Tetrapod extinction across the Jurassic-Cretaceous boundary

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ABSTRACT

Taphonomic filters can have a major affect on perceived patterns of diversity, and it has been suggested that many apparent extinction events in fact reflect biases in preservation and collection rather than genuine biological signals. Here we present the results of an analysis of tetrapod diversity across one such event, the Jurassic-Cretaceous extinction. Rather than constructing global diversity curves, our analysis is based upon α- (community) diversity within well-preserved and well-studied sites and faunas (e.g. Como Bluff, Tendaguru, Galve, Lujiatun). Our method minimizes the effects of taphonomic bias, commonly cited as a weakness of global diversity curves. Patterns of tetrapod α-diversity across the Jurassic-Cretaceous boundary are consistent with a mass extinction. A decrease in richness can be observed at most taxonomic levels. Large taxa, particularly theropods, experienced the greatest drop in diversity. Some groups, such as turtles and crocodilians, were largely unaffected. The reliability of these results is supported by comparisons with global diversity curves, as well as by cluster analysis, which shows that the patterns observed in this study are most likely shaped by a biological rather than a taphonomic signal.

INTRODUCTION

-While the Jurassic-Cretaceous (J-K) boundary has long been recognized as a mass extinction (Raup & Sepkoski 1984), some studies have suggested otherwise
-Plants show no evidence of extinction at the end of the Jurassic (Niklas 1988), while Marine invertebrates experienced regional rather than global extinctions (Hallam 1986)
-Calcareous nannoplankton (Tremolada *et al.* 2006), ammonoids (House 1989), insects (Labandeira & Sepkoski 1993, Vrsansky 2006), marine vertebrates (Bardet 1984), and tetrapods (Benton 1989) all appear to drop in diversity across the J-K boundary
-Among tetrapods, large dinosaurs (sauropods, ceratosaurians, and allosauroids) appear to have been most severely affected (Weishampel & Norman 1989), though this does not hold true on southern continents (Sereno 1999)
-The tetrapod fossil record from the Late Jurassic and Early Cretaceous is very incomplete and geographically disjunct suggesting that what appears to be an extinction may in fact be a taphonomic artifact (Fara & Benton 2000, Rees *et al.* 2004)
-We examine tetrapod diversity across the J-K boundary at the level of the community (α-diversity) in order to minimize preservation and collection biases

Hypotheses

H1) Tetrapod α-diversity should decrease across the Jurassic-Cretaceous boundary
H2) The most severely-affected groups should be large dinosaurs, particularly sauropods, ceratosaurians, and allosauroids

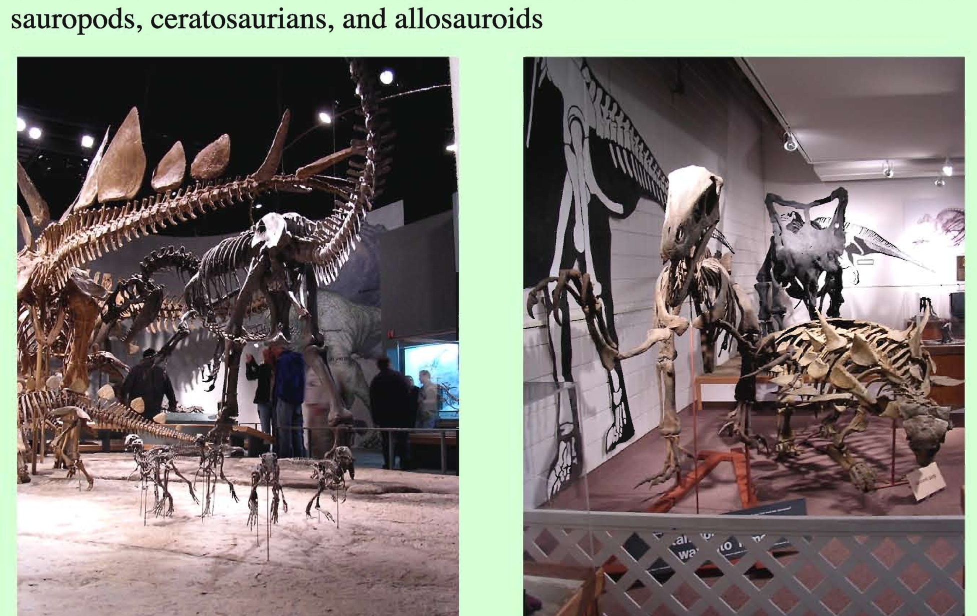

Figure 1 - Late Jurassic & Early Cretaceous Communities
Examples of typical Jurassic and Cretaceous faunas from North America. Left: Morrison Formation - *Allosaurus*, *Othnielia*, *Stegosaurus* (Denver Museum of Nature & Science). Right: Cedar Mountain Formation: *Utahraptor*, *Gastonia* (College of Eastern Utah Prehistoric Museum). Photos by the author (JDO).

METHODS

Data Collection

-Sites and faunas included were chosen based on quality of preservation, community completeness, and collection history using the criteria of Sahney & Benton (in preparation)
-Presence/absence data for each community were collected from published literature
-Study confined to Late Jurassic and "Neocomian" Early Cretaceous (Table 1)
-Data recorded in the Alpha Diversity Database (ADD)
  -Custom-designed relational database
  -http://palaeo.gly.bris.ac.uk/Sahney/index.php
  -Taxonomy based on Benton (2005)
  -Families tied to diet type and body size based on Benton (1993)

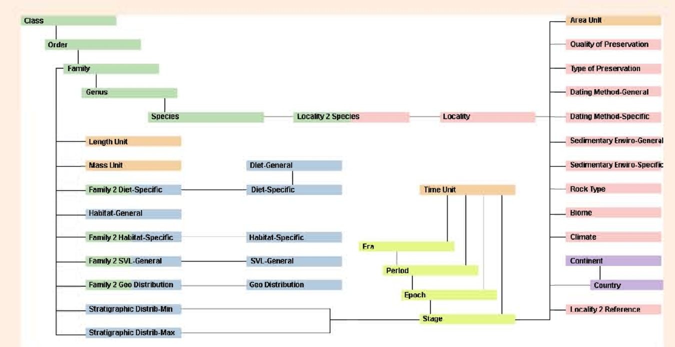

Figure 2 - Database Structure
Tables and connections within the Alpha Diversity Database. Colors indicate data types. Green = taxonomic, pink = geologic, blue = ecological, yellow = age, orange = measurement units. From Sahney & Benton (in preparation).

Age	Stage	Sites and faunas		
125.0 Ma / 130.0 Ma	Barremian	Chinese sites & faunas (3), China (Ch) Dalton Wells, USA (DW)	Grange Chine, UK (E) Kitadani, Japan (J)	Spanish sites (4), Spain (S)
136.4 Ma	Hauterivian	La Amarga, Argentina (LA)		
140.2 Ma	Valanginian	Phu Wiang, Thailand (PW) Shiramine, Japan (J)	Urho Fauna, China (Ch)	
145.5 Ma	Berriasian	Anoual, Morroco (A) Cornet, Romania (C)	Shokawa, Japan (J) Sunnydown Farm, UK (E)	
150.8 Ma	Tithonian	Morrison Formation sites (4), USA (M) Shar Teg, Mongolia (ST)		
155.7 Ma	Kimmeridgian	Guimarota, Portugal (G) Morrison Formation sites (4), USA (M)	Tendaguru Fauna, Tanzania	
161.2 Ma	Oxfordian	Qigu Fauna, China (Q) Tuo Jian Fauna, China (TJ)		

Table 1 - Temporal Scope of Project
Time scale of the seven stages included in this study. Bold line represents the Jurassic-Cretaceous boundary. Ages at left are based on Gradstein *et al.* (2004). Sites and faunas included in the study are listed at right. Letters in parentheses correspond with map in Figure 3.

Figure 3 - Geographic Scope of Project
Location of communities included in this study on a Late Jurassic (Kimmeridgian) world map. Letters correspond to those in Table 1; green = Jurassic, blue = Cretaceous. Map from Scotese (2001).

Analysis

-Diversity curves (Figures 4-6)
  -Constructed based on presence/absence of orders, families, genera, and species
  -Average curves show mean number of taxa per community per stage
  -Maximal curves show number of taxa in most diverse site within each stage
-Significance tests (Table 2)
  -Performed on body size, diet type, and niche (combination of body size and diet)
  -Kruskal-Wallis test used to identify significant differences between stages
  -Mann-Whitney test used to identify significant differences between periods
-Cluster analysis (Figure 7)
  -Used to determine whether primary signal is biological or taphonomic
  -Based on presence/absence of families, Bray-Curtis distance metric, and Ward clustering algorithm

RESULTS & CONCLUSIONS

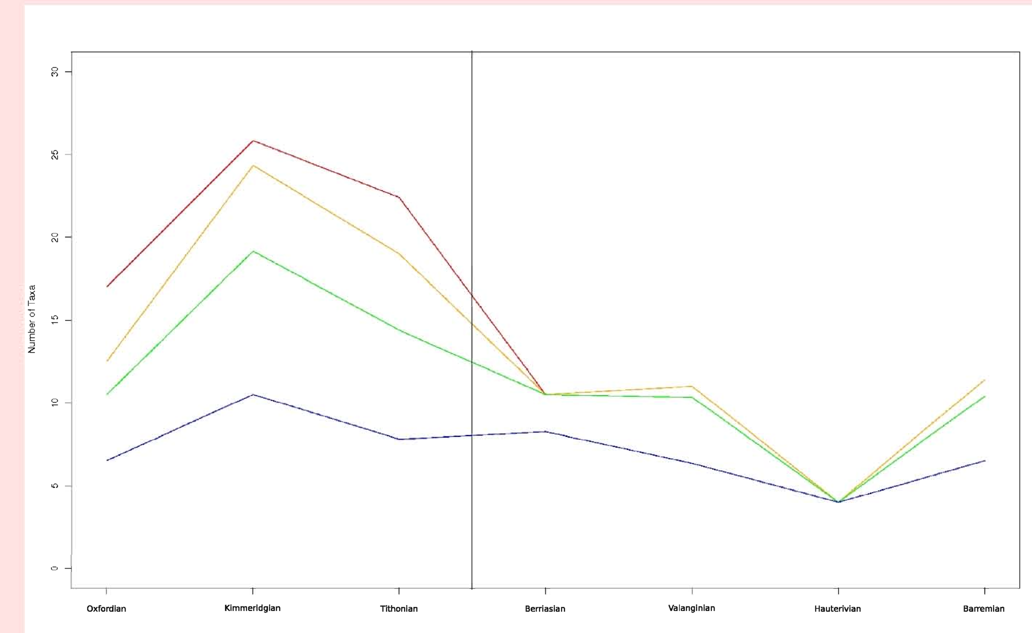

Figure 4 - Average Tetrapod Diversity
Shows the average number of taxa per community for each stage. Red = species, orange = genera, green = families, blue = orders. Vertical line represents the Jurassic-Cretaceous boundary.

Alpha Diversity in a Global Context

-Alpha diversity curves show almost identical topology to global tetrapod diversity curve
-Similar patterns also seen in marine animals (Sepkoski 2002), insects, (Labandeira & Sepkoski 1993), but not in plants (Niklas 1988)
-May indicate that knowledge of global diversity is heavily influenced by a few well-preserved communities (Sepkoski 2002)
-Gap between curves may serve as a measure of endemism (β-diversity)

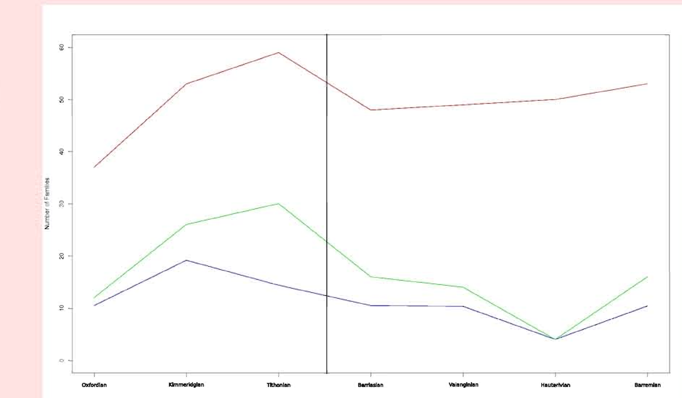

Figure 6 - Comparison to Global Diversity
Family α-diversity as estimated by this study (blue = average, green = maximal) plotted alongside global tetrapod diversity (red). Vertical line represents the Jurassic-Cretaceous boundary. Global data from Benton (1989).

Selectivity of Extinction

-Large carnivores - a group that in the Late Jurassic and Early Cretaceous was composed almost entirely of allosauroid and ceratosaurian theropods - are the most severely affected group, showing a highly significant decrease across the J-K boundary
-Change in relative abundance of sauropods and ornithopods is unclear because both are included in the "large herbivore" category
-Apparent extinction of mammals is likely due to the presence of two mammal-rich microvertebrate sites from the Late Jurassic (Guimarota and Quarry Nine) and the absence of comparable sites in the Early Cretaceous
-Some taxa - particularly turtles and crocodilians - show no significant change in diversity across boundary

Group	Composition	p
Large Herbivores	Sauropods Ornithopods	0.02439 (K-W)
Small Omnivores	Mammals Turtles	0.01015 (M-W)
Medium Insectivores	Mammals	0.03652 (M-W)
Large Carnivores	Theropods	0.008354 (K-W) 0.002595 (M-W)

Table 2 - Significance Tests
Shows groups of tetrapods with significant ($p < 0.05$) changes in diversity during the Late Jurassic and Early Cretaceous. K-W = Kruskal-Wallis test, M-W = Mann-Whitney test.

Diversity Curves

-Decrease in species, genus, and family diversity occurs at Jurassic-Cretaceous boundary
-Apparent drop in richness in Hauterivian likely due to very small sample size (n=1)
-No evidence of recovery in Early Cretaceous

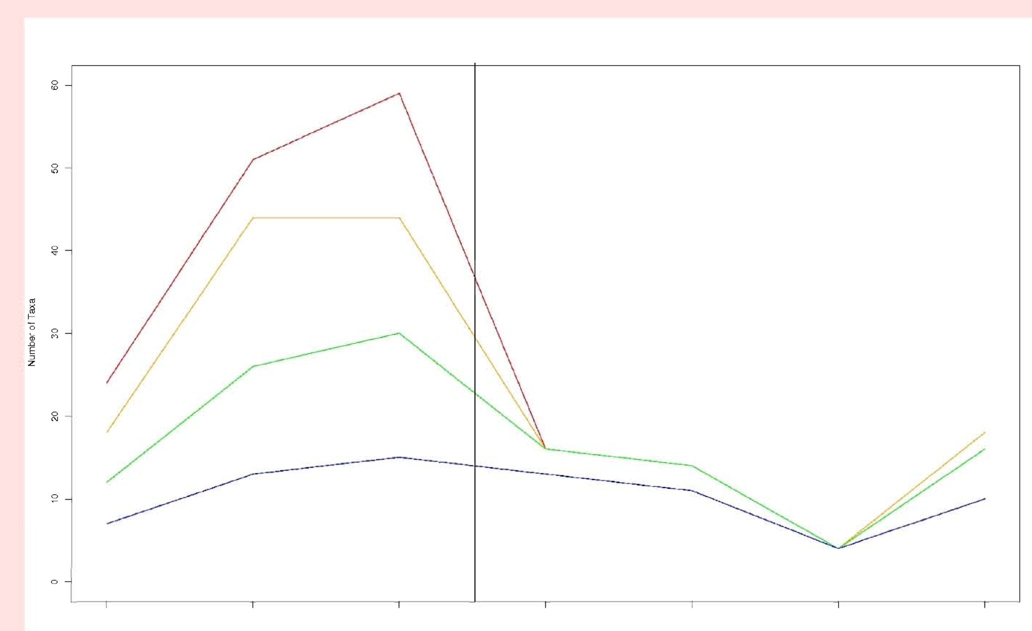

Figure 5 - Maximal Tetrapod Diversity
Shows richness within the most diverse community from each stage. Red = species, orange = genera, green = families, blue = orders. Vertical line represents the Jurassic-Cretaceous boundary.

Cluster Analysis

-Separation of communities into Jurassic and Cretaceous groups shows that the primary signal is temporal rather than geographic or taphonomic
-Within each major cluster, communities tend to group by continent, demonstrating the presence of a secondary geographic signal
-No evidence of a paleoenvironmental/lithological signal

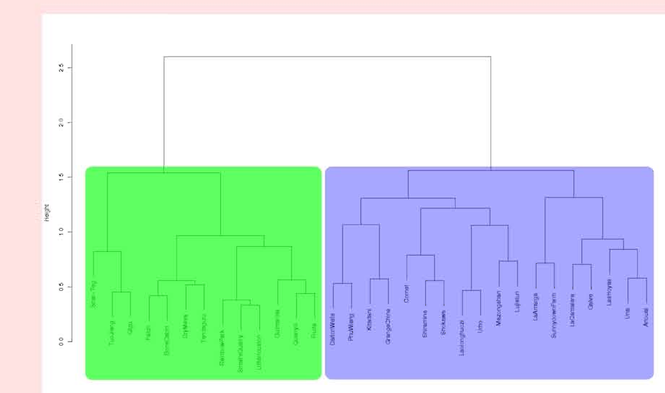

Figure 7 - Cluster Analysis
Cluster dendrogram of sites and faunas included in this study. The cluster highlighted in green is composed entirely of Jurassic communities while the cluster highlighted in blue is composed entirely of Cretaceous communities.

H1) Tetrapod α-diversity should decrease across the Jurassic-Cretaceous boundary
-Supported by topology of alpha diversity curves
-Global diversity curves (with exception of plants) show similar pattern
-Cluster analysis suggests that diversity curves reflect genuine biotic patterns rather than taphonomic signal

H2) The most severely-affected groups should be large dinosaurs, particularly sauropods, ceratosaurians, and allosauroids
-Statistical tests show a significant decrease in allosauroid and ceratosaurian richness
-More detailed analysis required to determine patterns of herbivorous dinosaur diversity across the J-K boundary
-Apparent drop in mammal richness is likely a sampling artifact

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