



Landscape Diversity of the Upper Cretaceous Judith River Formation

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Introduction

The Judith River Formation (JRF) is a historically important, fossiliferous Upper Cretaceous stratum, deposited ~72-80 million years ago on a swampy coastal floodplain with rivers and oxbow lakes. Since the 1850s, researchers have collected many vertebrate fossils including mammals and dinosaurs. More recently, abundant microvertebrate sites have allowed investigation of the paleoenvironment and paleoecology of the formation [1,2].

This project focuses on the taxonomic and ecological diversities and abundances of these microvertebrate assemblages. We make comparisons between sites to investigate differences within the formation and compare each site with collective data on this prehistoric ecosystem.

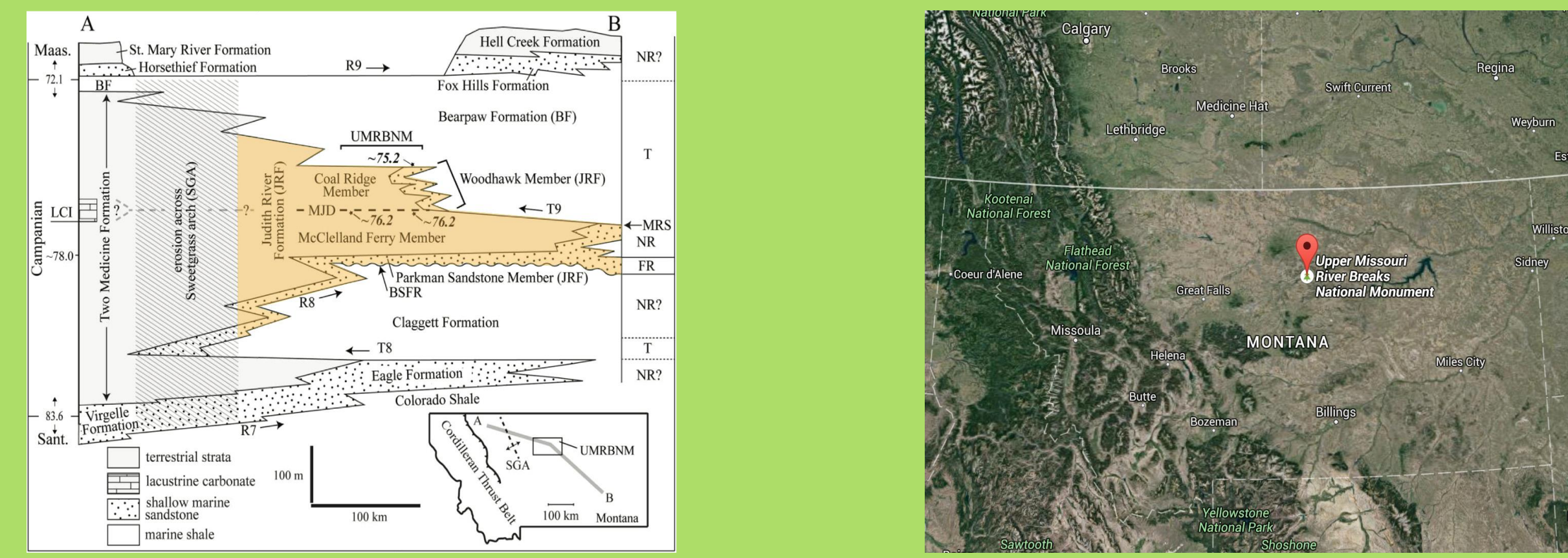


Figure 1: Geographic and geologic contexts. (A) Stratigraphic diagram of Upper Cretaceous rocks, with the JRF highlighted in orange [modified from 3]. (B) Location of field sites [Source: Google Maps].

Methods

Fossils from 13 sites in the JRF of the Missouri Breaks, central Montana were surface- and bulk-sampled (and sieved) in 1994-1996 and 2012-2015. For each fossil, element type and taxon were identified using a Zeiss Stemi SV 6 microscope, resulting in 7,694 identifiable specimens [4,5,6]. Surface and sieve samples were counted separately.

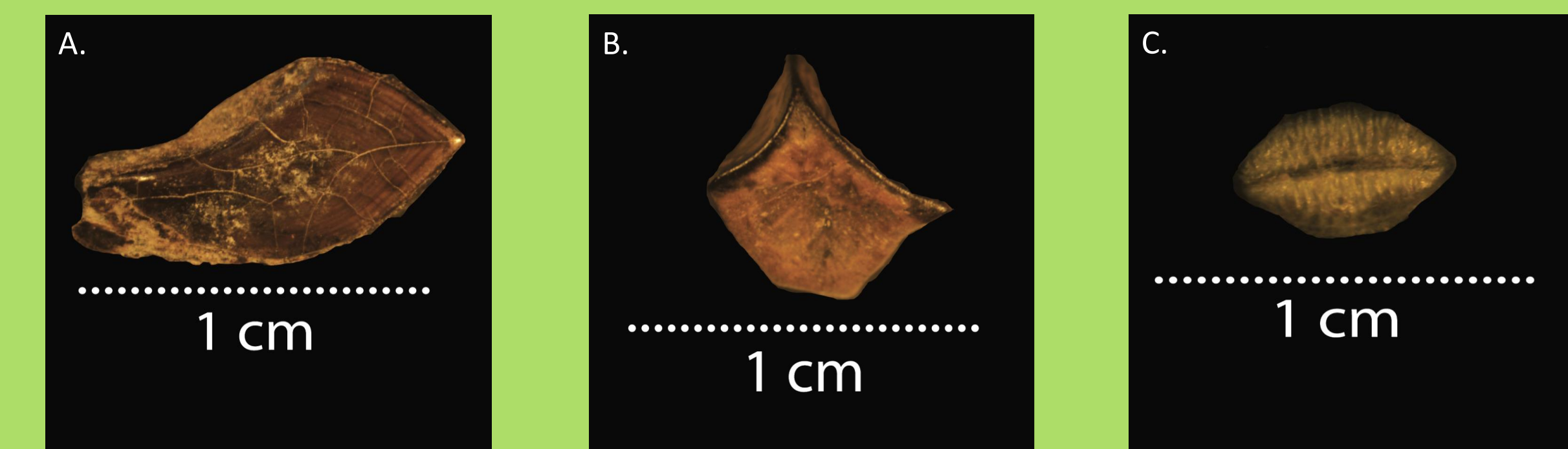


Figure 2: Images of a three common fossils, (A) a gar scale, (B) a hadrosaur tooth, occlusal view and (C) a ray tooth, occlusal view.

We compared sites using the *vegan*, *permut*, and *lattice* packages in the R program [7]. To determine how representative each site was of the overall ecosystem, we constructed rarefaction curves comparing sample size to number of taxa. We calculated cluster dendrograms based on the Jaccard, Sørensen, and Morisita's overlap indices, and used non-metric multidimensional scaling (NMDS) to determine the relationship between the sites and taxonomic abundances.

We also examined the abundances and diversities of taxa according to two ecological attributes, habitat and diet. Taxa were separated three habitat categories (aquatic, amphibious, terrestrial) and four diet categories (small carnivore, large carnivore, omnivore, herbivore). These ecological attributes were examined separately and in combination.

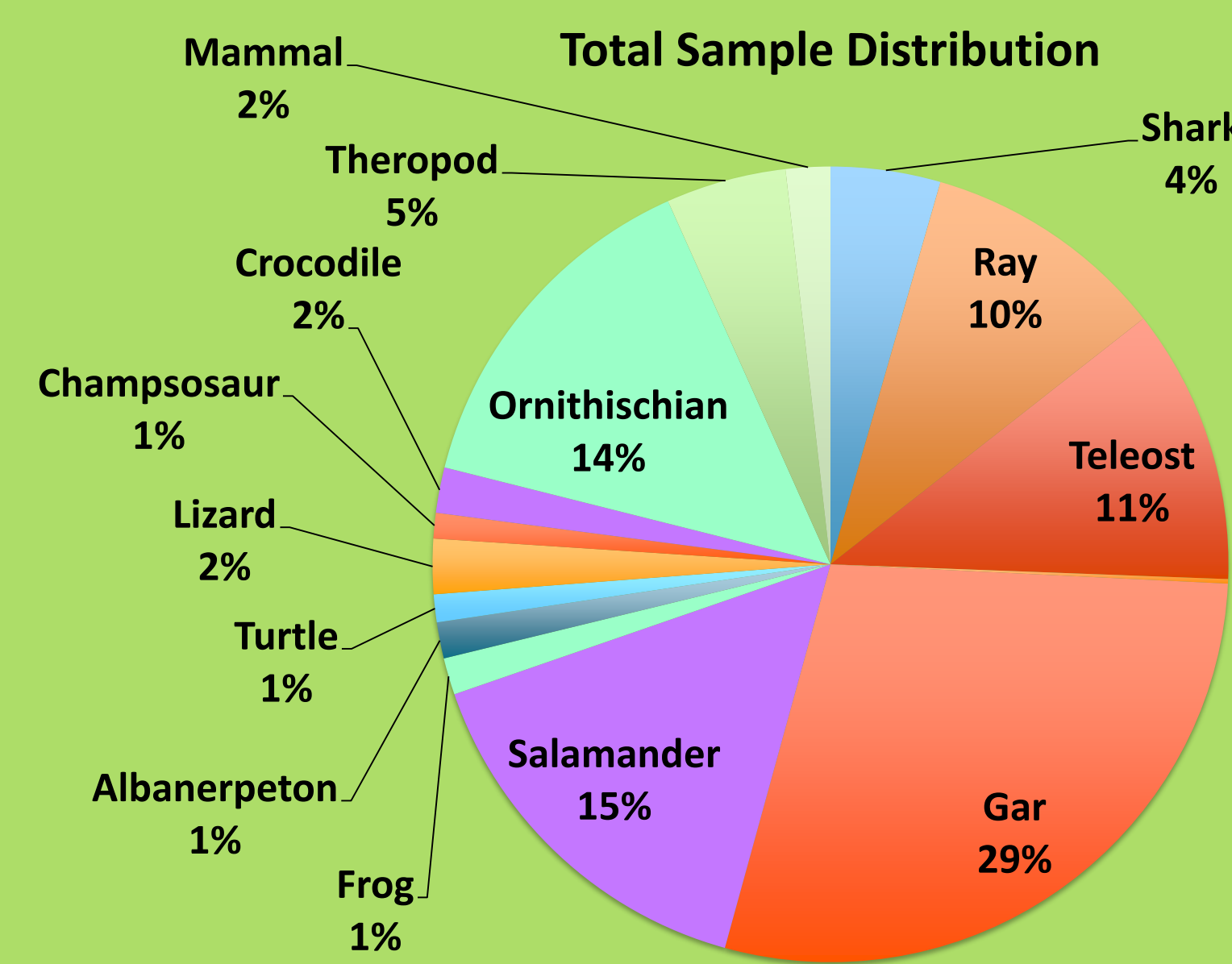


Figure 3: Relative abundances of taxa based on individual specimen counts from all sites.

Results

The most abundant taxa were gar, teleosts, salamanders, and ornithischian dinosaurs (Fig. 2). The rarefaction curves for several sites show evidence of an asymptote ≥ 14 taxa. UC-941, the site with the largest sample, is nearing an asymptote at about 15 taxa [8] (Fig. 3). Two sites may be genuinely less diverse (CBH, UC-914).

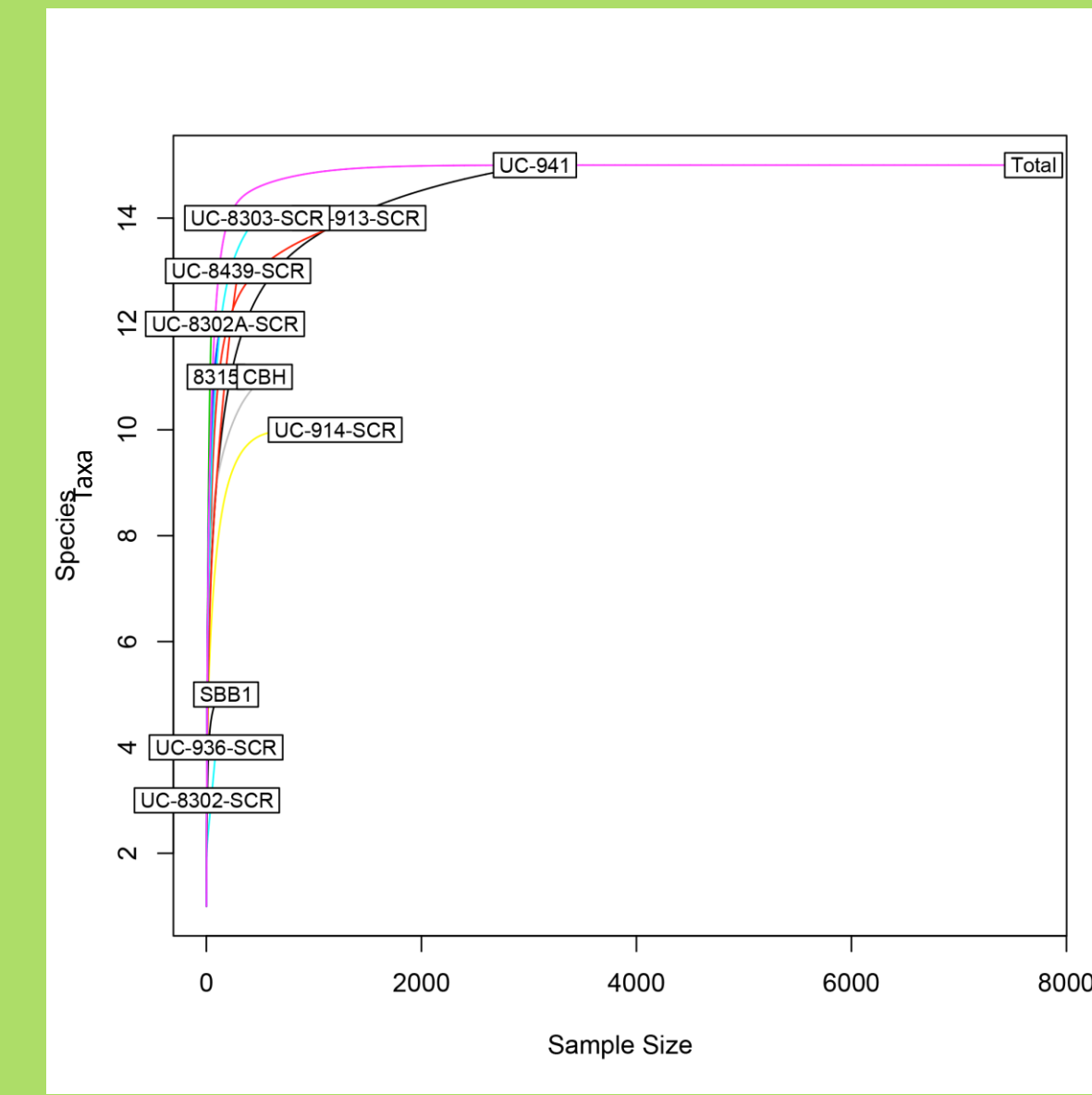


Figure 4: Rarefaction curves showing the relationship between sample size and number of taxa for each of the sites.

Results (cont.)

Aquatic taxa and small carnivores were the most abundant habitat and diet groups respectively. The combined abundance shows aquatic carnivores (small or large) had the highest totals. Terrestrial taxa and omnivores were the most diverse groups, and terrestrial omnivores were the most diverse when combined (Fig. 8).

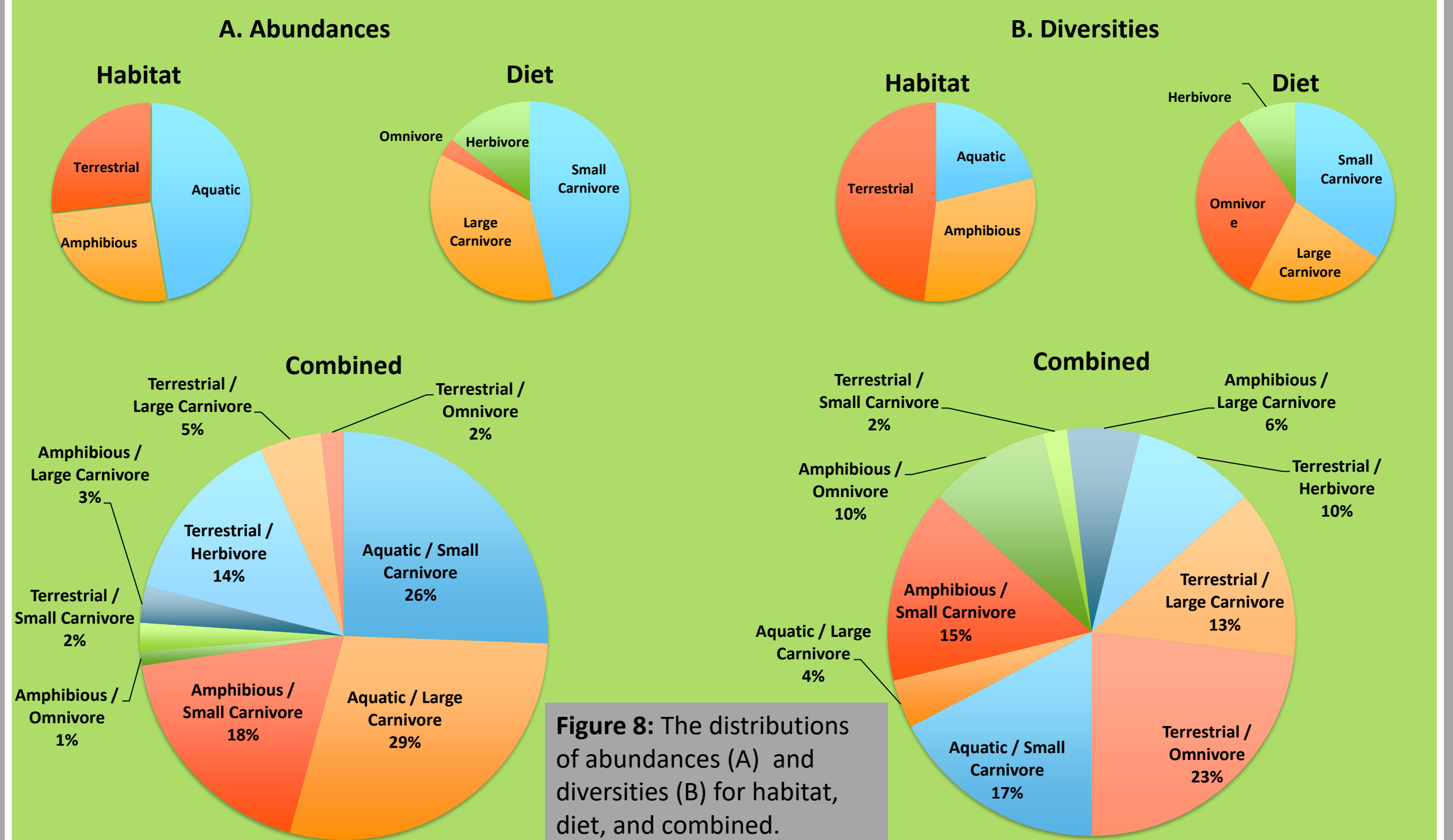


Figure 8: The distributions of abundances (A) and diversities (B) for habitat, diet, and combined.

The Jaccard and Sørensen indices were nearly identical, with clusters broadly distributed based on taxonomic diversity. The outliers UC-936 and UC-8302 contain the fewest number of taxa (4 and 3, respectively), whereas the large cluster 1 groups sites with ≥ 10 taxa (Fig. 4). Within the latter, cluster 1.1 contains high numbers of teleosts, while 1.2 contains high numbers of dinosaurs. In contrast, Morisita's overlap index clusters according to the most abundant taxa at each site. For cluster 1 these are dinosaurs, split between theropods and ornithischians. Cluster 2 is dominated by gar, and cluster 3 by salamanders (Fig. 5).

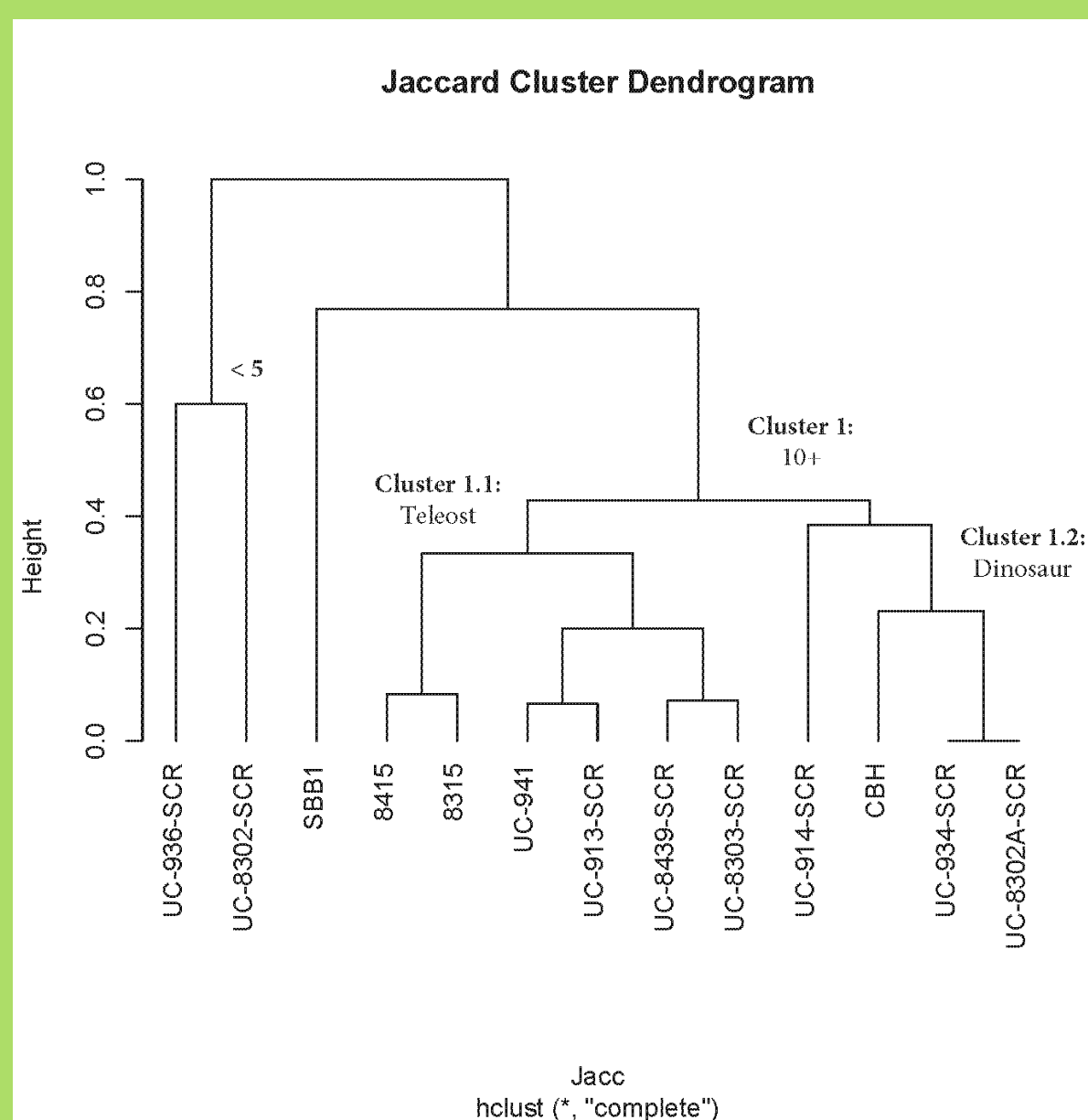


Figure 5: The Jaccard index cluster dendrogram organizes the sites based on the total number of taxa present.

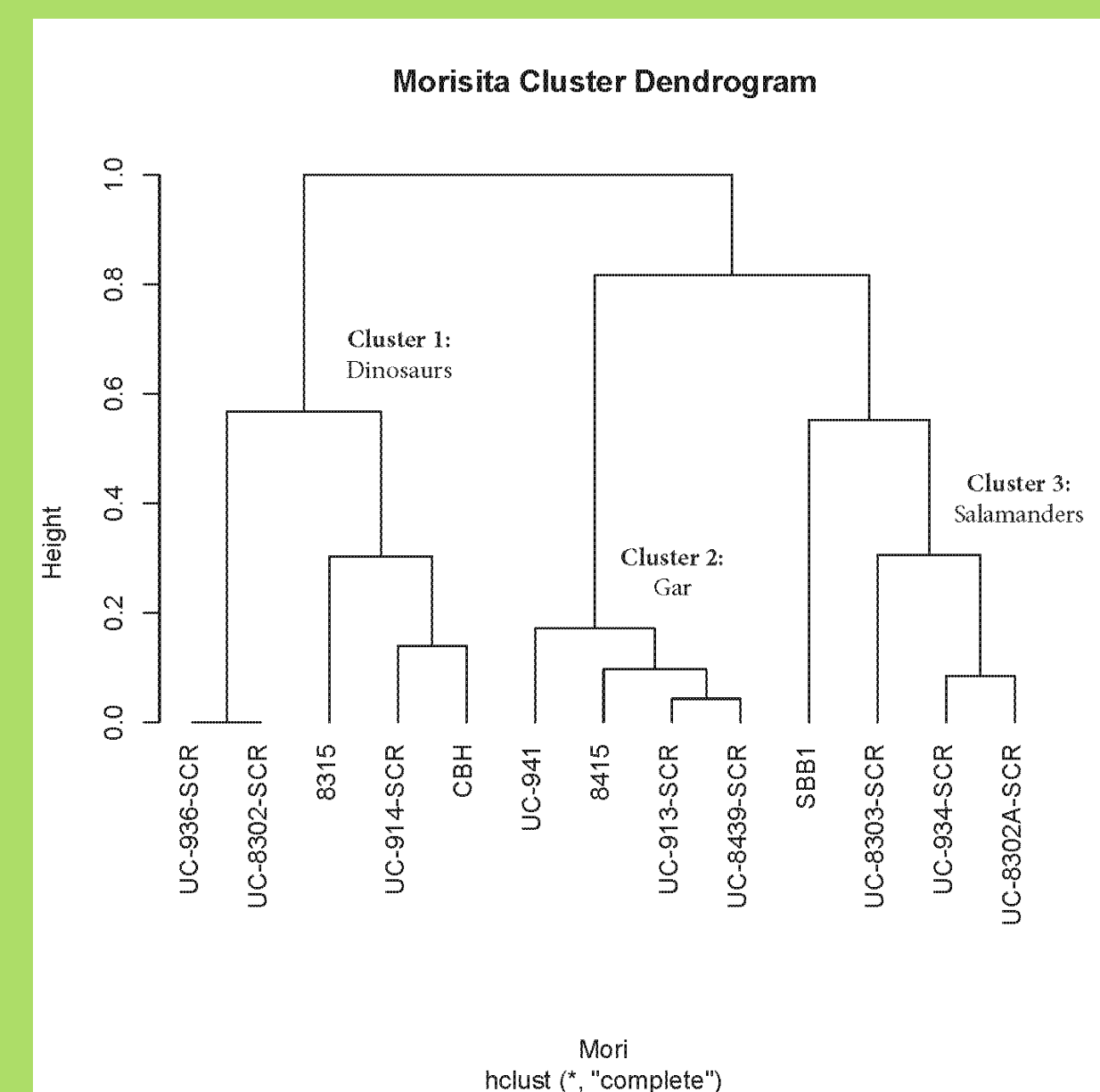


Figure 6: The Morisita's overlap index cluster dendrogram organizes the sites based on the dominant taxa.

NMDS1 separates the sites based on high abundances of theropods and ornithischians (positive) versus high abundances of smaller taxa such as salamanders, gar, and lizards. NMDS2 discriminates based on high abundances of terrestrial or amphibious taxa (positive) versus aquatic taxa (negative) (Fig. 7).

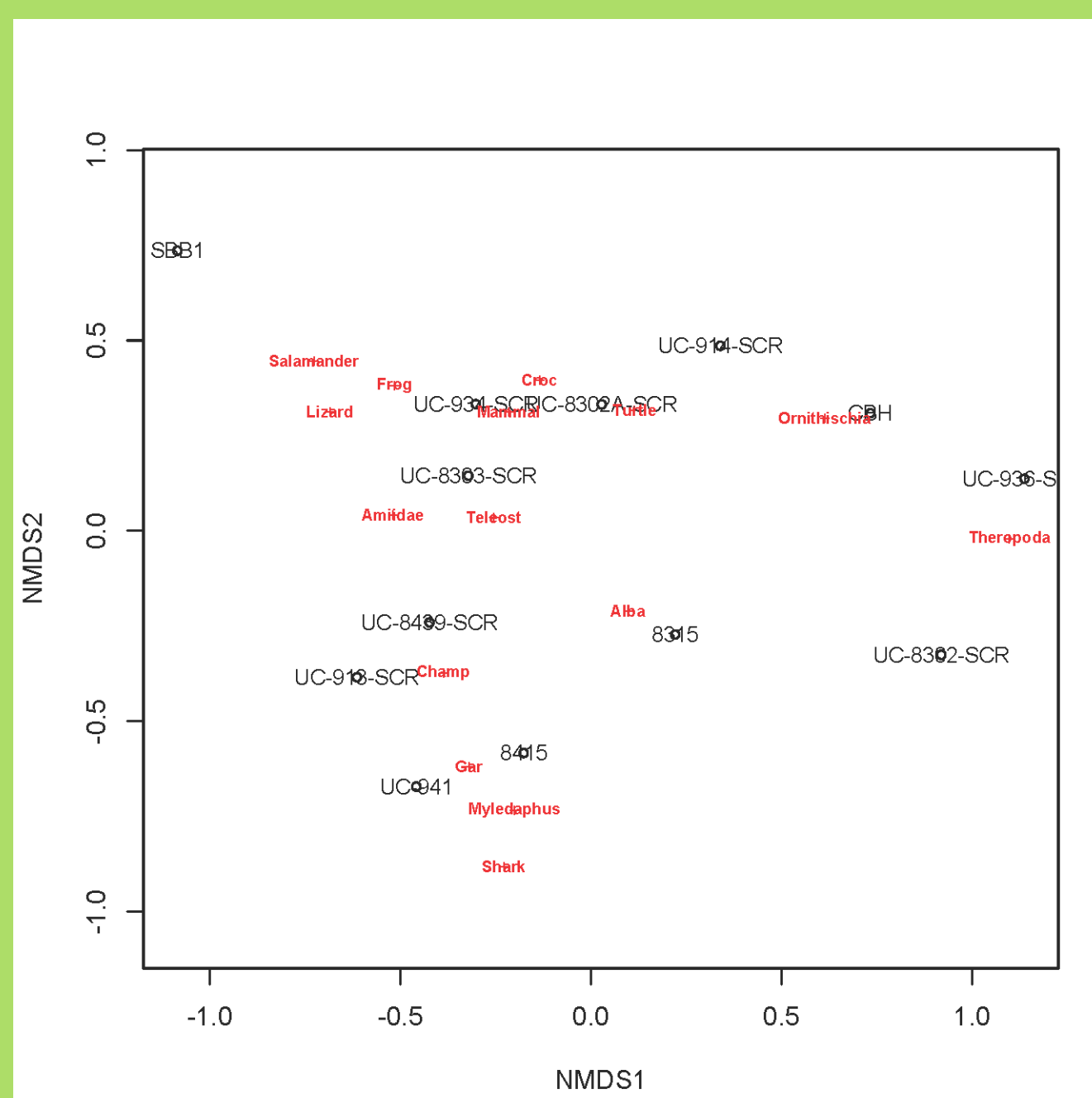


Figure 7: Nonmetric multidimensional scaling illustrates the relationships between the different sites and their taxonomic compositions.

Discussion

Rarefaction curves show evidence of an asymptote for sites with 14+ taxa, whereas some with fewer taxa do not appear to be as fully sampled. Comparison with the rarefaction curve for all sites combined suggests that many sites can be considered as thoroughly sampled.

One marked difference between sites is whether dinosaurs (terrestrial) or gar and salamander (aquatic/amphibious) are most abundant. Dinosaur-dominated sites often had lower sample sizes, and may have been skewed by a favorable taphonomy toward larger fragments. However, even better-sampled sites followed similar trends. Thus the variation in faunal composition across the sites is not entirely due to sample size. As a result we infer that some of these abundance and diversity variations may have been present in the original ecosystem.

Aquatic taxa were the most abundant, as were small carnivores, as would be predicted from the paleoenvironment. Diversity differed where terrestrial taxa dominated, due to the large number of mammal species identified. This is likely an artifact of our increased ability to identify mammal teeth versus other taxa. Identification of these fossils to lower-level taxa will allow more detailed investigation of these conclusions.

Conclusions

The samples include all broad taxonomic groups present in the larger ecosystem. The environment appears to be primarily aquatic with mainly small carnivores. Most sites follow similar trends, with smaller aquatic and amphibious taxa dominating. Although sample size is an important factor, the different abundances of gar, salamanders, or teleosts may reflect genuine landscape distinctions. However, until there are species level identifications of the different taxa, there is still a degree of uncertainty about the paleoenvironment.

References

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