Middle Jurassic (Benton, 1985). Taking a raw account of the tetrapod fossil record (Benton, 1989) found slightly elevated taxonomic extinction rates at the end-Tithonian, coinciding with a moderate peak in total and per-taxon extinction rates. Accounts like this, however, must be interpreted with caution for not considering the intrinsic nature of the fossil record in detail, or are at least in need of reassessment due to practical and theoretical developments in the field of macroevolution and sampling biases. The Jurassic-Cretaceous interval was entirely dismissed by Hallam and Wignall’s review on the correspondence between sea-level and mass extinctions, even as a minor event (Hallam & Wignall, 1999). Tying this all together, it strongly indicates that more work is needed investigating the environmental and biological patterns and processes over this important interval in Earth’s history.

## Case study: atoposaurid crocodylomorphs

The Family Atoposauridae (originally Atoposauridés) was erected by (Gervais, 1971) to describe a small animal, *Atoposaurus*, the type genus for the clade. Subsequent to this, the species was placed within Crocodylia by (von Zittel, 1890), and further work recognised atoposaurids as a group of ‘dwarfed’ neosuchians, the group including all extant crocodylians. Atoposaurids had a broad geographic distribution, and their fossil record spans the Late Jurassic through to the latest Cretaceous. Being less than one metre in length, they were clearly ecologically specialised, adapting to specific conditions that may reflect competition within often unusually high diversity crocodilian faunas. The number of putative taxa assigned to this small enigmatic family has increased in recent years, expanding their phylogeographic distribution out of Europe where the first four taxa were found into the rest of Laurasia and even possibly Gondwana (Buscalioni & Sanz, 1990).

The oldest known atoposaurid remains are from the Middle Jurassic (Bathonian) of England, *Theriosuchus*, and the precursor to a radiation into the northern hemisphere (Evans & Milner, 1994) (Thies, et al., 1997). *Theriosuchus* is well-known from a number of localities in mainland Europe and England (Owen, 1879) (Buscalioni & Sanz, 1984) (Buscalioni & Sanz, 1987) (Buscalioni & Sanz, 1987) (Salisbury, 2002) (Salisbury & Naish, 2011). Reports based on isolated teeth place this genus in North America (Pomes, 1990) (Winkler, et al., 1990) (Thies, et al., 1997), although affinities of this standard are somewhat dubious, and additional *Theriosuchus* species are known from Thailand (Lauprasert, et al., 2011). Ambiguous atoposaurids have been reported from North America (*Pachycheilosuchus trinquei* from the Glen Rose Formation, Texas) and additional isolated teeth from the Cedar Mountain formation of Utah (Cifelli, et al., 1999) (Eaton, et al., 1999) (Fiorillo, 1999) (Rogers II, 2003). Asian form persisted from the Upper Jurassic until the Lower Cretaceous, implying that atoposaurids dispersed out of Europe and into the rest of Laurasia during this period.

A recent analysis by (Lauprasert, et al., 2011) recognised only four valid genera within Atoposauridae: *Theriosuchus, Alligatorium, Alligatorellus* and *Montsecosuchus*, with the former-most being sub-divided into three valid species; *T. pusillus*, *T. ibericus* and *T. guimarotae* (see (Owen, 1878) (Owen, 1879) (Joffe, 1967) (Buffetaut, 1982) (Clark, 1986) (Buscalioni & Sanz, 1988) (Brinkmann, 1992) (Wu, et al., 1996) (Schwarz & Salisbury, 2005)), and a fourth being named as *T. grandinaris*. A fifth species is known, *T. sympiestodon*, but its taxonomic validity is uncertain (Martin, et al., 2010). The taxonomic identity of these specimens and internal relationships have not been comprehensively reviewed, which is somewhat paradoxical given their important phylogenetic position near the base of Neosuchia, their biogeographical implications and temporal span, and the clear need for systematic revision given the uncertainty surrounding the taxonomic identity of many species and specimens. They also provide an opportunity for more detailed assessment of their macroevolutionary patterns from the Jurassic through to the end Cretaceous.

# Hypotheses

Following, are the main hypotheses that will be tested during this thesis, along with secondary hypotheses that form under them, and null or alternative hypotheses where appropriate.

1. Over the Jurassic/Cretaceous interval, there was a mass extinction in tetrapods, on the order of 60% species biodiversity lost, when sampling biases are accounted for (minimum estimate for the end-Ordovician extinction);
   1. Null: There was no excursion from standardised background rates during this period;
   2. Alternative: Extinction rates were elevated over this period, but not sufficient to be formally classified as a mass extinction;
2. Different patterns of and processes of extinction can be detected between the broad marine and terrestrial realms, and within-groups where they occupy both;
   1. Null: There is no statistical difference between biodiversity patterns between the marine and terrestrial records;
   2. Alternative: There is no general pattern of differentiation between marine and terrestrial tetrapods, although differences are reflected within less inclusive groups;
3. Geography plays an important role in extinction rate, with the same groups in different regions experiencing different patterns of extinction and origination;
   1. Null: Geographical location has no correspondence with biodiversity patterns;
   2. Alternative: Some groups suffer different extinction and origination rates depending on geography, whereas others are unaffected;
4. A combination of extrinsic and intrinsic parameters covary with the biodiversity patterns resolved;
   1. Null: No factors correspond statistically with biodiversity patterns;
   2. Alternative: Some factors correspond with biodiversity patterns in some groups.

# Materials and methods

The collection and use of 'big data' in Palaeontology is on the rise. As computers have increased in their power and capability, the amount of data we have been able to feed into them and analyse has increased. Spearheading this is the Paleobiology Database (PaleoDB) (Alroy, 2003). This is an open database recording data such as specimen occurrences, collections information, taxonomic relationships, and other metadata including geological age, collection mode, and depositional environment. The goal is to have occurrence data for all fossil specimens spanning the marine and terrestrial realms during the Phanerozoic, including both vertebrates and invertebrates. It is worth noting here that the data compiled in the PaleoDB is different to that used by previous palaeodiversity analytics (e.g., Raup and Sepkoski), in that it is the individual taxonomic or specimen-based occurrences in a particular time and place that form the basis for estimating biodiversity, as opposed to the interpolation of lineage longevity using first and last occurrences. In total for this study, the PaleoDB has incorporates 5670 tetrapod taxonomic occurrences from the Callovian – Aptian. Many studies have incorporated the PaleoDB to analyse diversity patterns, both on a global (Alroy, et al., 2001) (Alroy, et al., 2008) (Wall, et al., 2011) and local scale. They provide baseline biodiversity curves for investigating the extrinsic and intrinsic controls or drivers, and correlates of macroevolutionary patterns through time (Payne & Finnegan, 2007) (Alroy, 2010). Note, however, that some of these studies, particularly more temporally expansive ones involving tetrapods, were undoubtedly conducted before the data were mature or complete enough for such analyses (e.g., (Wall, et al., 2011)).

Tetrapod diversity was calculated as the number of species within a number of fossil-bearing localities as a measure of species richness through different time slices. The three advantages of this approach are firstly, comprehensiveness, secondly, computationally simple approach, and thirdly, no requisite of phylogenetic relationships beyond higher inclusive taxa (Mannion, et al., 2011). This third point is actually a double-edged sword, as it makes the explicit statement that diversity is independent of phylogeny, which is rarely the case. Time-bins used followed the International Commission on Stratigraphy (Gradstein, et al., 2012) stage intervals to plot stratigraphic ranges, with 9 stage bins from the Callovian to the Aptian.

Much of the data recorded in the PaleoDB is diagnosed only to the level of genus, for example, as *Camarasaurus* sp. or higher taxonomic unit, for example as Sauropoda indet. This level of diagnosis reflects natural uncertainty from palaeontologists when it comes to taxonomic assignment. What it means, however, is that there is no standardised way of comparing these to diagnosed species, as they may or may not reflect new species. There are multiple approaches to overcoming this problem. The first would be to use a higher taxonomic unit which would then encapsulate more of the recorded data, such as genera. However, this would inflict the problem of the arbitrary nature of higher-level taxonomy on the data sample. A second approach, and a much more conservative one, would be to ignore any undiagnosed occurrences, with the implication that the probability of there being additional species in the data set is zero. A third approach would be to inflate the species data, based on what we know is present but not diagnosed to the species level in the individual bins. For example, if in one time bin there are 100 named species, and *Camarasaurus* sp. is present with no species-level diagnosed *Camarasaurus*, then we can assume that there is at least one additional, but unnamed species present and add this to the taxic list. This process can be repeated for all undiagnosed occurrences, and is a safe way of artificially inflating the species diversity without making any additional assumptions about taxonomy. As such, there are two raw data sets forming the basis of the taxic diversity assessments. The second inflated one of these is in preparation. An additional comparison will also be drawn between the species and genus level tetrapod data set to see if there’s a strong correlation between the two.

## Sample standardisation

In order to assess the impact of biased or uneven sampling of the tetrapod fossil record, multiple standardisation techniques were applied. This was to explore the range of differential influences that different sampling techniques can have on the shape of the tetrapod diversity curve over the J/K interval, and whether or not they converged on a common signal, or provide different accounts of the apparent trends. Sampling standardised curves are not designed to provide an absolute measure of predicted biodiversity given complete sampling; rather, they provide a best estimate of diversity given a particular level of sampling intensity. As such, they are purely methods for accounting for the inherent biases in sample size heterogeneity.

### Subsampling methods

Randomised subsampling methods are a relatively new approach to overcoming the biases inherent in the fossil record. They are designed to remove the effects of, or at least estimate a way of compensating for, uneven sampling of the fossil record, thereby allowing meaningful comparative analysis between time-series and interpretation of biodiversity trends. They work by removing data from relatively well-sampled lists of taxa, and reducing them to a state that is comparable to intervals that are relatively poorly sampled (Alroy, et al., 2001).

Rarefaction is a method of accounting for biases in sample sizes, coined by (Sanders, 1968) and first introduced into mainstream palaeontology for taxonomic purposes (Raup, 1975) (Tipper, 1979) and subsequently for assessments of morphology (Foote, 1996). It was initially designed as a method of assessing species richness based on the number of specimens in a sample, but can be applied to any analysis of samples within higher units (e.g., species occurrences per time bin; (Miller & Foote, 1996)). As an interpolation-based method for estimating richness at smaller sample sizes and exploring the impact of sample size on taxonomic richness, it is of considerable use in biodiversity studies, particularly in palaeontology where samples can be substantially limited in size (Foote, 1996) (Jackson & Johnson, 2001) (Johnson, 2003). The central goal, therefore, of rarefaction is to test the hypothesis that observed trends in biodiversity are the result of heterogeneous sample sizes. In tetrapods, its use has mainly focussed on dinosaurs on a global (Fastovsky, et al., 2004) (Lloyd, et al., 2008), regional (Sheehan, et al., 1991), or taxonomically constrained manner (Mannion, et al., 2011). The basis for rarefaction is that larger sample sizes are expected to yield higher numbers of taxa, and that sufficient sampling to include all taxa can only occur when sample sizes are consistently large enough. It works by estimating diversity by scaling samples to consistent sample sizes, and measuring the relative frequencies of species with respect to an inclusive ‘list’, such as a collection or taxonomic occurrences per time bin. By changing the scaling threshold, different subsampling patterns emerge, highlighting how differences in sample size are driving apparent diversity patterns. Preliminary analyses set this threshold at 30, 50, 70, 90 and 100 to assess the impact of these different limits on the geometry of the curve.

Rarefaction carries with it assumptions about the data, in that the samples must be taxonomically similar, all derived from the same habitats, and collected using comparable sampling techniques (Tipper, 1979) (Raup, 1975). Rarefaction techniques using the fossil record are conducted in relative terms, as there is always the perpetual issue of non-complete sampling which means that absolute sample sizes and species richness estimates will never be known absolutely (Raup, 1975). Additionally, Stage intervals are not equal, and it is typically expected that under standardised sampling conditions, more fossils will be collected from longer duration intervals. This has a negative implication for rarefaction analysis, which is time-dependent (Foote, 1996). A further assumption that rarefaction makes, along with occurrences weighted and occurrences-squared weighted subsampling methods is that alpha diversity has remained constant through time, and that patterns of beta diversity are being drive by incomplete sampling. A limitation of rarefaction is that while it does correct for differences in sample size, whether or not these differences can be accounted for by taphonomic biases, incomplete sampling, or true biological signals representing a change in species richness. As such, the sampling standardised interpretations of biodiversity will be compared with proxies that represent geological megabiases in the fossil record (e.g., via the residuals approach).

An interesting extension of this analysis was carried out by (Mannion, et al., 2011) involving sauropodomorph dinosaurs, whereby an additional taxon, in this case at the genus level, was added to each occurrence sample where a higher level but indeterminate specimen had been identified representing a clade that had no otherwise named specimens within that sample. This means that multiple new ‘species’ can be added to each sample, representing a variety of different indeterminate specimens.

The advantages of this methodological extension are twofold. Firstly, it provides an estimate of ‘cryptic’ diversity concealed within the global dataset, as in specimens that must represent distinct species within a locality, but for any number of reasons have not been identified as such. Secondly, increased sample sizes are beneficial for rarefaction analysis which relies heavily on the size of the smallest sample for performance efficiency (Mannion, et al., 2011). For the sake of completeness, a total evidence approach will also be conducted by rarefying the whole global occurrence dataset. This represents the maximum threshold that tetrapod biodiversity could have attained, if all indeterminate specimens transpired to be new species. Finally, it also does not inflict any artificial bias by ‘double-counting’ species, as higher taxa which already have a named inclusive taxon are not additionally counted.

Methods of standardisation vary between using the number of localities (e.g., PaleoDB collections), or the number of species within each time interval (in this case, stage bins). Each list is essentially a measure of alpha diversity, or within-habitat diversity, where each collection is considered to be a valid discrete correspondent for a habitat. Four modes of sub-sampling analysis were described and employed by (Alroy, et al., 2001) in an attempt to account for the various modes in which incomplete sampling can influence our reading of the fossil record. They form part of an essential protocol to standardise collecting effort through time so that relative diversity can be assessed independently of sampling effort. The first of these is rarefaction, as described previously. The remaining three are different methods of subsampling based on taxonomic occurrence lists and various weighting exponents. They are summarised by (Bush, et al., 2004) in their analysis of sub-sampling on different spatial scales. Each time interval is assigned a list of fossil-bearing collections (or irreducible localities) and a list of taxa within each collection. The first of these methods uses a by-lists unweighted algorithm (UW), whereby a number of collections-based taxonomic lists are drawn randomly and without replacement from each time period, to produce a matrix consisting of unique taxa (weight = 0.0) The second method uses a by-list weighted occurrences algorithm (OW). This is achieved by setting the weighting exponent to 1.0. Whole taxonomic lists are sampled from each time interval until a pre-defined sub-sampling quota is reached (can be set at different counts). For each method, by drawing at random from this matrix until this pre-defined count is reached, and iterating multiple times (which also gives a measure of confidence intervals), a relative measure of taxonomic diversity can be estimated. The by-list occurrences-squared weighting method sets the weighting exponent to 2.0, thereby squaring the number of taxa in each list to mimic increased sampling intensity (O2W). Variants can be produced between these three members by randomly changing the exponent until optimal weighting is achieved, but as these methods are those most covered in previous literature and understood the most, are adhered to for analyses here (Alroy, et al., 2001) (Bush, et al., 2004). However, (Bush, et al., 2004) did find that an optimal weighting exponent is around 1.5 - 1.3 for selective regional and global analyses, so a fourth sub-sampling analysis was conducted with the weighting exponent set to 1.4. The issue with determining the optimal value for *x* is that it requires collections-based abundance data per-taxon, which is a largely unattainable goal for tetrapods, and not required for understanding of regional to global scales of biodiversity. Furthermore, it is also not possible for the Paleobiology database, where taxonomic lists are by default restricted to a single occurrence per taxon per collection. The methods here will be expanded on further, including an assessment using the shareholder quorum subsampling (SQS) method (Alroy, 2010).

### Estimating phylogenetic diversity

The informal supertree method is effectively a way of stitching together complimentary and over-lapping portions of independently attained trees, to construct larger-scale series of relationships but without making any additional phylogenetic assumptions (Lloyd, et al., 2008) (Pisani, et al., 2002). To assess phylogenetic biodiversity through the J/K interval, trees were sourced from Graeme Lloyd’s personal website (downloaded in Newick format, and redrawn in Adobe Illustrator CS5). No large tetrapod tree currently exists, so a new one was reconstructed by ‘bolting’ together regions of overlap in trees from the following sources: Crocodylomorpha (Cau & Fanti, 2011), (Choiniere, et al., 2013), (Adams, 2013), (Andrade, et al., 2011) Ichthyosauria (Fischer, et al., 2013), Dinosauria (Carrano, et al., 2012) (Mannion, et al., 2012) (Mannion, et al., 2013), (Godefroit, et al., 2013), (Coria, et al., 2013), (Brusatte & Benson, 2013), Plesiosauria, (Ketchum & Benson, 2011), (Benson & Druckenmiller, 2013), Testudines, (Perez-Garcia & Murelaga, 2012), Squamata, (Daza, et al., 2012), and Pterosauria, (Lu, et al., 2012). Trees were modified in terms of their predicted ghost lineages to make the least assumptions about the cryptic temporal duration; for example, in (Godefroit, et al., 2013) lineages are extended back through multiple time slices in a seemingly arbitrary fashion (see Troodontidae), instead of minimum divergence times following the bifurcation model of speciation, as ghost lineage reconstruction necessitates. Ranges were restricted to between the Callovian and Aptian.

These trees are of course restricted by taxonomic sampling for the capacity and availability of analysis, but provide a strong basis for reconstructing ghost lineages and an assessment of lineage reconstruction and phylogenetic diversity compared to sampling standardised time-series based estimates of diversity. Stratigraphic calibrations were co-ordinated using data from the PaleoDB and from the source trees where provided. This method provides an estimate of raw taxic diversity through time. Constructing ghost lineages on to this, which will be necessary to fill in the ubiquitous stratigraphic gaps between related lineages, will artificially inflate this to produce an estimate of phylogenetic diversity. Naturally, this skews the inflation of diversity backwards in time. The following rules are applied for the ghost lineages: stage-intervals are divided into quartiles to represent the field of uncertainty regarding the precise extension of lineages; if a taxon appears to pervade into the previous time-slice, it is restricted to purely the upper quartile of that interval in terms of temporal expansion of that lineage, to make minimal assumptions about divergence times of known lineages and hypothetical divergence points. If a lineage appears to go beyond this, it is assumed to be part of the ‘middle’ part of time slice, and the range extended to the mid-point of the stage.

Phylogenetic diversity reconstruction is, however, not without its flaws, as summarised by (Mannion, et al., 2011). Firstly, lineages can only be extended back to the basal minimal stratigraphic occurrence of the sister taxon, which neglects errors in first occurrence for the sister taxon extrapolated backwards towards. This is somewhat overcome by correcting with ghost lineages between successive hypothetical ancestors. By only applying ghost lineages, and not the opposite ‘zombie lineages’, a back-projected skew is applied to the data set by only inflating diversity backwards in time with respect to terminal taxa. Methods of compensating for this could including the probabilistic assessment of whether a species existed further forward in time, using a function of specimen density over their given occurrence range and using this to assess the likelihood of pseudo-absence in time. The magnitude of this issue is probably not as large as has been previously discussed, as to an extent ‘zombie lineages’ are constructed too between hypothetical ancestors (i.e., hypothetical nodes), which may act to counter-balance the asymmetry of a pure ghost lineage approach. In effect, each branch projecting forward from a hypothetical ancestor, but constructed as a ghost lineage, is a zombie lineage. The problem arises when trying to extend lineages forward for terminal taxa in non-ultrametric trees. Additional issues, such as lack of definitive ancestors in the fossil record, or the misdiagnosis of phylogenetic relationships, have been raised before, but their direct quantitative impact on reconstructed phylogenetic diversity trends has yet to be explored in terms of possible solutions (Lane, et al., 2005), and again, our knowledge of the fossil record may be sufficient that such minor discrepancies will not have an influential impact on diversity trends (Benton & Storrs, 1994).

One benefit of taxic diversity estimates over phylogenetic diversity estimates is that they include all named and described taxa, as opposed to those included in the most recent or comprehensive phylogeny. Therefore, it has the benefit of including newly named or redescribed taxa, and may be a more faithful representation of the range of species diversity. The two can, to a degree be integrated. If the relationships of a species are known to a higher taxonomic level (e.g., genus or family) then the species can be superficially ‘glued’ to the tree, but in a place where it makes the least phylogenetic assumptions, so at the least inclusive node as a polytomy. This has the potential to create large ghost lineages, but has the advantage of using all available information with the last number of assumptions made. The alternative to this method is to prune the taxic diversity data to match the data used for phylogenetic diversity. This has the advantage of making the two directly comparable at a species level, but comes with the obvious caveat that diversity estimates are being deliberately deflated to allow this.

### Residual diversity

A suite of methods involves constructing models that perfectly predict sampling, which can be subtracted from raw diversity counts to leave a portion of diversity that must represent an auxiliary signal, usually attributed to biology. This ‘unexplained diversity signal’ approach is known as the residuals method as it is these remaining data after the subtraction that purportedly reflects a genuine biodiversity signal (Smith & McGowan, 2007) (Barrett, et al., 2009) (Butler, et al., 2009) (Benson, et al., 2010) (Wall, et al., 2011) (Mannion, et al., 2011).

The number of fossil-bearing formations or collections has shown to be a meaningful proxy for the amount of rock available for sampling of particular fossil groups (Barrett, et al., 2009) (Mannion, et al., 2011) (Upchurch & Barrett, 2005). This protocol has to be defined with respect to each group being analysed, due to the potential different ways in which each group is preserved, for example based on size differences. Therefore, a suite of proxies is required for all tetrapods, such as crocodyomorph-bearing formations (CBFs), dinosaur-bearing collections (DBCs), and so on for all groups, and an inclusive tetrapod-bearing formations (TBF) proxy for all inclusive groups. Global terrestrial outcrop area throughout the Jurassic and Cretaceous does show a marked trend from relatively low during the Late Jurassic to around a four-fold increase during the lower Cretaceous, not taking into account the relative interval widths (Wall, et al., 2011). The individual terrestrial and marine outcrop data will be used to independently assess the nature of this variable on the biodiversity curves, particularly with respect to the standardised curves.

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