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Perception of paleocommunities at different taxonomic levels: How low must you go?

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ABSTRACT

To obtain meaningful information from paleocommunities, researchers must collect assemblages that are sufficiently complete to accurately represent the once-living community and large enough to produce statistically robust results. A key decision in community paleoecological research is the level of taxonomic identification. Here, we conducted a meta-analysis of 28 datasets from the Paleobiology Database (PBDB) to determine whether paleocommunity analyses at higher taxonomic levels produce similar results to those analyzed at the generic level. For each dataset, we composed taxon-sample matrices (series of samples containing multiple taxa of varying abundances) at the genus-, family-, order-, and class-levels. We then compared the multivariate paleocommunity results of each of the three higher taxonomic levels (family, order, and class) to the genus-level result. High goodness-of-fit statistics (using three different statistical comparison methods) resulted between comparisons of genus- and family-level taxonomic identifications for 28 paleocommunity datasets. However, 15 of the 28 genus- and family-level taxonomic identification comparisons were determined to produce different paleocommunity results based on qualitative-visual comparisons. Thus, family-level identification of specimens may often lead to the same paleocommunity conclusions as genus-level identification; however, inconsistencies generate enough uncertainty that paleocommunity research would benefit from genus-level identification of specimens. Due to the moderate-to-low goodness-of-fit statistics between genus–order and genus–class comparisons of paleocommunities as well as the clear differences found in the qualitative-visual comparisons, order and class did not reliably reproduce genus-level results. Thus, family-level identifications may be sufficient some of the time for studies employing multivariate statistical methods to compare paleocommunities that would otherwise use the genus level; order- and class-level identifications are probably never sufficient.

1. Introduction

Community paleoecology utilizes fossil assemblages to examine the mechanisms of ecological and environmental variation through space and time. Such data provide insight into the processes that structure ecosystems and the causes of ecosystem collapse and extinction (Olszewski and Patzkowsky, 2001; Kowalewski et al., 2002; Bonelli et al., 2006; Redman et al., 2007; Clapham and James, 2008; Leighton and Schneider, 2008; Heim, 2009). In addition, paleocommunity data provide a wealth of information about ecological interactions and environmental tolerances on local scales and help researchers understand how these processes scale up to regional, continental, and global scales (Kowalewski et al., 2002; Bambach et al., 2004; Clapham and Bottjer, 2007). Furthermore, in the face of the rapid tempo of the current biodiversity crisis, conservation science will benefit from increased productivity by paleoecological researchers and quick dissemination of their findings (Bennington and Aronson, 2012). Conducting examinations of how ecosystems were affected by events of rapid warming in the past can lead to predictions regarding how current ecosystems will change (Louys, 2012). This could provide information important to preserving the natural world and counteracting anthropogenic influence.

To obtain meaningful information, researchers must collect samples of fossil assemblages that are sufficiently complete to be an accurate representative and large enough to produce statistically robust results (Forcino et al., 2010; Forcino, 2012). Most community paleontological research is resource-intensive, both in terms of travel and in time spent collecting and analyzing data. Therefore, researchers must strike a balance between economy of collection and quantity of data.

A key decision in community paleoecological research is the level of taxonomic identification. Most studies identify specimens to the genus (Olszewski and Patzkowsky, 2001; Forcino et al., 2012) or species (Schneider, 2003). However, some studies use taxonomic families, or non-Linnaean clades or guilds (Kowalewski et al., 2002; Lebold and Kammer, 2006; Forcino et al., 2012). Here, we conducted a meta-analysis of 28 datasets from the Paleobiology Database (PBDB) to determine whether paleocommunity analyses at higher

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taxonomic levels produce similar results to those analyzed at the genus level. For each dataset, we composed taxon-sample matrices (series of samples containing multiple taxa of varying abundances) at the genus-, family-, order-, and class-levels. Species were not examined, as genus is the lowest taxonomic level included in the PBDB. Genus is also the lowest taxonomic level to which paleocommunity researchers typically identify specimens. We then compared the multivariate paleocommunity results of each of the three higher taxonomic levels (family, order, and class) to the genus-level result. If the higher-level identifications produce the same multivariate results as those at the genus-level, such higher-level classification may be sufficient for community paleoecological research. Simplification of the identification process would conserve resources for researchers. On the other hand, if higher-level identifications do not produce the same multivariate results as the genus-level, then researchers should invest time and effort into lower-level identification in order to produce the most accurate paleocommunity results from the available material.

Identification of fossil specimens to taxonomic levels above genus may provide information as meaningful as information derived from genus- or species-level identification. More closely related organisms tend to be ecologically similar (Darwin, 1859; Cadotte et al., 2008; Cavender-Bares et al., 2009; however, see Cahill et al., 2008 for a counter-argument); two genera of rhynchonellate brachiopods have more in common in terms of natural history, feeding strategy, and environmental preferences than either genera may have with two genera of fish, and vice versa. In addition, identification of specimens at lower taxonomic levels requires much more specialized knowledge than identification to higher levels; a paleocommunity assemblage can contain dozens of genera in several families within multiple phyla, while a typical paleontologist may specialize in only one or two taxonomic groups. When non-specialists attempt to identify specimens to genus or species, identifications may take longer and are more likely to be incorrect. If higher-level classification is sufficient for paleocommunity research, researchers could save significant resources on research projects and reduce inaccurate identification.

Conversely, the taxonomic resolution of paleocommunity data may affect the quality of the paleoecological information derived from the assemblage. While more closely related organisms may tend to be more ecologically similar, even closely related genera can have different ecological functions within a community (Cahill et al., 2008). Lumping these separate genera within a single higher taxon would mask any effect their differing ecologies may have had on the community composition as a whole. The result would be a loss of ability to resolve paleoecological parameters and to detect ecological differences between samples, regions, and formations, degrading the value of the paleocommunity data, and therefore, any conclusions based on those data. Ultimately, the issue is to determine which taxonomic level is more likely to provide the most reliable ecological signal.

Forcino et al. (2010) examined the effect of taxonomic level of identification in paleocommunities from the Finis Shale of Texas, finding a strong correlation between results derived from genus-level identification and results derived from higher-level identifications. Greffard et al. (2011) compared the results of community analyses of chironomid flies (Class Insecta) identified at different taxonomic levels. Although Greffard et al. (2011) concluded that finer taxonomic resolutions should be employed, the multivariate results of the fine- and coarse-taxonomic resolutions were strongly correlated (PROTEST $m^2 = 0.93$, $p < 0.001$). De Biasi et al. (2003) found similar community results among species-, genus-, and family-level identifications, and a somewhat similar result at the level of taxonomic order. Warwick (1988) found no loss of information (i.e., the same multivariate community results) among species-, genus-, and family-level identifications for five modern marine benthic community datasets.

Alternatively, if a study was to examine a wider range of paleoecological data than those studies described above, it may be discovered that community resolution is lowered when taxa are identified to higher taxonomic levels (e.g., family, order). Combining taxonomic units that may represent different ecological aspects of a community may mask a paleocommunity signal that would be clear when conducting analyses at the genus- or species-level. If the meta-analysis we conduct here finds that higher taxonomic resolution leads to different paleocommunity results, this may reassure researchers that the current paradigm (identifying fossil taxa to genus or species) is necessary to obtain meaningful ecological information from paleocommunities.

2. Methods

Twenty-eight datasets were acquired from the PBDB (Table 1). The datasets contained a range of numbers of samples (16 to 162 samples) and generic richness (21 to 244 genera). The datasets represented a wide range of time periods and featured a diversity of taxonomic groups. Each dataset was used to create four taxon-sample matrices — one for each of the taxonomic levels: genus, family, order, and class. The higher-level groupings (family, order, and class) were based on the most up-to-date classifications in the PBDB. Two datasets (Crame, 1981; Budd et al., 1999) contained only one taxonomic order, so no order-level taxon-sample matrices were created from these datasets. Three datasets (Ruzhencev and Bogoslovskaya, 1978; Crame, 1981; Budd et al., 1999) contained only one taxonomic class, so no class-level taxon-sample matrices were created from these datasets.

For each taxonomic-level comparison (family–genus, order–genus, and class–genus) of each dataset, three multivariate statistical comparisons were conducted (Table 2):

(1) Using the vegan package in R 2.4 (Oksanen et al., 2011; R Development Core Team, 2011), we performed Mantel Tests of correlation between Bray–Curtis dissimilarity indices (values that quantify the dissimilarity between each object in a taxon-sample matrix). The Mantel Test tests the similarity of two matrices of dissimilarity indices by permuting each of the elements in the dissimilarity matrix 999 times to derive a distribution of correlation values (Mantel, 1967; Fall and Olszewski, 2010). The resulting R-statistic is similar to the Pearson's Product Moment Correlation Coefficient (r); with increasingly similar dissimilarity matrices, the Mantel R-statistic will approach 1. The Mantel Test evaluates the goodness-of-fit of two datasets of non-ordinated data. The remaining two methods evaluate the goodness-of-fit of ordinated data.

(2) We produced non-metric multidimensional scaling (NMDS) ordinations of the samples using the Bray–Curtis dissimilarity index (Clarke and Ainsworth, 1993; Legendre and Legendre, 1998; Bush and Brame, 2010). The NMDS axis-one ordination scores of each taxonomic level were compared to each other pairwise using a Pearson's product–moment correlation.

All NMDS ordinations were run examining the taxonomic distributions among samples. Ordination is an exploratory multivariate visualization tool that allows multidimensional relationships of samples to be examined in fewer dimensions (McCune and Grace, 2002). Because ecological datasets contain samples with taxonomic objects, each with some abundance, ordination is the standard way to visualize the similarities and differences among samples or taxa. Samples that have more similar taxonomic distributions plot closer together in the ordination space.

NMDS ordination iteratively searches for a best-fit solution between the rank dissimilarity indices and the distribution of samples in a low-dimension ordination space. This non-parametric approach is appropriate for community data, which are typically non-normally and non-linearly distributed (Bush and Brame, 2010). The best-fit solution is assessed by the “stress” of the ordination; low stress represents a better NMDS solution (Kruskal, 1964). Stress levels varied from dataset to dataset and from