

**UTILIZING VERTEBRATES TO UNDERSTAND THE
FACTORS THAT INFLUENCE TERRESTRIAL ECOSYSTEM STRUCTURE**

A Dissertation

by

CORY MARTIN REDMAN

Submitted to the Office of Graduate Studies of
Texas A & M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May 2012

Major Subject: Geology

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ABSTRACT

Utilizing Vertebrates to Understand the Factors that
Influence Terrestrial Ecosystem Structure. (May 2012)

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Conserving biodiversity in the current global ecological crisis requires a robust understanding of a multitude of abiotic and biotic processes operating at spatial and temporal scales that are nearly impossible to study on a human timescale and are therefore poorly understood. However, fossil data preserve a vast archive of information on past ecosystems and how they have changed through time. My PhD research is composed of three studies that look at biogeographic distribution, ecosystem structure, and trends in richness and diversity.

Identifying organisms to the species level is a common practice in ecology when conducting community analyses. However, when species-level identification is not feasible, higher level taxonomic identifications are used as surrogates. This study tests the validity of supraspecific identifications for vertebrates in regional biogeography studies, using the recorded occurrences of terrestrial and aquatic taxa from 16 national parks on the Colorado Plateau and culling the data set based on a series of taphonomic processes to generate fossil assemblages.

Changes in community structure as a result of increased magnitude and/or frequency of perturbations have been well documented in terrestrial and marine ecosystems. Unfortunately, the long-term effects of sea-level rise on vertebrate communities in coastal habitats are poorly understood and difficult to study on a human time scale. This study examines the long term effects of relative sea-level change on coastal plain ecosystems of the Belly River Group (Campanian) in southern Alberta using microvertebrate fossils.

Most Cretaceous freshwater deposits in North America produce only a couple of articulated fish skeletons. Because of this preservational bias many workers suggested that freshwater teleosts were largely absent from North America until the Eocene or later. Late Cretaceous fish assemblages are of particular interest, because these assemblages undergo a major compositional change. Pre-Cretaceous fish assemblages are dominated by non-teleosts, while Paleogene assemblages are dominated by teleosts that are members of extant families. This study provides a first approach in characterizing long-term trends in richness and the distribution of Late Cretaceous, nonmarine actinopterygians of the Western Interior of North America.

ACKNOWLEDGEMENTS

This dissertation is dedicated to my family, who has always supported my educational and career goals. I am indebted to my major advisor, Thomas Olzsewski, for giving me the freedom to make my own way, but always having the time for me when I needed guidance.

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CHAPTER I

INTRODUCTION

My research focuses on using fossil data of terrestrial organisms to understand how ecological processes have influenced diversity, ecosystem structure, and biogeography through Earth's history. Conserving biodiversity in the current global ecological crisis requires a robust understanding of a multitude of abiotic and biotic processes operating at spatial and temporal scales that are nearly impossible to study on a human timescale and are therefore poorly understood. However, fossil data preserve a vast archive of information on past ecosystems and how they have changed through time. My research combines field work, sophisticated statistical analyses, and process-based modeling applied to whole assemblages in order to understand biodiversity in the past and present.

My dissertation work has been focused on Late Cretaceous deposits of western North America, which has one of the best-known records of vertebrate fossil material as well as extensive research into its ancient sea level and climate. This foundation of previous work makes it an ideal natural laboratory to study ancient ecological and evolutionary responses of vertebrates to environmental change that can serve as analogues for understanding present-day biotic change. My research focuses on terrestrial, vertebrate ecosystems, because basic ecological principles have rarely been

This dissertation follows the style of *The American Naturalist*.

tested using fossil vertebrates. My PhD research is composed of three studies that look at biogeographic distribution, ecosystem structure, and trends in richness and diversity. I use a modern data set from the North Colorado Plateau to test whether higher-level taxonomic identifications greatly affect the observed pattern of relationship among sample sites in regional biogeographic studies. I also examined the long term effects of relative sea-level change on coastal plain ecosystems using Late Campanian vertebrate fossils from southeastern Alberta. Finally, I examined changes in the composition of freshwater fish communities for the Late Cretaceous, in order to study the transition from a nonteleost dominated assemblage to the teleost dominated assemblage that is seen today.

CHAPTER II

THE INFLUENCE OF TAXONOMIC LEVEL ON BIOGEOGRAPHIC PATTERNS

Introduction

Studies of mass extinctions in the fossil record are usually conducted at the family to genus level due to the volatile nature and the limited geographic distribution of most species (Archibald and Fastovsky 2004; Bambach et al. 2004; Benton et al. 2004; Clapham et al. 2009; Barnosky et al. 2011). In contrast, community analyses are typically performed at the genus or species level because these studies sample a small geographic area over a short duration and sampled genera typically do not contain more than one species (Holland 2005; Redman et al. 2007; Barrett and McGowan 2009; Olszewski and Erwin 2009; Forcino et al. 2010). In order to bridge the gap between global and local study scales, it is necessary to understand how a change in the taxonomic level of identification can influence observed biogeographic patterns and relationships. Numerous studies have demonstrated the validity of supraspecific identifications of extant macroinvertebrates (Ferraro and Cole 1990; Andersen 1995; Bamford et al. 1996; Roy et al. 1996; Cardoso et al. 2004; Torres Mendes et al. 2007; Heino and Soininen 2007; Jimenez et al. 2010; Schipper et al. 2010), but the validity of supraspecific identifications for vertebrates has largely gone untested (Wilson 1974; Rabinovich and Rapoport 1975; Hadly et al. 2009). The goal of this study is to test the validity of supraspecific vertebrate identifications by examining whether higher-level

taxonomic identifications greatly affect the observed pattern of relationship among sample sites in regional biogeographic studies.

Identifying organisms to the species-level is not always feasible, because of limited taxonomic expertise, time, money, sampling resolution, or the preservation of morphological features needed for species-level identification. In order to overcome these limitations, higher-level taxonomic identifications (i.e., genus- or family-level) are used as surrogates. Supraspecific identifications of vertebrates are most commonly used in paleoecological studies, because the incomplete and/or disarticulated nature of the fossil record makes species-level identification impossible for most taxonomic groups, unless partial skull and skeletal material is recovered. The validity of supraspecific identification for vertebrate fossil assemblages is tested here by culling a modern data set based on a series of taphonomic processes (i.e., size sorting, depositional environment, preservation potential of taxonomic groups).

Study Area

This study was conducted using the recorded occurrences (i.e., 103 Families; 327 Genera; 558 Species) of all terrestrial and aquatic vertebrates found within the boundaries of 16 federal management areas (Fig. 1) on the Northern Colorado Plateau (NCP). All 16 management areas belong to the same National Park Service inventory and monitoring network (i.e., Northern Colorado Plateau Network), which means that comparable sampling strategies, taxonomic nomenclature, and environmental assessments were applied to each (O'Dell et al. 2005). This study area was chosen because it represents a unique effort to document the occurrence of all vertebrates across

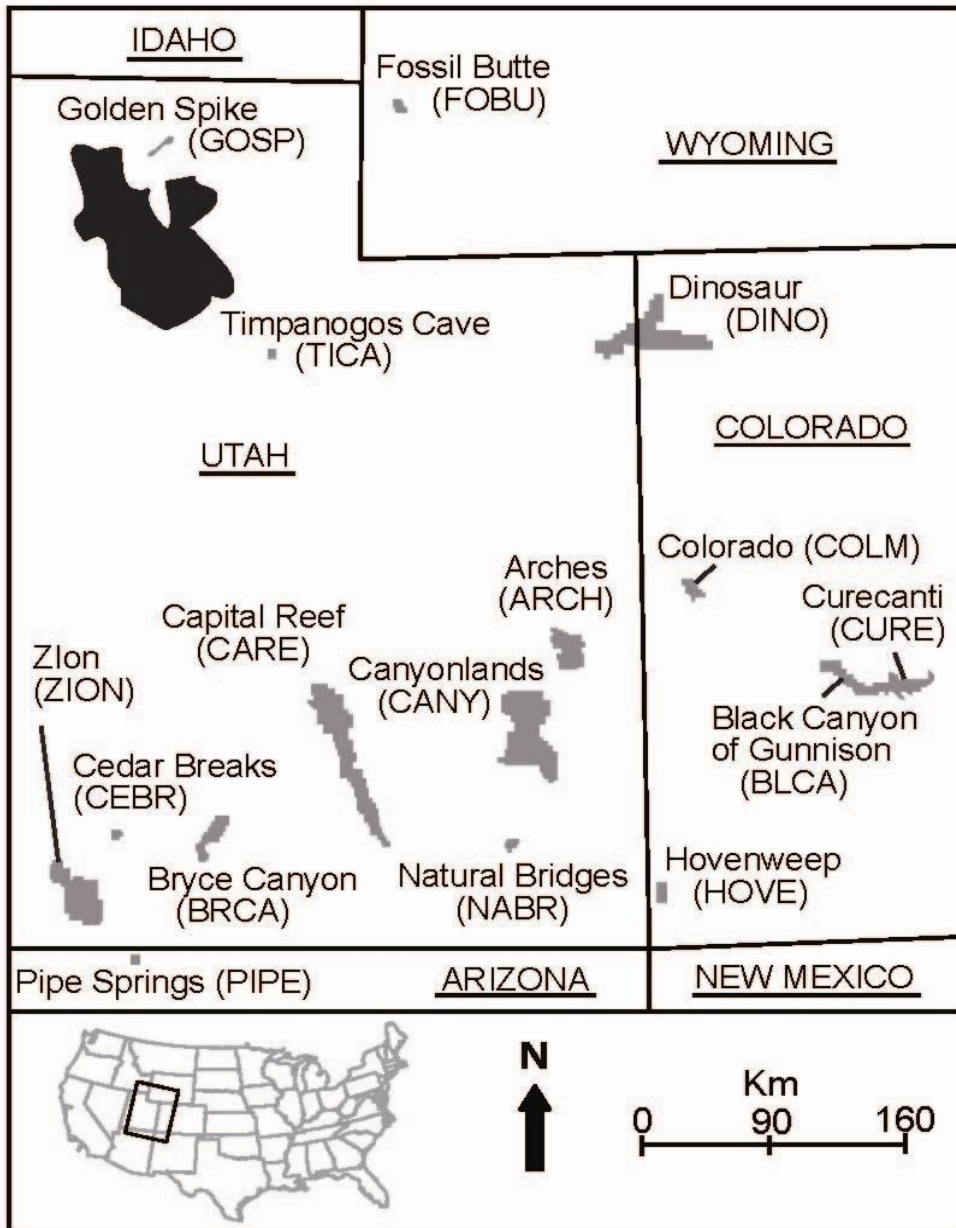


Figure 1: Geographic position of the 16 management areas on the Northern Colorado Plateau that are used in this study.

a wide-range of habitats (desert, grasslands, forests, lakes, rivers, etc.) over large geographic areas (Table 1).

Table 1: Best estimates of completeness for the biological inventory by taxonomic groups for the 16 management areas. (~~) Denotes that no fish have been documented. Data from O'Dell et al. 2005.

<u>Park Code</u>	<u>Birds</u>	<u>Mammals</u>	<u>Herps</u>	<u>Fish</u>	<u>Park Area (ha)</u>
ARCH	90%	85%	85%	90%	30,974
BLCA	80%	65%	70%	80-90%	11,439
BRCA	90%	90%	80%	~~	14,613
CANY	90%	85%	80%	90%	135,201
CARE	94%	65-70%	50%	90%	98,650
CEBR	80%	50%	66%	~~	248
COLM	90%	80%	80%	~~	8255
CURE	80%	75%	0%	90%	16,612
DINO	70%	90%	80-90%	90%	87,308
FOBU	80%	80%	85-90%	~~	3353
GOSP	50%	50%	50%	~~	1075
HOVE	90%	75%	70%	~~	326
NABR	90%	85%	85%	~~	2993
PISP	98%	20%	40%	~~	16
TICA	50-60%	50-60%	50%	90%	98
ZION	98%	75%	70%	90%+	59,813

Methods

Before the validity of supraspecific identifications can be assessed, two factors need to be accounted for: ubiquitous higher taxa and environmental homogeneity. Due to the close geographic proximity of the 16 management areas used in this study, these two factors could cause a strong similarity in observed pattern of relationship among sample sites that is unrelated to the validity of supraspecific identifications. Similarity in

the composition of the management areas could occur if all higher taxa are ubiquitous and variation is between cogenetic species or cofamilial genera (Fig. 2). While ubiquitous higher taxa are not usually a concern with extant taxonomic groups, this can be a major issue when dealing with extinct groups. To assess whether more and more genera and families are being represented as species richness increases, taxon richness at each taxonomic level was cross-plotted. If the NCP is environmentally homogeneous, similarity in the composition of the management areas could also occur because all the parks are sampling the same species pool. This was tested by constructing species-area curves (Fig. 3), to determine if the data used in this study fit the power model of species-area relationship at all taxonomic levels. The power-model relationship predicts that with increasing sample area an increased number of taxa are being captured, suggesting that as the sample area increases a larger variety of environments are being sampled and therefore a larger number of distinct communities (He and Legendre 2002; Tjørve 2003; Martin and Goldenfeld 2006; Stiles and Scheiner 2007; Guilhaumon et al. 2010).

Ordinations

The biogeographic patterns among the 16 parks on the Northern Colorado Plateau were characterized using Nonmetric Multidimensional Scaling (NMDS) ordination (Fig. 4), to visually compare the grouping pattern between sample sites using species-, genus-, and family-level identifications. NMDS places samples in multidimensional space to minimize the difference between rank similarities in the original distance matrix and the rank Euclidean similarities in ordination space.

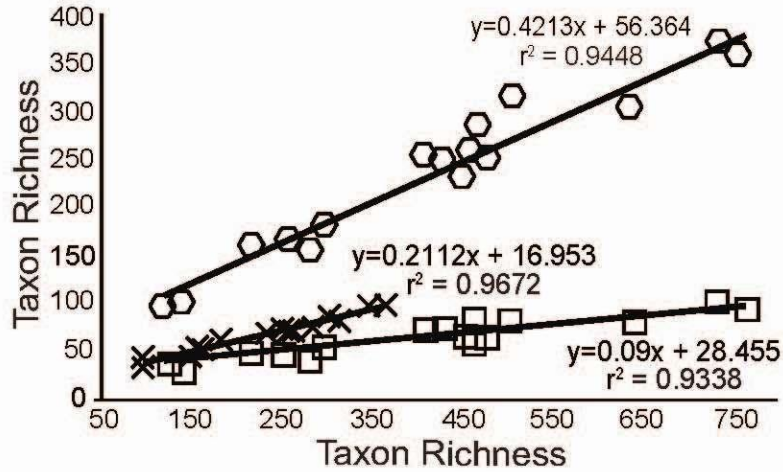


Figure 2: Cross-plot of taxon richness at each taxonomic level. All r^2 values are statistical significant (p-values < 0.001). Hexagons, X's, and squares denoted taxon-level correlations between species-genera, families-genera, and species-families, respectively.

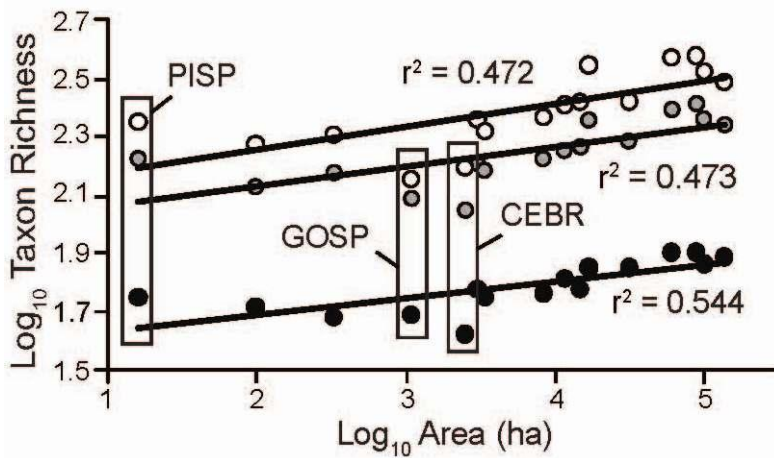


Figure 3: Taxon-area richness for each park at the species- (open circle), genus- (gray circle), and family- (solid circle) level of identification. All r^2 values are statistical significant (p-values < 0.005).

Goodness of fit is measured using stress, which is calculated based on the sum of square differences between the ordination-based distance and the distance predicted by the regression. NMDS was chosen, because it is commonly regarded as one of the most robust unconstrained ordination methods in community ecology and is extremely effective at reducing the complexity of multivariate ecological data and elucidating underlying ecological patterns (Kruskal 1964; Minchin 1987; Clarke 1993; McCune et al. 2002). NMDS was performed using Sørensen dissimilarity. The Sørensen dissimilarity measure is based on shared abundance of taxa among a pair of samples divided by their combined total abundance, treating only mutual occurrences as positive associations (Beals 1984; McCune et al, 2002). NMDS analyses were performed using 100 iterations for 20 runs with 3 axes.

Procrustes and Mantel Test

Procrustes analysis and Mantel tests were used to calculate whether NMDS dissimilarity matrices at the species-, genus-, and family-level were statistically significantly different. Procrustes analysis is a goodness-of-fit statistic that describes the degree of concordance between the two matrices. Procrustes analysis maximizes the similarity between two matrices through matrix translation, reflection, rigid orthogonal rotation, dilation, and contraction. Procrustean randomization test (PROTEST) was used to determine the statistical significance of m^2 , the sum of squares (m^2) differences between the original values and the best-fit solution for each observation (Jackson 1995; Peres-Neto and Jackson 2001; McCune et al. 2002). Each observation from one matrix is permuted randomly so the within-matrix covariance structure is not changed

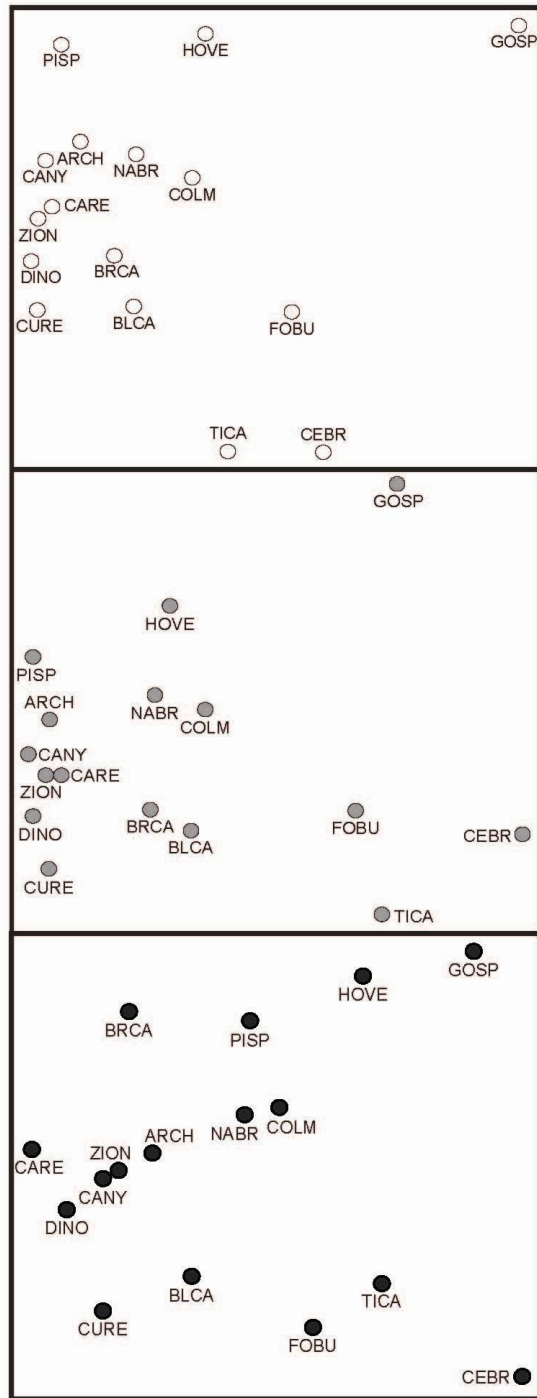


Figure 4: Observed pattern of relationship among the parks in NMDS ordination space at the species- (open circles), genus- (grey circles), and family-level (black circles), with stress values of 8.64, 9.27, and 10.90, respectively. This is based on 558 species, 327 genera, and 103 families. Taxa occurring in two parks or less were culled.

(i.e., the concordance between the resultant randomized matrix and the original target matrix). PROTEST is a one-tailed test that counts the number of random m^2 statistics that are smaller than or equal to the observed m^2 value (Jackson 1995).

Mantel statistical tests the hypothesis of no relationship between two symmetrical matrices with repeated randomization (i.e., covariance structure is not held constant), determining whether the correlation between the two matrices is stronger than the observed correlation (z). In the study, Pearson's correlation coefficient (r) is used to measure the similarity between the randomly generated matrices and the original dataset (Sokal and Rohlf 1995; McCune et al. 2002). PROTEST and the Mantel test were assessed based on 999 permutations.

Artificial Fossil Dataset

Culling the modern dataset based on a series of taphonomic processes serves two purposes (Table 2). 1) It allows the validity of supraspecific identification for fossil assemblages to be tested and 2) tests the robustness of the observed pattern of relationship among the sample sites in ordination space. A taxon has a higher probability of being preserved in the fossil record if it has a large population size, its remains are permanently buried shortly after death, it is found in a variety of environments that experience frequent episodes of sediment deposition, and it has multiple skeletal elements that are resistant to mechanical and chemical degradation (Olszewski and Kidwell 2007; Kidwell and Rothfus 2010). Since this study is conducted using recorded occurrences, rare taxa are considered to be taxa that occurred in two parks or less. Taxa were divided into two size groups, based on whether they were smaller or greater than

Table 2: Number of taxa that were eliminated to approximate taphonomic biases commonly found in the fossil record. (Environment- probability of burial & between habitat transport; Taxon's body size- size-sorting & resistance to degradation; Abundance- loss of rare taxa; Taxonomic group- robustness of skeletal elements).

<u>Environments:</u>	Species	Genus	Family
River Systems	162 (29%)	125 (38%)	64 (62%)
Ponds/Riparian	215 (39%)	153 (47%)	63 (61%)
Lakes	133 (24%)	96 (29%)	46 (45%)
Grasslands/Meadows	248 (44%)	170 (52%)	67 (65%)
Forests/Thickets	284 (51%)	180 (55%)	65 (63%)
Deserts/Chaparral	172 (31%)	120 (37%)	61 (59%)
Aquatic Systems	279 (50%)	192 (59%)	78 (76%)
Terrestrial Systems	435 (78%)	255 (78%)	80 (78%)
<u>Body Size:</u>			
Small (<488 g or <37 cm)	419 (75%)	234 (72%)	71 (69%)
Large (>500 g or >40 cm)	139 (25%)	93 (28%)	32 (31%)
<u>Rarity:</u>			
≤ 2 parks	158 (28%)	63 (19%)	11 (11%)
≤ 4 parks	233 (42%)	105 (32%)	18 (17%)
<u>Taxonomic Group:</u>			
Amphibians	11 (2%)	6 (2%)	5 (5%)
Birds	346 (62%)	197 (60%)	52 (50%)
Fish	48 (9%)	33 (10%)	13 (13%)
Squamates	42 (7%)	30 (9%)	12 (12%)
Mammals	111 (20%)	61 (19%)	21 (20%)

500 grams in mass or 40 centimeters in length. Large taxa are generally considered to have more robust skeletal elements and be more resistant to degradation, so culling based on size allowed for fossil assemblages to be generated that have been hydraulically sorted or have endured a significant amount of mechanical and/or chemical destruction. Body size was determined using two different metrics because length is more commonly measured in fish, amphibians, and squamates, while weight is more

commonly measured in birds and mammals. Taxa were culled based on their environmental restrictions because environments that have higher rates of sediment deposition are more commonly preserved in the rock record than environments that experience long periods of nondeposition or a high degree of erosion (Behrensmeyer et al. 2000; Western and Behrensmeyer 2009; Turvey and Blackburn 2011). The mixing of faunal assemblages from multiple environments due to postmortem transportation is also addressed by culling taxa based on their environmental restrictions. The faunal list compiled for each park represents a mixture of faunas from multiple environments found within a park's boundary (i.e., equivalent to a fossil assemblage that has undergone a high degree of transportation before being permanently buried). This habitat mixing effect is significantly diminished by only including the taxa found in one environment, but cannot entirely be removed, because environments are relatively broadly defined (O'Dell et al. 2005). However, this is appropriate for the purposes of this study because of the difficulty in assigning extinct, nonmarine taxa to specific habitats in the fossil record. All statistical analyses conducted in this study were implemented using the R statistical programming environment (R 2.12.0)

Results

Figure 2 shows that higher taxa are not ubiquitous. The regression slopes between taxonomic levels are positive and all r^2 values are significant at 0.001, indicating that as species richness increases, more and more genera and families are being represented.

Figure 3 shows that a majority of the parks used in this study fit the power model for the species-area relationship, but there are three outliers, PISP, GOSP, and CEBR. PISP has a higher taxonomic richness than would be predicted by the species-area model because it contains a series of springs representing a rare water source for the desert region and thus a focal point for wildlife (O'Dell et al. 2005). GOSP has a lower taxonomic richness than predicted because it has only been a protected historical site since 1965, prior to which the area endured over a century of human-related disturbances as a result of the transcontinental railroad and associated settlements (O'Dell et al. 2005). CEBR also has a lower taxonomic richness than predicted because 99% of the monument occurs above 2500 meters of elevation, receiving more annual snow fall (i.e., > 9 m) and having the lowest mean annual temperature (i.e., 1.9°C) of all the NCP management areas. This results in CEBR having long, cold winters and short, cool summers that few taxa can tolerate (O'Dell et al. 2005).

Figure 4 shows how the pattern of relationship among the 16 parks changes in Nonmetric Multidimensional Scaling (NMDS) ordination space as higher taxonomic levels of identification are used. The overall relationship of the 16 parks does not change as a result of using supraspecific identifications. There is a counter-clockwise rotation in the position of the parks from species- to genus-level, but a rotation between NMDS plots is not significant because the orientation of NMDS axes is arbitrary with respect to the shape of the cloud of site points. There is a shift in the position of the parks from being more tightly packed in the lower left-hand corner to becoming more spread out and moving towards the upper right-hand corner from genus- to family-level,

but the overall relationship of the parks relative to one another in ordination space does not change. Overall, the degree of similarity for any pair or triplet of parks is consistent regardless of the taxonomic-level of identification used. This is confirmed by Procrustes and Mantel tests (Table 3), with 87-98% of all PROTEST-generated matrices having a m^2 value equal to or smaller than the observed and having high Pearson's correlation coefficient value between the randomly-generated matrices and the originals. These results demonstrate that there was no statistical difference between the species, genus and family matrices (i.e., PROTEST) and this similarity was not due to randomness (Mantel). All Procrustes and Mantel results are significant to 0.001.

Table 3: Results of Procrustes and Mantel tests, based on 999 permutations and significant to 0.001.

	<u>Species-Genus</u>	<u>Species- Family</u>	<u>Genus-Family</u>
m^2 :	0.03538	0.2473	0.1914
PROTEST:	0.9821	0.8676	0.8992
r^2 :	0.9655	0.8084	0.8682

The observed pattern of relationship in ordination space is extremely robust, despite the culling of taxa based on rarity, body size, taxonomic group, or environment, which eliminates 2-82% of the original dataset in a given run (table 2). The observed pattern of relationship among the 16 parks is only dramatically altered, when all endotherms (i.e., birds and mammals) are removed, representing 71-82% of the taxa. Even with the elimination of endotherms, much of the observed pattern of relationship is

still preserved, with CARE, DINO, CANY, ARCH, and ZION still forming a tight grouping in ordination space. The observed pattern of relationships among the parks in ordination space is also consistent using only birds, which represent the best surveyed and most abundant taxonomic group (50-62%) across the 16 parks. The observed pattern of relationship is not dramatically altered with the removal of environments, because most taxa are found in multiple environments. For example, forested habitats have the highest richness (53-61%), but only a small minority (5-29%) of taxa is restricted to that habitat. Sorting taxa into various size categories were used to approximate physical processes that cause fossil elements to be concentrated by size and the increased probability of smaller or more delicate skeletons being destroyed. Up to six different size categories (three for mass and length) at each taxonomic level were used to cull taxa (2-64%), but the observed pattern of relationship did not change.

Discussion

Figure 4 demonstrates the validity of supraspecific identifications for vertebrates in regional biogeographic studies. The observed pattern of relationship for the 16 parks in ordination space is congruent using species-, genus-, and family-level identifications, with the stress values well within the recommended range (<20) for ecological data (McCune et al. 2002). This congruency is statistically significant and not the result of randomness, ubiquitous higher taxa, or a homogeneous environment across the NCP.

While not all taphonomic biases are accounted for in this study (e.g., time-averaging) the robustness of the observed pattern of relationship among sample sites supports the working hypothesis that supraspecific identifications are valid for vertebrate

fossil assemblages in regional biogeographic studies. This is not entirely surprising, since numerous live-dead studies that have shown that death assemblages can approximate snapshots of ecosystems (Olszewski and Kidwell 2007; Western and Behrensmeyer 2009, Terry 2010, Tomašovych and Kidwell 2010; Tomašovych and Kidwell 2011).

The results of this study suggest that the observed pattern of relationship would be even more robust for studies covering broader geographic, temporal, and environmental ranges, since faunal assemblages that are farther apart would have greater differences due to the small geographic area and short temporal duration of most species. Whether that observed pattern of relationship would hold up at the family or order-level has yet to be tested; though previous studies utilizing mammalian and avian taxa suggests they would (Rabinovich and Rapoport 1975; Balmford et al. 1996; Clarke and Warwick 1999). Future work should examine the validity of supraspecific identifications for vertebrates across a larger geographic area (e.g., continental & global), using whole-assemblage data compiled at the local community level from multiple environments.

Conclusions

This study has demonstrated that taxonomic level (i.e., species, genus, or family) need not influence the pattern of regional biogeographic relationships between sample sites. While the results of this study have direct applications to regional biogeographic studies of modern taxa, especially with respect to the management and preservation of threatened ecosystems, these results are especially exciting when applied to the fossil

record. Many fossil taxa can only be identified to the family-level due to poor preservation or a poor understanding of a group's systematics. The results of this study suggest that even such limited data can provide useful information on biogeography in Earth's past and how it has changed through time.

CHAPTER III
THE RESPONSE OF COASTAL ECOSYSTEMS TO SEA-LEVEL CHANGES
BASED ON MICROVERTEBRATE ASSEMBLAGES OF THE BELLY
RIVER GROUP (CAMPANIAN) OF SOUTHEASTERN ALBERTA

Introduction

Changes in sea-level influence biota through their affect on the distribution and areal extent of terrestrial and marine habitats, dispersal routes and connectivity of populations, and regional and global climate (Alroy 2008; Benton 2009; Hughes 2003; Miller et al. 2005; Miranda et al. 2005; Worm et al. 2006; Dominici and Zuschin, 2007; Solomon et al. 2007; Nicolles et al. 2010). However, the long term effects of sea-level change on the conditions and distribution of coastal habitats are difficult to assess on a timescale easily accessible to ecologists (Wu et al. 2002; Moniful and Mirza 2003; Dolan and Walker 2004). Under these circumstances, the fossil record can address the affect of sea level change on ecosystems, since paleoecological studies are commonly conducted at local (i.e., single habitat), landscape (i.e., multiple habitats), and regional (i.e., multiple landscapes) spatial scales, over temporal durations that can capture the evolutionary effect(s) of disturbances on an ecosystem (Powell and Kowalewski 2002; Bush and Bambach 2004; Olszewski and Erwin 2004; Patzkowsky and Holland 2007; Redman et al. 2007; Alroy 2010). This study examines the long term effects (~2 m.y.) of relative sea-level change on the terrestrial community structure of a coastal plain

ecosystem using Late Cretaceous, microvertebrate fossils from the Belly River Group (Campanian) of southern Alberta.

The Belly River Group represents one of the best sampled (both temporally and spatially; Figs. 4 and 5) coastal plain successions in the rock record. A coastal plain refers to an extensive, low-relief area that is bounded by the sea on one side and a high-relief province on the other (McGraw-Hill 2009). Microvertebrate assemblages (i.e., fossil sites that produce an abundance (>150) of small (1mm–100mm) skeletal elements) were used for this study, because they contain a diverse range of taxa of various body sizes and produce the large sample sizes needed for quantitative analyses of ecological changes through time (Brinkman 1990; Jamniczky et al. 2003; Brinkman et al. 2004; DeMar and Breithaupt 2006; Sankey and Baszio 2008). In addition to the robust sampling of the Belly River Group, detailed systematic, taphonomic, sedimentological, and stratigraphic work has been conducted on each sample site (i.e., microsite) (Wood et al. 1988; Eberth 1990; Eberth and Hamblin 1993; Eberth 1996; Hamblin 1997; Eberth and Brinkman 1997; Brinkman et al. 1998; Brinkman and Neuman 2002; Eberth 2005; Neuman and Brinkman 2005). This allows for a high degree of confidence that any changes in diversity will reflect ecological changes, since taphonomic biases have previously been examined and accounted. Changes in ecosystem structure were evaluated by partitioning diversity into within-community and between-community components. Partitioning diversity is important to understanding how changes in diversity were accommodated, since different biophysical processes (e.g., substrate, topography, rainfall, etc.) will manifest at different spatial scales (Willis and Whittaker

2002; Crist et al. 2003; Magurran 2004; Legendre et al. 2005; Patzkowsky and Holland 2007; Scarponi and Kowalewski 2007; Bonelli and Patzkowsky 2008; Jost et al. 2010).

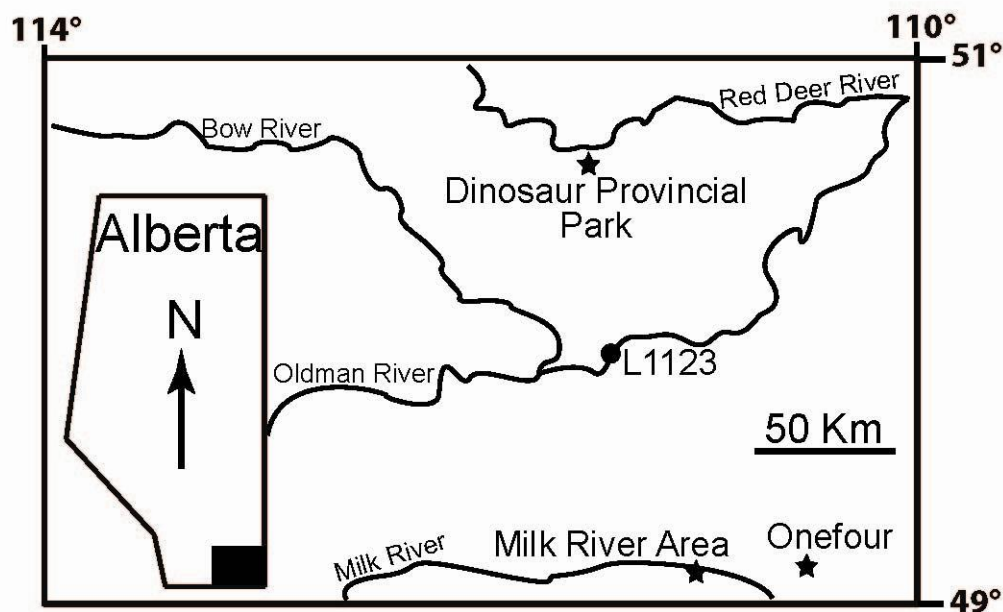


Figure 5: Microsites come from three main regions of southern Alberta (modified from Sankey et al., 2005).

The absolute abundance data set used in this study was compiled from previous published data and additional collections. Taxonomy was updated and rationalized to facilitate regional scale analyses, resulting in 65 taxa from 63 localities from three main regions in southeastern Alberta (Fig. 4): Dinosaur Provincial Park (DPP), the Milk River area, and near the town of Onefour (Brinkman 1990; Eberth and Brinkman 1997; Brinkman et al. 1998; Beavan and Russell 1999; Brinkman et al. 2004; Brinkman et al. 2005; Sankey et al. 2005; Brinkman 2008). All microsites were bulk sampled and

disaggregated in water using screens with seven to nine openings per centimeter.

Specimens were identified to the lowest taxonomic level and abundance counts were

based on the number of identifiable skeletal elements.

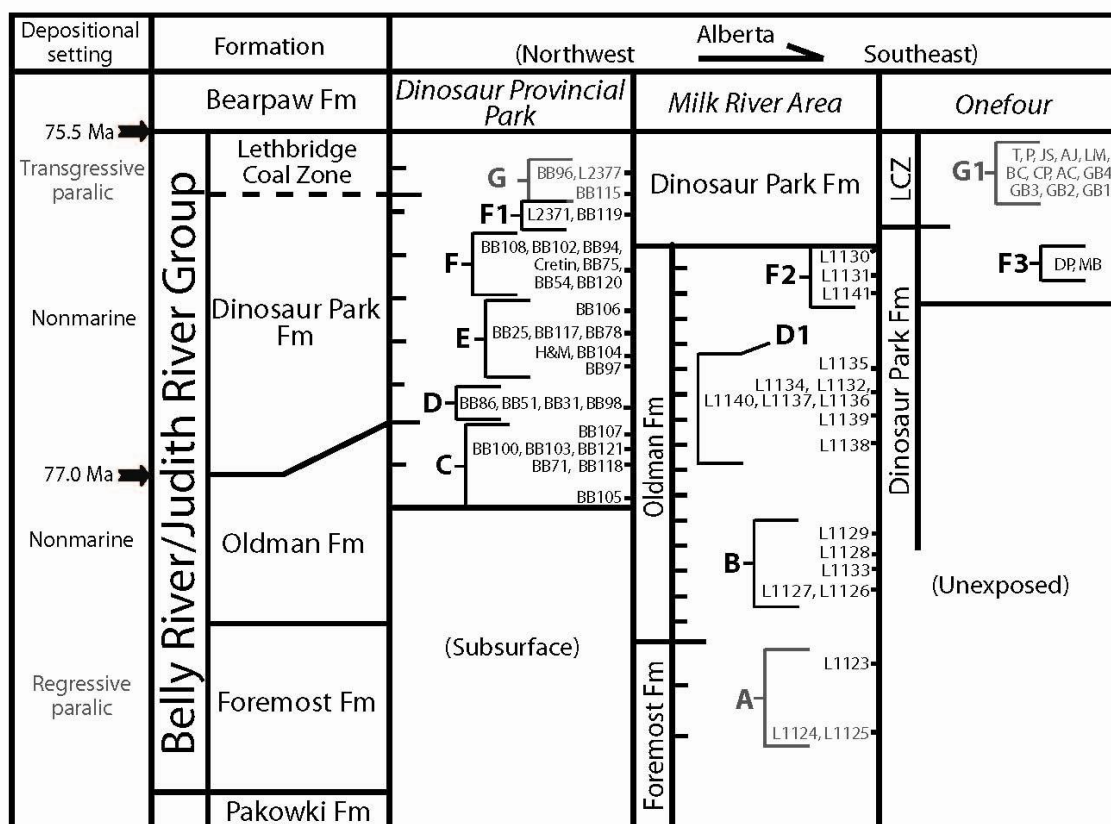


Figure 6: Stratigraphic distribution of microsites. Alphabetical letters refer to the stratigraphic bins, with approximately temporally equivalent bins denote with a number. Stratigraphic sections are divided into 10 meter intervals (left-hand side of column).

The Belly River Group (formerly referred to as the Judith River Group) records a regressive-transgressive cycle of the Western Interior Seaway (Bearpaw Sea) and is

composed of the Foremost, Oldman, and Dinosaur Park Formations (Wood et al. 1988; Eberth 1990; Hamblin 1997; Eberth 2005; Fig. 5). The Foremost Fm. is composed of coarsening-upward, progradationally to aggradationally stacked parasequences of interbedded coals, shales, and sandstones, representing back-barrier facies and overlaid by stacked paleochannels. The Oldman Fm. is composed of alluvial sandstones and mudstones, represented by lenticular to sheet-shaped paleochannels and overbank facies of an ephemeral-flow, low-sinuosity fluvial system. The Oldman Fm. represents the maximum basin ward extent of the Belly River Group's nonmarine clastics. The Oldman-Dinosaur Park contact is a regionally extensive, diachronous discontinuity that becomes younger to the south-southeast. The majority of the Dinosaur Park Fm. is composed of single to multistoried paleochannels and over-bank deposits, representing a low- to high-sinuosity meandering system. The Lethbridge Coal Zone (LCZ) forms the upper fifteen meters of the Dinosaur Park Fm. and is composed of nonmarine laminated sandstones and shales, fully-marine mudstones, and coal beds, representing a tidally-dominated estuarine system. The LCZ records a series of flooding and infilling events, due to rapid changes in relative sea level prior to the final transgression represented by the overlying Bearpaw Fm.

Previous faunal analyses of the Belly River Group demonstrated that the stratigraphic distribution of taxon abundances tracked environmental shifts related to the regressive-transgressive cycle of the Western Interior Seaway (Brinkman 1990; Brinkman et al. 1998; Brinkman et al. 2004; Sankey et al. 2005). Two separate paleocommunities were identified, coastal and inland. Coastal communities referred to

vertebrates (aquatic and terrestrial) that had higher abundances in estuarine-dominated areas of the coastal plain. Inland communities referred to vertebrates that had higher abundances in fluvially-dominated areas of the coastal plain.

Methods

Regional trends in the paleocommunity structure of the coastal plain was examined using Nonmetric Multidimensional Scaling (NMDS) with Sørensen (i.e., Bray-Curtis) dissimilarity. NMDS plots samples as points in a multidimensional space to minimize the difference between rank similarities in the original dissimilarity matrix and the Euclidean distance in ordination space. Goodness of fit is measured using stress, which is calculated based on the sum of square differences between the ordination-based distance and the distance predicted by the regression. The Sørensen dissimilarity measure is based on shared abundance of taxa among a pair of samples divided by their combined total abundance, treating only mutual occurrences as positive associations. NMDS was chosen, because it is commonly regarded as one of the most robust, unconstrained ordination methods in community ecology and is extremely effective at reducing the complexity of multivariate ecological data and elucidating underlying ecological patterns (Beals 1984; Clarke 1993; McCune et al. 2002). NMDS ordinations were run using two axes with a maximum of fifty random starts.

The effect of sample-size on diversity trends through time was evaluated using individual-based rarefaction, which uses the abundance of each taxon in a sample (i.e., microsite) to calculate the expected richness for any subsample that is smaller than the entire collection. Statistically significant differences in richness for a given subsample

size was evaluated using 95% confidence interval based on the expected variance of sample richness. Rarefaction curves also provide an unbiased sample-size measure of evenness (i.e., relative abundance or proportion of individuals among taxa); a curve with the steeper, initial slope has a more even distribution of species abundances (Magurran 2004; Gotelli and Colwell 2001; Shen et al. 2003; Olszewski 2010).

Changes in diversity partitioning were evaluated using effective richness based on Shannon and Simpson entropies (Jost et al. 2010). The Shannon entropy measures the mean uncertainty of identifying the next taxon in a series of individuals from an infinitely large community. Collections with high richness and high evenness have a higher Shannon index, because there are many different taxa that can be drawn from the collection (Keylock 2005; Ben-Naim 2008; Olszewski 2010). The Simpson index measures the probability that any two individual drawn at random from an infinitely large community belongs to the same taxon (Lande 1996; Legendre and Legendre, 1998; Keylock 2005). All Shannon and Simpson indices' values were converted into effective richness, because collections with different richness could have the same entropy value depending on the evenness of the taxa. Effective richness estimates the number of equally common taxa required to produce a particular value of the index (Jost 2006; Jost 2007; Olszewski 2010). Statistically significant differences in the effective richness were determined at the 95% confidence level by randomly subsampling all microsites to 500 specimens 1000 times, without replacement, and examining the distribution of entropy values.

Results

NMDS ordinations (Fig. 6) showed a gradual change from more brackish or marine dominated fauna (i.e., coastal community) to more terrestrially or freshwater dominated fauna (i.e., inland communities). This pattern is consistent regardless of a microsite's geographic location. LCZ microsites are separated from the other DPP microsites in ordination space, because L2377 and BB96 are dominated by marine and brackish tolerant elasmobranchs (e.g., Elopiformes, Hybodus, Lamniformes, Odontaspidae, Rajiformes), while BB115's faunal assemblage only has one elasmobranch (e.g., Rajiformes) and a higher proportion of nonmarine taxa (e.g., Hadrosauridae, Scapherpeton). Onefour's LCZ microsites come from muddy channel fill deposits and show a gradational change from having a higher proportion of marine and brackish tolerant taxa (i.e., GB1-4) to an increased presence of rare, nonmarine taxa (i.e., T, BC, CP). Foremost microsites, L1124 and L1125 come from shoreface deposits and have a similar faunal composition (e.g., Hadrosauridae, Crocodilia, Champsosaurus) to nonmarine microsites of the lower Oldman Fm., but have a higher abundance of marine and brackish tolerant taxa (e.g., Belonostomus, Rajiformes, Elopiformes). The other Foremost microsite L1123 comes from a channel deposit and has a nearly equal abundance of freshwater-restricted (Scapherpeton, Opisthotriton, Holostean A) and brackish-tolerant taxa (Rajiformes; Lepisosteus; Elopiformes), clustering with the nonmarine Oldman microsites. Nonmarine microsites from the Dinosaur Park and Oldman Fms. form a tight cluster in ordination space, but are separated by geographic region, because of 15 nonmarine taxa that are unique to DPP. L2371, Cretin, and BB54

plot in ordination space between brackish- and terrestrial-dominated assemblages, but they do not represent a mixed fauna and are dominated by nonmarine taxa. L2371 and BB54 probably cluster more closely to Onefour's LCZ microsites, due to similarities in depositional environment. L2371 represents the only nonmarine microsite from a muddy-channel fill microsite and BB54 is the only microsite from an abandon channel (i.e., oxbow lake). Cretin's ordination position is probably a reflection of its faunal assemblage having low evenness and being dominated by *Lepisosteus*, which are two characteristics of the Onefour's LCZ faunal assemblages. Ordination patterns are robust to the exclusion of rare taxa (≤ 18 specimens or occurring in ≤ 8 microsites), using taxon occurrence data, or eliminating microsites from fully marine sediments (i.e., L2377 and BB96).

Individual-based rarefaction curves show that microsites from the regressive and transgressive paralic facies (i.e., coastal communities) generally have a lower richness and evenness than microsites from the nonmarine facies (inland communities), independent of the depositional environment being sampled. However, there was statistically significant overlap in richness between the two communities. Richness increases from the upper Foremost Fm. to the middle of the Dinosaur Park and Oldman Fms. at DPP and the Milk River area, respectively (Fig. 7). Richness then begins to decrease, reaching its lowest value within the LCZ. The LCZ's microsites vary widely in their richness due to their proximity to the shoreline, which was rapidly changing during the deposition of this unit. Onefour's microsites AC and GB 1-4 have the lowest richnesses, but are considered to be in a more distal position on the coastal plain and

experienced stronger tidal influences. The initial slope of the rarefaction curves show that the LCZ microsites tend to have the lowest evenness, due to being dominated in abundance (43-98%) by one taxon (i.e., *Lepisosteus*, Rajiformes, or Elopiformes). There are three nonmarine microsites (i.e., Cretin, BB118, BB119) that have an evenness comparable to the LCZ, due to being dominated in abundance (40-70%) by one taxon (i.e., *Lepisosteus* or Hadrosauridea), but these represent the exceptions (3 out of 46).

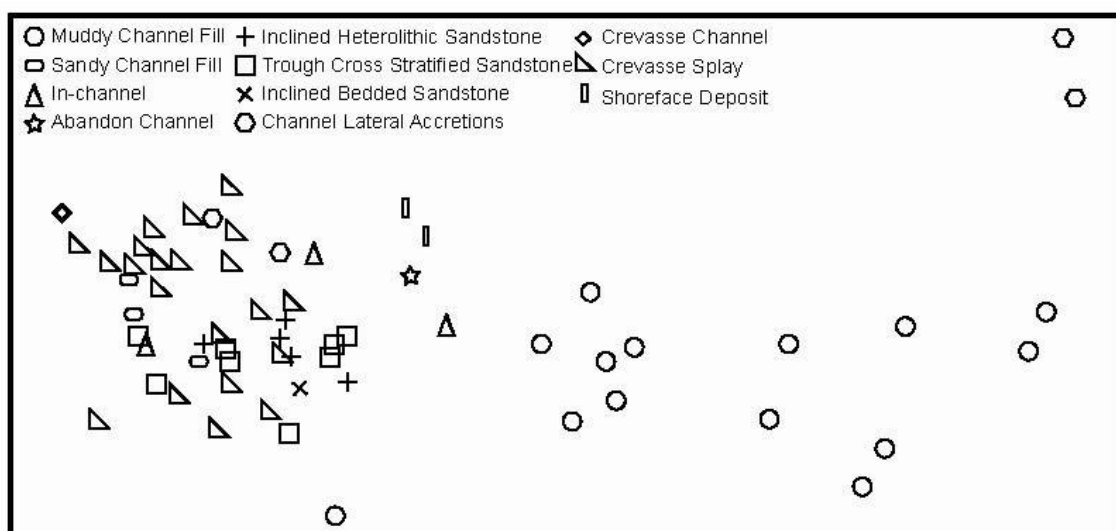


Figure 7: NMDS ordination shows a gradual change from more brackish or marine dominated fauna (i.e., coastal community) to more terrestrially or freshwater dominated fauna (i.e., inland communities). This pattern is consistent regardless of a microsite's geographic location or depositional environment.

Statistically significant changes in diversity partitioning were evaluated by grouping microsites into discrete stratigraphic bins and calculating the effective richness based on Shannon and Simpson indices. Each bin represents the diversity of part of the

Cretaceous landscape over a discrete interval of time. Grouping microsites into discrete stratigraphic bins did not change the overall trend in richness (Fig. 8). Regional and within community diversity reached a maximum in the middle of the Dinosaur Park Fm. and then begins to decrease reaching its lowest value in the LCZ. The drop in diversity in the C bin is due to the low evenness of microsite BB118 and the drop in diversity in the D1 bin is due to the elimination of microsites L1135 and L1136, because those microsites had less than 500 specimens. Effective richness shows that inland communities in the middle of the Dinosaur Park Fm. (i.e., stratigraphic bin D and E) are two to five times more diverse than coastal communities in the upper Foremost (i.e., stratigraphic bin A) and LCZ (i.e., stratigraphic bin G), respectively (Fig. 8). These trends are consistent for both the Simpson and Shannon indices. Regional and within community diversity follow the same trends, because diversity between communities is largely constant until the uppermost Dinosaur Park Fm. and the LCZ, where there is a slight, but statistically significant drop. These results demonstrate that the relative rise of the Western Interior seaway at the end of the Campanian caused a reorganization of the coastal landscape by decreasing diversity and evenness within local communities, but not by affecting their relative compositional differences. Low diversity and evenness and dominance by generalist taxa (i.e., taxa that have a wide habitat range or food preferences) are all features of the LCZ coastal communities and typical for the estuarine systems they represent.

Discussion

Recent studies have shown that microvertebrate assemblages are dominated by autochthonous taxa and composed of minimally transported skeletal elements. Size frequency distributions (i.e., relative abundance of skeletal elements of similar size, shape, and density) of the Belly River Group's microvertebrate assemblages have shown that differences in taxon abundances between microsites are not a taphonomic artifact (Eberth 1990; Rogers 1993; Blob and Fiorillo, 1996; Wilson 2008; Vasileiadou et al. 2009; Rogers and Brady 2010; Peterson et al. 2011).

Tomašových and Kidwell (2009; 2010a; 2010b; 2011) have found that diversity is partitioned differently between live and death assemblages in shallow marine molluscan assemblages, with diversity transferred from between communities to within communities due to time averaging. These authors have also shown that time averaging (>1000 yrs) increases evenness within communities (i.e., decreased the proportion of abundance species and increased the proportion of rare species) and decreases diversity between communities. To minimize this effect, Tomašových and Kidwell (2010a) recommended analyzing paleontological data at multiple spatial scales by combining multiple bulk samples from a habitat (e.g., stratigraphic bins).

Regional and local community diversity (Fig. 5) rises from the upper Foremost to the middle of the Dinosaur Park Fm, but differentiation among local communities remains constant. All diversity decreases from the middle of the Dinosaur Park Fm. to the LCZ, but within community evenness also decreases, which suggests these microsites are not more time averaged than the microsites in the lower part of the

section. Diversity trends of the Belly River Group are reconstructed using multiple bulk samples from multiple environments and grouping them into discrete stratigraphic bins, minimizing the effect of time averaging. While the microvertebrate fossil assemblages of the Belly River Group have experienced some amount of time averaging, it is not enough to dramatically influence changes in diversity through time.

The Belly River Group was deposited on an extensive (>200 km), low-gradient coastal plain dominated by straight to meandering fluvial systems and tidal-dominated estuarine systems with extensive upstream tidal backwaters (Eberth and Brinkman 1997; Eberth 2005). Changes in the spatial distribution and extent of these two environments are reflected in the stratigraphic distribution of vertebrate abundances, allowing the identification of two distinct paleocommunities (inland and coastal; Fig. 6). Diversity curves show an inverse relationship between relative sea-level and both local and regional diversity (Fig. 8). Despite rapid fluctuations in relative sea-level (40,000-400,000 year durations; Eberth 2005), faunal assemblages show gradational changes in richness and evenness, regardless of geographic region or the depositional environment being sampled. This is significant because changes in community structure occurred prior to any sedimentological indications that the shoreline was retreating from or encroaching on a given area. The gradual shifts in the community structure of a largely terrestrial succession served as an early warning signal to environmental changes related to sea level fluctuations. Community structure of was not significantly altered until an area became flooded with marine waters. Significant overlap in fauna assemblages between the two communities and across the three sampled areas help demonstrates that

rising sea-level did not fragment the landscape. Changes in community structure as a result of increased magnitude and/or frequency of perturbations have been well documented in fossil and modern, terrestrial and marine ecosystems (Halloy and Barratt 2007; McGill et al. 2009; McElwain et al. 2009; Foster and Dunstan 2010; Webb and Leighton 2011), but this study represents one of the first times the response of terrestrial coastal ecosystems to relative sea-level fluctuations have been quantitatively documented at a regional scale.

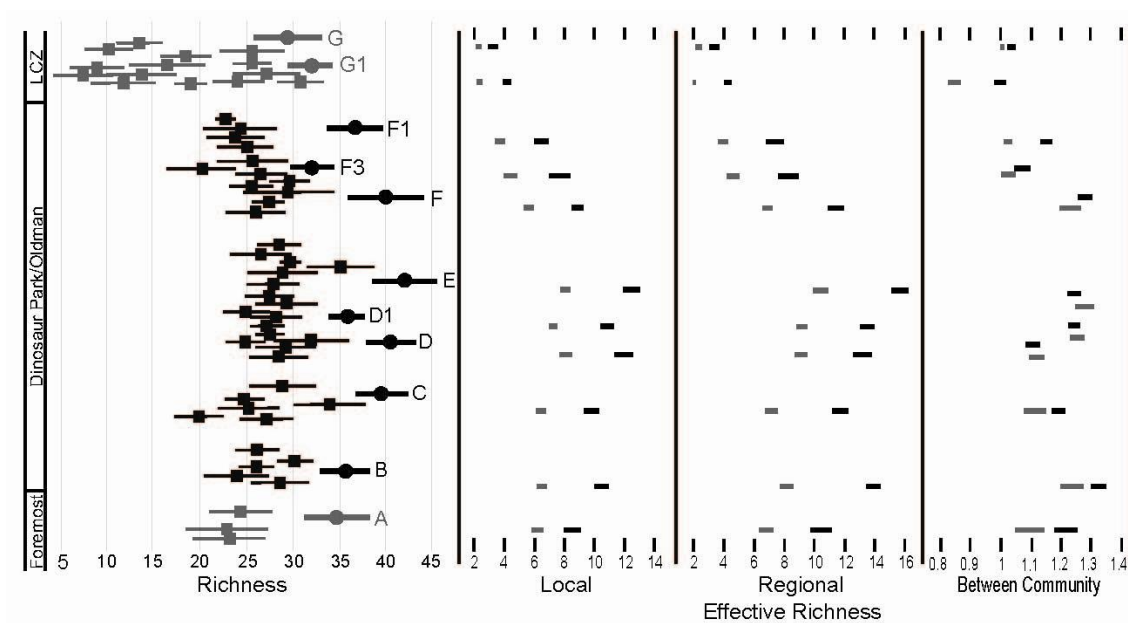


Figure 8: Trends in richness and diversity for the Belly River Group. Microsites were subsampled to 500 specimens, except for the richness of the stratigraphic bins. (denoted by gray circle), which were subsampled to 2000 specimens. Effective richness based on Shannon (black lines) and Simpson (grey lines) entropies, respectively. All error bars represent 95% confidence intervals.

Conclusions

The affect of sea-level fluctuations on terrestrial, vertebrate ecosystems has received surprisingly little attention relative to research on marine invertebrates, fisheries, or coastal wetland habitats to rising sea-levels. This study examined the long term effects (~2 m.y.) of relative sea-level fluctuations on terrestrial community structure of a coastal plain ecosystem at a regional scale. Partitioning diversity revealed that the flooding of the coastal plain leading up to the last major transgression of the Western Interior Seaway affected the landscape by restructuring local coastal communities, represented by estuarine systems. Despite the rapid fluctuations in relative sea-level, fluvial-dominated systems showed gradational changes in richness and evenness, serving as an early warning indication of the encroaching shoreline on a particular region. The gradual change in ecosystem structure of terrestrial-dominated assemblages has the potential to serve as an important indicator for the health of coastal systems in the modern. The challenge will be constructing a long-term baseline for comparison and distinguishing environmental stresses related to a sea-level fluctuations opposed to other disturbances commonly found on modern coastlines (e.g., pollution, habitat lost, lack of freshwater input, etc.).

CHAPTER IV
LONG TERM TRENDS IN THE RICHNESS OF LATE CRETACEOUS
(CENOMANIAN-MAASTRICHTIAN) ACTINOPTERYGIANS
OF NORTH AMERICA

Introduction

Fishes are core members of nonmarine, aquatic communities. In order to reconstruct these ecosystems, it is critical to have a firm understanding of fishes' diversity and distribution and how it has changed through time (Wilson et al. 1992; Wilson and Murray 1996; Grande and Grande 1999; Brinkman and Neuman 2002; Neuman and Brinkman 2005; Hilton and Grande 2006; Cavin et al. 2007; Brinkman 2008; Newbrey et al. 2008). This presents a significant challenge, since most taxonomic identifications require articulated skeletons, which are usually only preserved in large, deep water lakes and only represent one of the habitats fish occupy. However, isolated skeletal elements such as dentaries and centra are usually abundant and distinctive elements that often have autapomorphic features that allow them to be assigned to an established taxonomic group (Brinkman and Neuman 2002; Brinkman 2008).

Late Cretaceous fish assemblages are of particular interest, because these assemblages undergo a major compositional change. Pre-Cretaceous fish assemblages are dominated by non-teleosts (i.e., ichthyodectiformes, elopomorphs, salmoniforms), while Paleogene assemblages are dominated by teleosts (i.e., ~23,000 species) that are members of extant families (i.e., 90% extant taxa) (Wilson et al. 1992; Grande and

Grande 1999; Neuman and Brinkman 2005; Cavin et al. 2007). Understanding the timing, geography, and phylogenetics of this faunal change is critical to understanding nonmarine, aquatic ecosystems and teleost evolution. This study provides a first approach in characterizing long-term trends in richness and the distribution of Late Cretaceous, nonmarine actinopterygians (i.e., ray-finned fishes) of the Western Interior of North America.

To define stratigraphic distribution and richness, nonmarine fish assemblages from the Late Cretaceous deposits of southern Utah (Dakota, Straight Cliffs, Wahweap, & Kaiparowits Fms.), Montana (Hell Creek Fm.), and Wyoming (Lance Fm.) are compared (Fig. 9). The Paunsaugant and Kaiparowits Plateau in southern Utah provides a unique opportunity to examine long-term trends (Cenomanian-Campanian) in the diversity of Late Cretaceous nonmarine vertebrates, because it is the most complete, nonmarine Late Cretaceous sequence of rocks known to date (Eaton 1991). Actinopterygians from the Hell Creek and Lance Formations (Latest Maastrichtian) were included in this study, so trends in richness could be evaluated for the whole of the Late Cretaceous.

Geological Background

The west side of the Kaiparowits Plateau exposes approximately two kilometers of a nonmarine siliciclastic succession (Dakota, Straight Cliffs, Wahweap, & Kaiparowits Fms.), interrupted only by 200 meters of fully marine deposits from the latest Cenomanian to middle Turonian, represented by the Tropic Shale (Fig. 10). These terrestrial sediments were deposited as part of an eastward prograding clastic wedge

deposited in a subsiding foreland basin bounded to the west by the Sevier orogenic belt and to the south by the Mogollon Highlands (Eaton and Nations 1991).

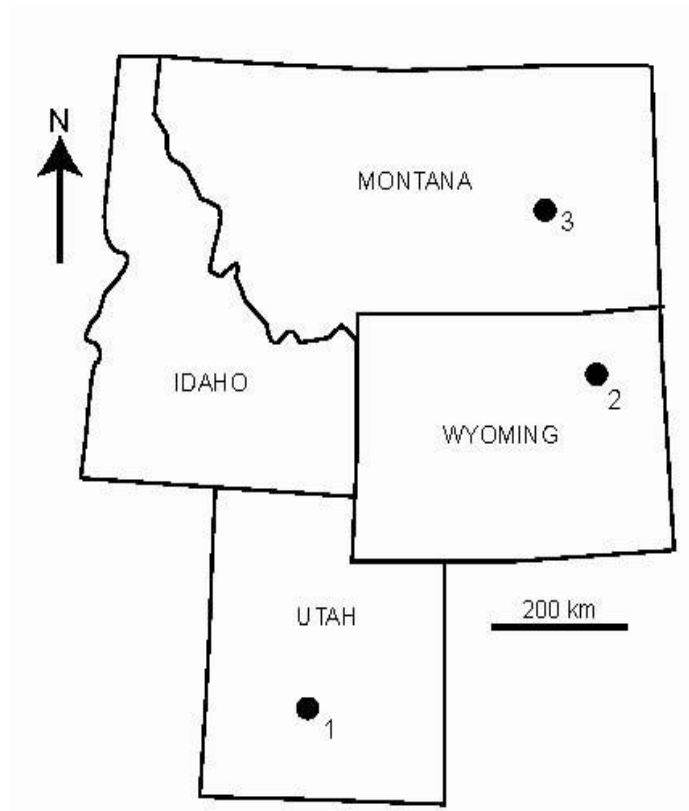


Figure 9: Geographic distribution of sample sites. #1- Kaiparowits Plateau; #2- Lance Fm.; #3- Hell Creek Fm.

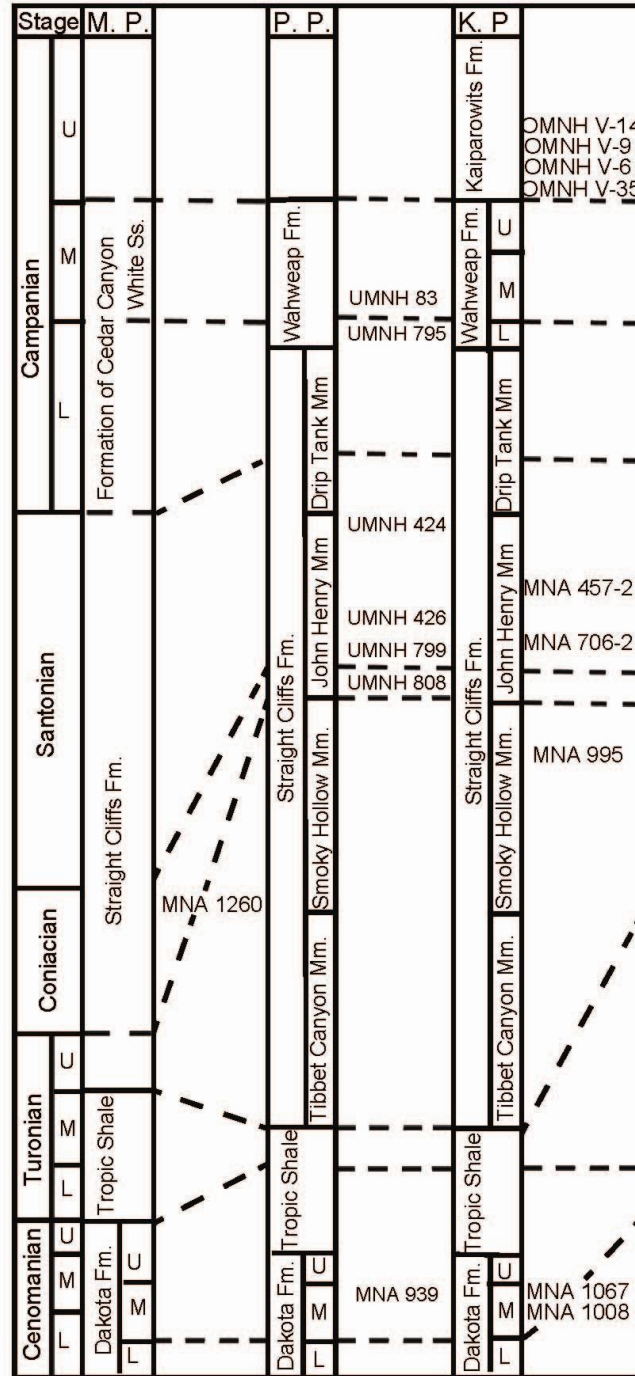


Figure 10: The approximate stratigraphic position of vertebrate microfossil localities used in this study. Abbreviations: M.P.= Markagunt Plateau; P.P.=Paunsaugunt Plateau; K.P.=Kaiparowits Plateau.

The Dakota Formation is divided into three informal members and unconformably overlies the middle Jurassic Entrada Sandstone and interfingers with the Tropic Shale (Peterson 1969). The Dakota is composed of sediments representing fluvial, paludal, lacustrine, brackish, and fully-marine environments (Eaton 1991). All nonmarine vertebrates are recovered from floodplain and levee deposits found in the upper 10-20 meters of the middle member (Eaton et al. 1993). A late Cenomanian age has been assigned to the Dakota's middle member based on ammonites and inoceramids (i.e., *Dunveganoceras pondi* through *Metoiceras mosbyense* ammonite zone) that occur in the overlying marine sands of the upper member and ^{40}Ar - ^{39}Ar dates of 94.7 ± 0.2 Ma and 94.5 ± 0.2 Ma from ash beds low in the overlying Tropic Shale (Tibert et al. 2003). Since the middle member gradually transitions from fluvial to more brackish conditions and there is no indication of a significant time gap, the middle member of the Dakota is considered to be late Cenomanian in age, though could be as old as middle Cenomanian (Eaton 1999a).

The Smoky Hollow Member of the Straight Cliffs Formation is informally divided into three units and overlies the Tippet Canyon Member, which is a sandstone-dominated unit interpreted to represent upper shore face deposits (Peterson 1969; Eaton 1991). The Smoky Hollow is composed of a largely terrestrial sequence of interbedded sandstones, mudstones, and coals, with the basal part dominated by coals and brackish paludal sediments and the upper part dominated by lacustrine and floodplain deposits. The majority of the late Turonian, nonmarine vertebrates come from the floodplain deposits in the middle unit of the Smoky Hollow. The age of this unit is based on the

late middle Turonian index fossil *Inoceramus howelli*, found in the underlying Tibbet Canyon Member (Peterson 1969). As there is no marked unconformity between the Tibbet Canyon and the Smoky Hollow Member, it is considered to be late Turonian in age (Eaton 1999a).

The John Henry Member of the Straight Cliffs Formation unconformably overlies the upper unit of the Smoky Hollow Member called the Calico beds (Peterson 1969). This unconformity appears to span the late Turonian based on the occurrence of a middle Coniacian inoceramid *Volviceramus involutus*, found in the lower part of the John Henry. The upper age limit of the John Henry is considered to be latest Santonian based on the presence of inoceramids (i.e., *Cordioceramus mulleri*, *Endocostea flexibalticus*, *Endocostea balticus*, *Platyceramus cycloides*, and, *Cordioceramus mulleri*) and an ammonite *Desmoscaphites*, recovered from the very upper part of the John Henry (Eaton 1991). The John Henry Member was deposited during a significant transgression of the Western Interior Seaway that began in the Coniacian and reached the middle of the Kaiparowits Plateau by the Santonian. As a result of this, the John Henry Member is primarily composed of marine sediments along the eastern margin of the Kaiparowits Plateau and brackish and non-marine sediments along the western margin. Due to the close proximity of the shoreline, there is a large brackish-tolerant component to the John Henry fauna and fully nonmarine fauna are relatively rare (Eaton 1999a). All the nonmarine vertebrates recovered from this member come from floodplain and paludal deposits, occurring high in the section and are thus considered to be late Santonian in age (Eaton 1991).

Coniacian fish assemblages are included in this study, represented by material from one locality (1260) in the Straight Cliffs Formation (or its equivalent) on the Markagunt Plateau. The age is constrained by a biotite ash that has been dated at 86.72 ± 0.58 Ma (Eaton et al. 1999b; Eaton et al. 2001), placing this locality in the Coniacian. The samples available for study are large, but consist mostly of teeth, scales, and compact bones.

The Wahweap Formation consists largely of interbedded sandstones and mudstones that were predominantly deposited by a meandering river system (Eaton 1991). Nonmarine vertebrates are mainly recovered from basal sandstone lag deposits and floodplain mudstones in the middle and upper part of the formation (Eaton 1999a). An ash bed 60 meters from the base of the formation produced an ^{40}Ar - ^{39}Ar date of 80.1 ± 0.3 Ma. The majority of the 400 meter thick Wahweap Formation is considered to have been deposited between 80.8 and 76.1 Ma, based on estimated rates of deposition (i.e., 8.4 and 13.1 cm/ka) using the radiometric date obtained from Wahweap and the overlying Kaiparowits Formation (Jinnah et al. 2009). This would suggest the majority of the Wahweap is middle Campanian, though some of the most basal localities could be lower Campanian (Eaton 1991).

The Kaiparowits Formation is 860 meters thick, comprised of sandstones, mudstones, and siltstones that were deposited within the relatively low-relief alluvial plain of a meandering river system. The majority of the nonmarine vertebrates are recovered from the fluvial sandstones or the floodplain mudstones in the lower 400 meters of the formation. The entire Kaiparowits Formation is late Campanian in age,

based on the ^{40}Ar - ^{39}Ar dating of four bentonite beds dispersed throughout the formation. These bentonite beds yielded ages ranging from 75.96 ± 0.14 Ma to 74.21 ± 0.18 Ma (Roberts et al. 2005). Estimated rates of deposition based on the ^{40}Ar - ^{39}Ar dates suggest a very high rate of deposition 39 to 42 cm/ka. The poor soil development that is seen throughout this formation supporting this interpretation (Eaton 1999a).

This study also includes seven fossil localities (Late Maastrichtian) from fluvial deposits of the Hell Creek (6 localities) and Lance Formations (1 locality). These localities were chosen, because they yield an abundance of actinopterygian specimens (>200 specimens), have been placed in a robust stratigraphic framework, and come from the same depositional environments as the fossil localities sampled on the Kaiparowits Plateau. The fossil localities from the Hell Creek Formation come from a sandy-siltstone facies commonly associated with organic material and cross-stratified sandstones with mud rip-up clasts. These facies are interpreted to represent crevasse splays and the lag deposits of thalweg infillings, respectively (Wilson 2005). The Lance Formation is composed of thick-bedded sandstone with thin coal and carbonaceous shales, representing a coastal floodplain and is considered to be the temporal equivalent to the Hell Creek Formation (Clemens 1964).

Methods

All the fossil material included in this study was recovered from microvertebrate localities (i.e., fossil sites that produce an abundance (>100) of small (1mm–50mm) skeletal elements) that were bulk sampled (up to 3 metric tons), disaggregated, and screen-washed using 0.3 mm mesh screen (Eaton 2006). Because microvertebrate

assemblages are composed of disarticulated skeletal elements and most taxonomic identifications require partially articulated skeletons, a parataxonomic approach was used to identify this material (Krell 2004). Since many taxa are represented by morphologically distinct elements that can only be identified at higher taxonomic levels (i.e., order, family, & genus), recognizing these distinct morphotypes allows for easy comparison between stratigraphic units and inferences about changes in taxonomic diversity, without erecting redundant taxonomic names on the basis of isolated skeletal elements (Brinkman and Neuman 2002; Brinkman 2008). To interpret the relationships of the remains of fish as fully as possible, extensive comparison with recent osteological and fossil material was undertaken utilizing collections at the Royal Tyrrell Museum of Palaeontology, University of Alberta Laboratory of Vertebrate Paleontology, University of Utah, Museum of Northern Arizona, and Sam Noble Natural History Museum. Trend in richness of actinopterygians through the Late Cretaceous are based on 58 taxa from 25 fossil localities (Fig. 10).

To account for the effect of different sampling intensities between stratigraphic units, actinopterygian abundance data was subsampled to a standard size equal to that of the smallest collection. The Lance Formation had the smallest collection, with 368 identifiable skeletal elements, so each stratigraphic unit (i.e., collection) was subsampled to 350 individuals. Statistically significant differences in richness for a given subsamples was evaluated using the expected variance of sample richness at 95% confidence intervals (Magurran 2004; Gotelli and Colwell 2001; Shen et al. 2003; Olszewski 2010).

Individual-based rarefactions were constructed at the substage level, because the number of fossil localities within a given stratigraphic unit (i.e., 1-4 localities) and their sample sizes (i.e., 40-3000 specimens) varied dramatically. Examining long term trends in richness using samples lumped at such a coarse scale is not ideal, but the results of this study are still informative, because it represents the first analysis using absolute abundance counts of all actinopterygians for the entire Late Cretaceous (Cenomanian-Campanian) from a limited geographic area. Most vertebrate studies that examine long-term trends through time use taxon occurrence data (i.e., presence/absence rather than counts of individuals) and are conducted on a continental or global scale due to the lack of temporally continuous fossiliferous units in a single area.

Effective richness based on Simpson index was also calculated for each substage to evaluate any changes in community structure. Shannon's index was not used, because it is more susceptible to large differences in sample size, even though the Simpson's index is weighted more heavily to the most abundant taxa (Magurran 2004). The Simpson index measures the probability that any two individually drawn at random from an infinity large community belong to the same taxon. Effective richness estimates the number of equally common taxa required to produce a particular value of the index (collections with different richnesses could have the same index value depending on the evenness of the taxa) (Jost 2007; Jost et al. 2010; Olszewski 2010). The results of the Simpson index will be only a working hypothesis, since confidence intervals cannot be applied, due to several substages only having two collections or less.

Results

Results of individual-based rarefaction show significant changes in richness throughout the Late Cretaceous. Richness is highest in the Late Cenomanian, Santonian, and Campanian, with the rarefaction curve for these subsamples still rising. The effective richness of aquatic communities is highest in the Late Cenomanian and the late Campanian, being four to six times richer than Turonian or Early Campanian aquatic communities (Fig. 11). The loss of richness in the Turonian appears to be a local extinction, since only two taxa (Ellimmichthyiform centra type LvD & Amiidea centra type ASWW) are lost. The restructuring of nonmarine aquatic communities from the Cenomanian to the Turonian is reflected in the appearance of Lepisosteidae (i.e., gar), Ostariophysis (i.e., catfish), and Vidalamiinae (i.e., *Melvius*), and the decrease in abundance of *Coelodus* and *Lepidotes*. From the Turonian to the early Campanian, effective richness appears to be largely constant, but there is the appearance of new *Lepisosteus* species and the percentage of acanthomorpha centra (6-16%) increases. Differences in faunal assemblages from the Kaiparowits and Wahweap Formations suggest that a significant faunal turnover occurred during the mid to late Campanian, with the first appearance of five taxa in the Kaiparowits Formation: a new Esocoid, *Estesesox* sp., a characiform, a clupeiform, and an osteichthyan of uncertain relationships represented by a saber-like tooth. The decrease in richness from the late Campanian to the late Maastrichtian results from the absences of teleost centra types O and BvA, *Lepidotes*, and *Coelodus*. There is also an increase in abundance of BvA and

BvE teleost centra, Amiidae (60%) centra, and the presence of a large acanthomorpha in the late Maastrichtian deposits.

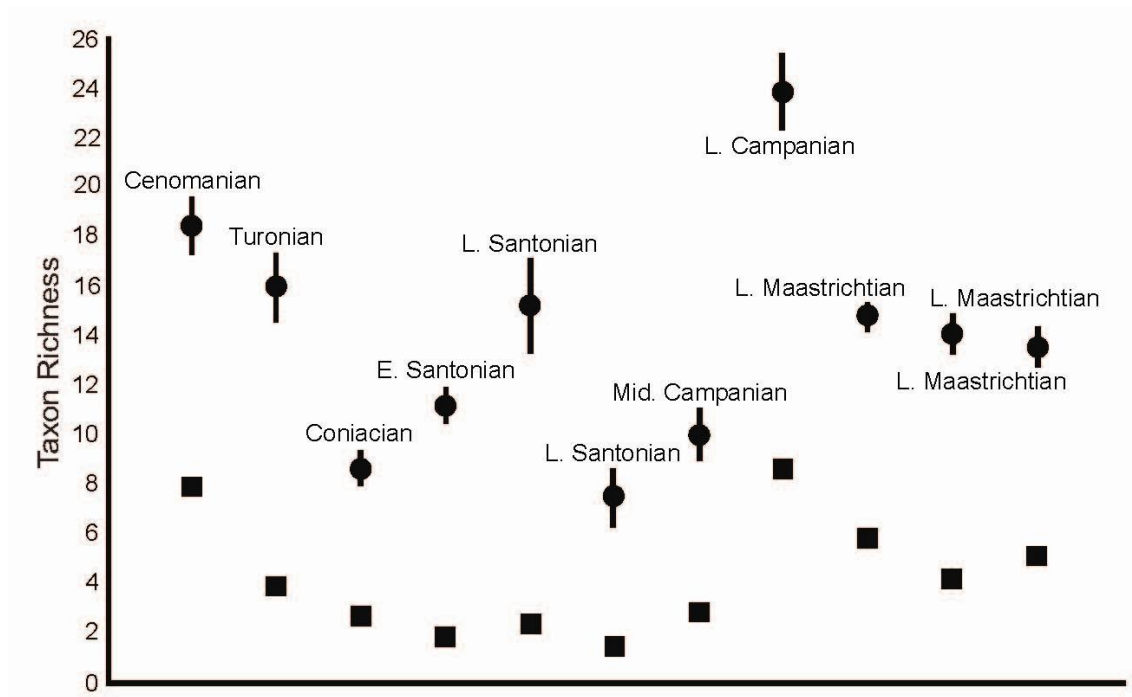


Figure 11: Trends in the richness of actinopterygians for the Late Cretaceous based on 350 specimens, denoted by black circle. Vertical bars represent 95% confidence intervals. Effective richness of Simpson's index is denoted by the black box.

Discussion

Most Cretaceous freshwater deposits in North America produce only a couple of articulated fish skeletons. Because of this preservational bias many workers suggested that freshwater teleosts were largely absent from North America until the Eocene or later (i.e., Green River Formation). Recent work utilizing isolated skeletal elements and a

parataxonomic approach has revised this interpretation. The results of this study demonstrate the teleosts were a significant component of North American, nonmarine fluvial communities for the entire Late Cretaceous. The long duration dataset that was used in this study also suggests that the transition from nonteleost-dominated to teleost-dominated aquatic communities during the Late Cretaceous was not a gradual transition, but occurred as a series of events marked by significant shifts in ecosystem structure and richness (e.g., Cenomanian-Turonian & middle to late Campanian), separated by long periods (millions of years) of relatively stability (e.g. Turonian to mid Campanian). However there does appear to be a lot of variability, depending on the actinopterygian group. Acanthomorphas show a gradual increase in abundance from the Turonian to the Maastrichtian, but Escocoidea rapidly diversify shortly after they appear in the late Campanian. High resolution sampling at the regional scale will be needed to develop a robust understanding of the timing and sequence of events leading up to a teleost-dominated ecosystem.

Eaton et al. (1997) were the first to report a drop (25% families) in the diversity of freshwater vertebrates across the Cenomanian-Turonian boundary. Since the diversity of terrestrial and brackish-tolerant taxa did not change across the boundary, Eaton et al. (1997) considered that the loss of freshwater-restricted taxa was due to the loss of coastal plain habitats during the transgression of the Western Interior Seaway. Brinkman (2008) considered the drop in richness at the Cenomanian-Turonian boundary to be related in part to the high global temperatures in the late Turonian reflected in the first appearance of *Melvius*, *Lepisosteus*, and ostariophysans (i.e., catfish), three taxa

commonly found in more southern assemblages. *Coriops* has a temporally disjunct distribution in Utah, being present the Cenomanian and Campanian, but not in any intervening assemblages. This may be a reflection of *Coriops* being a member of a northern, cool-temperature assemblage, with the presence of *Coriops* in Utah in the Cenomanian prior to Turonian thermal maxima, and during the relatively cooler late Campanian, can be interpreted as a southern shift in distribution of a northern taxon in response to cooling temperatures. The loss of habitat due to changing sea-level or the shift in the geographic range of taxa are not mutually exclusive, but the results of this study does not support one of the hypotheses over the other.

Conclusion

The fish assemblage of the Paunsaguant and Kaiprowits Plateau demonstrate that teleosts are much more significant members of fish assemblages that what has historically been thought to be the case. This study demonstrates that the richness of actinopterygians fluctuated greatly through the Late Cretaceous, with peak diversity occurring in the Late Cenomanian and the Late Campanian. A major faunal change occurred between the Cenomanian and Turonian assemblages. Amiids decrease in diversity, pycnodonts and *Lepidotes* become rare, and the Lepisosteidae, Vidalamiinae, and ostariophysan type U3/BvD all first appear in the Turonian. A significant faunal turnover also occurred in the mid to late Campanian, when esocoids and a characiform first appear. Whether this study represents the typical trends in Late Cretaceous aquatic communities will require sampling additional fossil assemblages.

CHAPTER V

CONCLUSIONS

The goal of my research is to use fossils to develop models based on fundamental ecological principles of long-term (i.e., evolutionary) biological change for terrestrial ecosystems through deep time. Using the distribution of modern terrestrial vertebrates from the Northern Colorado Plateau, my dissertation research has demonstrated that higher taxonomic levels can preserve the species-level pattern of regional biogeographic relationships among sites, meaning that it should be possible to study changes in fossils using higher taxonomic identifications. Partitioning diversity of the Late Campanian, terrestrial vertebrates from the Belly River Group, demonstrated that the flooding of the Alberta coastal plain leading up to the last major transgression of the Western Interior Seaway affected the landscape by restructuring local coastal communities, with an inverse relationship between relative sea-level and ecosystem richness and evenness. Despite the rapid fluctuations in relative sea-level, fluvial-dominated systems showed gradational changes in richness and evenness, serving as an early warning indication of the encroaching shoreline on a particular region. Utilizing isolated skeletal elements and taking a parataxonomic approach to studying Late Cretaceous, North America actinopterygians, demonstrated that teleosts were a significant component of nonmarine fluvial communities for the entire Late Cretaceous. The long duration dataset that was used in this dissertation suggests that the transition from nonteleost-dominated to teleost-dominated aquatic communities during the Late Cretaceous was not a gradual transition,

but occurred as a series of events marked by significant shifts in ecosystem structure and richness, separated by long periods (millions of years) of relatively stability.

Conserving biodiversity in the current global ecological crisis requires a robust understanding of the multitude of abiotic and biotic processes operating at different spatial and temporal scales. Unfortunately, many of these processes and their long-term impacts are not well understood and are nearly impossible to study on a human timescale. This work helps address this gap in knowledge, by developing a better quantitative understanding of how ecological processes and their changes have influenced diversity, ecosystem structure, and the distribution of species across a landscape through time.

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