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The sensitivity of paleocommunity sampling strategy at different spatiotemporal scales

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ABSTRACT

One of the primary differences between paleoecological and modern ecological research is the added dimension of deep geological time. The temporal dimension of paleoecological research can create added difficulties when determining the appropriate spatiotemporal sampling procedures required for any particular study. Previous paleocommunity studies have found that the spatial extent of sampling can have a grave impact on the multivariate analytical results. Here, we expand spatially on the previous paleocommunity study of Forcino et al. (2010) to determine the importance lateral variation may have on the paleocommunity signal within the Pennsylvanian Finis Shale. Spatial and temporal community gradients of bulk sediment shale samples from six localities were examined using ordinations and ANOSIM. The expanded spatial examination of the Finis Shale reveals the same two distinct communities separated at the mid-point of each sampled stratigraphic section. Thus, lateral variation did not have an effect on the primary multivariate result for the Finis Shale communities. At the temporal scale of the complete stratigraphic section, a temporal factor has the greatest influence on the community result. However, based on separation of samples in ordination space with respect to location and based on a significant difference between locality-based groupings using ANOSIM, the primary influence on the paleocommunity result at a finer temporal scale, containing 19 samples from only the lower half of each stratigraphic section, is a spatial factor. This minor variation in scale leading to a major change in the primary factor affecting the multivariate paleocommunity result is evidence that the paleocommunity results are extremely sensitive to the temporal scale of sampling. Thus, this differs from previous research; there are cases in which fewer laterally-equivalent samples are required per stratigraphic horizon, bed, or unit, because the temporal signal overwhelmed the spatial signal.

1. Introduction

Community paleoecology utilizes complete fossil assemblages to determine the mechanisms of spatiotemporal ecological and environmental variation, aiding in the pursuit of the processes that structure ecosystems and the causes of ecosystem collapse and extinction (Jablonski, 1998; Olszewski and Patzkowsky, 2001; Bonelli et al., 2006; Clapham et al., 2006; Clapham and James, 2008; Heim, 2009). Paleocommunities (herein referring to marine invertebrate fossil assemblages used to infer environmental or ecological gradients) provide a wealth of information regarding taxonomic interactions and environmental tolerances on local scales and how these processes scale up to regional, continental, and global scales (Bambach, 1993; Kowalewski et al., 2002; Bambach et al., 2004; Clapham and Bottjer, 2007).

Because modern ecological research is limited to human time scales, modern ecologists usually examine community relationships through space (Downes et al., 1993; Rosenzweig, 1995; Bustamante and Branch, 1996; Boström and Bonsdorff, 1997; Broitman et al., 2001; Harte et al., 2005; Hereu et al., 2008). A primary difference between paleoecological studies and modern ecological studies is that paleoecological studies have the added dimension of deep geologic time, which enables examinations of ecological persistence, turnover, and extinction effects through time (Pandolfi, 1996; Boyer et al., 2004; Clapham and James, 2008; Heim, 2009; Layou, 2009; Olszewski and Erwin, 2009). However, having to take into account both temporal and spatial dimensions also leads to complications when determining the most appropriate sampling and analytical methods required for conducting paleocommunity research.

Forcino et al. (2010) examined marine invertebrate paleocommunity variation through a 5 meter stratigraphic section of the Virgilian (Gzhelian) Finis Shale of Texas and identified two distinct paleocommunities, one occupying the lower portions of the section (older) and one the upper (younger). Although this temporal change in paleocommunity structure was clear at this one stratigraphic section, this result does not provide any evidence for the distribution of communities over broader spatial scales of the Finis Shale. Thus, additional sampling of the Finis Shale laterally would add the supplementary dimension that might lead to a different result.

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Recent studies examining the spatial sampling procedures required for studying paleocommunities have demonstrated that smaller, replicate (within bed or unit) samples produce more robust community patterns than one large bulk sample (Lafferty et al., 1994; Bennington, 2003; Webber, 2005; Zuschin et al., 2006; Zambito et al., 2008). The argument of the above studies is that large, single samples do not recover the complete diversity of a paleocommunity because such samples fail to capture variation caused by faunal patchiness and the sparse distribution of rare taxa. Based on the results of these studies, Forcino et al. (2010) may not have fully captured the structure of the Finis Shale paleocommunities because only one stratigraphic section was examined.

Here, to capture possible community changes through time in the Finis Shale more completely, we explore the lateral variation of the Finis Shale communities. Because the Finis Shale outcrops at convenient locations along strike at approximately regular intervals, the exposures provide an opportunity to examine how, and if, the temporal change in paleocommunities within the Finis Shale varied through space. For the present study, we collected 29 samples from six localities of the Finis Shale and conducted multivariate paleocommunity analyses in order to determine if additional lateral sampling leads to a change in the paleocommunity signal (the information and patterns produced based on the taxonomic distribution within and among samples) determined by Forcino et al. (2010). A difference in paleocommunity signal would be evidence of the importance of spatial sampling; any ecological conclusions based on only the original section would be based on incomplete data. In contrast, a consistent and laterally persistent paleocommunity signal would serve as evidence that complete spatial sampling may not always be necessary for all paleocommunity studies. However, such a result would not be very informative, as it would not be clear to a researcher whether lateral sampling was necessary a priori. Thus, it would be of additional interest to determine under what circumstances extensive spatial sampling might no longer be essential. One possibility may be the scale of the study, especially the temporal extent of sampling.

Paleocommunity studies examining faunal persistence, coordinated stasis, and high-resolution environmental variables (e.g., within-stratigraphic-unit depth gradient) often are examining communities within only a few stratigraphic horizons, beds, or units (Zambito et al., 2008). Often such studies limit themselves to one stratigraphic formation. The influence of the processes operating at these finer scales is inherently different (or at least less averaged by spatiotemporal variables) than those at larger scales (multiple stratigraphic formations). At small spatial scales, fine-scale controls on community composition may include microhabitat or biotic interactions, while at coarser scales water depth is often perceived as a primary controlling factor because it takes into account many other oceanographic parameters (Holland, 2005; Redman et al., 2007). Therefore, the types of ecological explorations and hypotheses examined are often quite different between smaller and larger scales.

Communities ordinated along a gradient reflect changes in taxonomic composition driven by some environmental variable or variables. Although the variables driving the gradient may be unknown (and cannot be identified based on the ordination alone without independent data), the processes underlying the gradient may operate on different scales, such that a change in sampling or analytical scale would alter the paleocommunity signal. For example, would communities sampled at a greater temporal scale be more likely to reveal a gradient indicative of a change in environment through time, rather than through space? In other words, would the spatial signal be obscured at greater temporal scales? If so, then there would be some temporal scale at which spatial variation within a single point in time would be reduced to noise in comparison to the overriding signal through time. As the choice of operational scale is dictated by the question of interest, scale considerations of this sort could affect decisions regarding sampling strategy.

Because Forcino et al. (2010) found two distinct paleocommunity sets separated by the approximate mid-point of the stratigraphic extent of the Finis Shale, there is the potential for a test of the hypothesis that the importance of lateral sampling may vary with the temporal scale under study. The stratigraphic section can be divided into two halves, and the multivariate analysis repeated only on one half. This second analysis would examine how changing the temporal scale (reducing it to approximately one half of the previous analysis) might affect any signal derived from lateral variation.

2. Methods

2.1. Geologic background

The Finis Shale was deposited along the paleoequator on the Eastern Shelf of the Midland Basin in what is now Texas, USA (Fig. 1). During the Virgilian (Gzhelian), tectonic activity was occurring paleonorth, paleoeast, and paleosouth of the Midland Basin (Brown, 1973; Heckel, 1977). The Amarillo–Wichita Uplift separated the Midcontinent and the Midland Basin and was active during the Late Pennsylvanian, leading to massive amounts of fine siliciclastic input into the smaller Midland basin (Algeo and Heckel, 2008). However, the Finis Shale lacked coarse siliciclastic input; rather, terrigenous mud settled out of suspension in a calm, low-energy environment over approximately 2 million years (Cheney, 1940; Brown, 1973). As a result, sediment grain size remains relatively constant, both laterally (>10 km) and vertically (>5 m), within the Finis Shale. Finis Shale strata are essentially flat-lying over great distances, with only local variations in dip attributed to either syndepositional topographic variation or post-burial sediment compaction. Within the Finis Shale, we chose outcrops on a transect paralleling the shoreline of the shallow Eastern Shelf. Thus, we are able to compare spatial and temporal variation at multiple scales within a system in which sedimentary regime and water depth is a relatively controlled factor.

Each stratigraphic section sampled ranged in vertical extent from ~4 m to 6 m. The base of each stratigraphic section was the lowest exposed point of the Finis Shale. The contact between the Finis Shale and the underlying Homecreek Limestone was not exposed at any

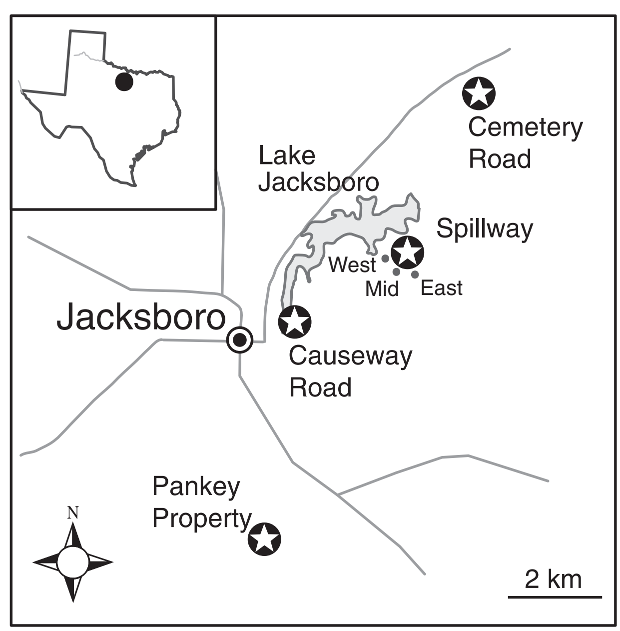

Fig. 1. The four sampled localities and specific sample collection spots within and around the area of Jacksboro Texas represented by large circles with stars inside. The small gray circles at the Jacksboro Spillway locality are the three within-outcrop locations sampled at that one locality. Dark gray lines represent roadways, and the light gray area represents water.