Palaeoecology is based on the documentation of occurrences and abundances of taxa across time and space. Although methodologically similar to the techniques of neontological ecologists, the discipline is distinct in its integration of a deeper time axis into our understanding of the processes shaping the earth’s ecological patterns. Taphonomy is the study of the processes by which organic remains become incorporated into the fossil record. Since this record is both incomplete and biased, multiple taphonomic approaches have been developed to quantify the reliability of the ecological information it preserves. As such, a fundamental issue in paleoecology relates to the sampling and counting of individuals. Although the nature of the preserving sediments often exerts the primary control on how data are collected, techniques exist to standardize sampling and counting strategies to maximize our ability to detect ecological patterns and gain insight into the processes shaping both ancient and modern communities.

Introduction

Paleoecology can be defined as the study of ancient ecosystems and organisms and their interrelationships with the paleoenvironments of the past. Modern biological patterns we study today have been shaped by the combination of ecological and evolutionary processes that have unfolded over tens to millions of years. The study of paleoecology melds this axis of time with ecological perspectives and analytical techniques, providing a framework for studying both ancient and modern organisms, communities and the paleoenvironments in which they occurred. At its core, paleoecology is built on the field-based documentation of the occurrences and abundances of taxa through time and across space.

History of Methodological Developments

Patterns of faunal succession in rock sequences have been recognized since the 1700s, most famously through the work of William Smith, commissioned to survey canal excavations across England. The beginnings of paleoecology thus were intimately tied with the application of fossil data to biostratigraphy, correlating contemporaneous rock units across space based on sets of fossil indicator taxa (Shaw, 1964; Prothero, 1998). With the development and refinement of radiometric dating techniques, regional stratigraphic correlation began to rely less on faunal zonation (Stanley, 1993). By the 1960s, paleoecology was primarily focused on the task of confidently recognizing distinct paleocommunities in the fossil record (Boucot, 1953; Ziegler, 1965). At the same time, neontologists began investigating the patterns and processes driving community succession along environmental gradients (Whittaker, 1975). The focus of paleontological research also shifted and researchers began to extend ecological principles to the fossil record to interpret the paleoecology of fossil assemblages (Valentine, 1973). The following decades witnessed an increasing emphasis on the axis of time and the development and application of new quantitative methods that facilitated rigorous spatio-temporal comparisons of systems. Seminal examples include (1) multivariate approaches to documenting taxonomic diversity through time (Sepkoski, 1978, 1979, 1981; Figure 1), (2) ecospace-utilization analyses which use natural history information of taxon life-histories (inferred from skeletal remains, depositional contexts and modern analogues) to compare temporally successive faunas (Bambach, 1983, 1985; Figure 2), (3) reconstruction of vegetation dynamics, paleobiogeography and non-analogue climate regimes using pollen cores (Jackson, 2006) and (4) faunal gradient analyses that incorporate spatial dynamics into our understanding of community
evolution (Miller et al., 2001; Holland and Patzkowsky, 2007). See also: Geological Time: Dating Techniques; Geological Time: Principles; History of Ecology

A rapidly emerging theme in modern paleoecology is the application of the recent fossil record to the study of human-induced environmental impacts (Swetnam et al., 1999; Barnosky et al., 2003; Jackson, 2007; Kidwell, 2007). The fossil and subfossil records offer unique and unparalleled insights into the functioning of ecological communities before the onset of intense anthropogenic modification (Kowalewski et al., 2000). Understanding the natural variability of ecosystems and how they responded to environmental perturbations in the past is critically needed to accurately predict the future fates of species and their ecosystems.

Taphonomy and Preservation

Paleoecological data typically consist of time-averaged occurrence and abundance records of the skeletal remains of taxa. As with surveys in modern systems, data from the fossil record are incomplete and biased. One of paleoecology’s strengths lies in the time and effort that has been devoted in understanding how and why such biases arise and how they might impact analysis and interpretation. For example, we know paleoecological data are temporally and spatially averaged (Figure 3). Although often considered an impediment in recovering ecological dynamics, such natural averaging can actually be beneficial; for example, damping short-term ‘noise’ for questions posed at longer temporal scales (Peterson, 1977; Terry, 2008).

Taphonomy (the study of the fossilization process) investigates the ‘filters’ that skeletal remains pass through before being recovered by eager paleontologists: death, decomposition, entombment in sediments, fossilization and diagenesis (Figure 4). See also: Exceptional Preservation; Fossils and Fossilization

Although all filters can impact the quality of preserved information, we can often determine the magnitude and direction of an expected bias. By quantifying the local environmental controls of preservability, and the entombment probabilities of taxa with differing skeletal mineralogies and life-histories, we can thus test and correct our interpretations of data accordingly. For example, we know that marine fossil assemblages typically lack soft-bodied taxa since skeletal hard-parts are much more likely to be preserved than soft tissues (Prothero, 1998). Within moluscan taxa that have a mineralized shell, those made of apatite are more prone to degradation and removal from the record than those made of calcite. Furthermore, infaunal benthos are more likely to be preserved when dead than

---

**Figure 1** History of Phanerozoic diversity and the three ‘evolutionary faunas’ as revealed by a factor analysis of data compiled from the literature. The grey area immediately below the curve for total diversity represents the residual diversity not accommodated by the first three factors in the analysis. The number ‘1750’ in the upper left-hand corner is the approximate number of metazoan families that have been described from the modern oceans. Reproduced from Sepkoski (1981), with permission from The Paleontological Society.
shells of epifaunal organisms which are exposed to physical and biological weathering processes present at the sediment–water interface (Foote and Miller, 2007). In terrestrial systems, dense mineralized tissues such as tooth enamel are less prone to postmortem degradation than tissues such as bone (primarily composed of apatite) (Benton, 1997; Kardong, 2002). Similarly, lignin in plants is less likely to decompose than cellulose, biasing preservation towards lignin-rich vascular plants and against their nonvascular counterparts (Foote and Miller, 2007). See also: Fossil Record

Taphonomic studies include ‘actuopaleontological’ analyses where decay processes and the fates of organic tissues are monitored in real time (e.g. the Shelf and Slope Experimental Taphonomy Initiative, Powell et al., 2002) and experiments performed under controlled laboratory conditions (Briggs, 2003). Many comparative approaches also exist, such as the use of ‘taphonomic control taxa’ to assess the true absence of taxa from an assemblage (Bottjer and Jablonski, 1988). The most direct method for assessing the fidelity of paleoecological data to source communities, however, is through ‘live-dead analysis’ (Kidwell and Flessa, 1996). Modern ‘death-assemblages’ represent the initial input of skeletal material into the fossil record, but are typically time-averaged (incorporating the remains of multiple generations). Various metrics (e.g. similarity indices and Spearman’s rho) are commonly used to assess

Figure 2  Ecospace utilization analyses showing the changes in the average relative abundances (based on specimen counts) of tiering (a), motility (b) and feeding types (c) between mid-Paleozoic (461–359 Ma) and late Cenozoic (23–0.01 Ma) fossil assemblages. For the two Cenozoic data sets, the 95% error bars represent simple sampling uncertainty, and they were calculated by a two-stage bootstrap procedure that resampled (with replacement) both the specimens in each sample and the samples used to calculate each mean, thus adding together the uncertainty generated by both stages of sampling (number of iterations = 50,000). For the Paleozoic data (third row), the error bars represent the range of values resulting from different assumptions about the strength of the bias against aragonite preservation. The shaded bars show the bias-simulated results assuming that 40% of the individuals in the average original community were aragonitic. The ‘taphonomic error bars’ encompass the raw data (bases of triangles; assumes no dissolution bias) and the bias-simulated data for 70% aragonitic specimens (uncapped ends of lines). The Paleozoic data do not have sampling error bars, but they would be of the same magnitude as those shown for the Cenozoic data. Reproduced from Bush et al. (2007), with permission from the Paleontological Society.
the concordance between the taxonomic composition of these death-assemblages and that of their contemporaneous living communities. Results from studies spanning a wide range of environments (marine to terrestrial) and taxa (marine invertebrates to large-bodied ungulates) have consistently shown remarkably high live-dead agreement within each habitat – as high as the agreement seen between replicate surveys of living communities within the same habitat (Johnson, 1957; Behrensmeyer and Dechant Boaz, 1980; Hadly, 1999; Kidwell, 2001, 2002; Terry, in press; Western and Behrensmeyer, 2009). Live-dead analysis of the distributions of trophic guilds, body sizes and population age structures are additionally informative. This is great news for paleoecology, suggesting that, despite potential obstacles to the recovery of ecological information from the fossil record, the information is preserved and can be interpreted with confidence.

**Where are Fossil Deposits Found?**

The preservation potential of skeletal remains is variable across different environments. The terrestrial realm is characterized by net sediment erosion, while lakes and seas are characterized by sediment deposition. Thus, terrestrial organisms are more likely to be fossilized if they undergo transport to a subaqueous environment (Lyman, 1994a). Subaqueous environments such as lakes also trap pollen, which can then be incorporated into finely laminated sediments accumulating on the lake bottom. Other terrestrial
environments that have high preservation potential include caves (where skeletal and macrofloral remains are collected by predators and/or packrats and incorporated into middens; Betancourt et al., 1990; Hadly, 1996; Grayson, 2000; Pokines and Peterhans, 2007) and tar pits or muddy areas (where animals become trapped in viscous sediments; Friscia et al., 2008). In marine systems, low-energy environments such as carbonate platforms accumulating behind reefs are more likely to preserve organisms than high-energy environments such as the rocky intertidal (Stanley, 1993). At a broader spatiotemporal scale, tectonic events such as episodes of mountain building or rifting exert a strong regional control on the spatiotemporal distribution of terrestrial fossil deposits (Rogers, 1993). Similarly, patterns of sea-level rise and fall shape the distribution of fossiliferous deposits in marine systems and influence the amount of time-averaging encompassed by a rock unit (Holland, 1995). See also: Sea Level Change

Primary Methods

Paleoecological methods trace their origin to the application of ecological analyses to fossil data. Paleoecology and ecology retain many analytical similarities today. For example, ecological metrics such as species richness and community evenness (the equitability of the distribution of individuals among species within a community) as well as similarity and distance metrics such as Jaccard and Bray-Curtis are commonly used in paleoecological analyses to compare paleocommunity composition across space and through time (Peters, 2004; Olszewski, 2004). Furthermore, ordination techniques such as Multidimensional Scaling and Principal Components Analysis have a long history in paleoecological research (Foote and Miller, 2007). See also: Ecological Methods; Multivariate Techniques in Ecology

In addition to drawing inferences about community composition and structure, paleoecologists are also interested in reconstructing the life histories of extinct taxa (Figure 2). Body size trends have yielded much insight into the dynamics of extinction and recovery events in the fossil record (Payne et al., 2009). Predation in terrestrial systems can be inferred by the breakage patterns of prey skeletal remains in mammals (Terry, 2007; Faith et al., 2007), as well as by microscopic traces indicating skeletal remains were digested before fossilization (Andrews and Nesbit Evans, 1983; Rensberger

Figure 4 The taphonomic processes and circumstances that, during the fossilization of organic remains, have potential to modify the original biological signal at different postmortem phases. Reproduced from Behrensmeyer and Kidwell (1985), with permission from the Paleontological Society.
and Krentz, 1988). In marine systems, predation has been studied by tabulating the frequency of drill holes and repair scars (Kelley et al., 2003). Furthermore, inferences about the diet and trophic level of extinct organisms can be made using a diverse array of isotopic proxies (Koch et al., 1989; Clementz et al., 2003; Fox-Dobbs et al., 2007; Rountrey et al., 2007). Finally, functional morphological studies of the bones and teeth of both extant and extinct organisms have provided much insight into the locomotor strategies of fossil taxa, as well as patterns of growth, age of reproduction and diet (Foote and Miller, 2007). See also: Biomechanical Studies of Food and Diet Selection; Biomechanics: Principles; Dinosaur Locomotion; Functional Morphology and Physiology: Comparative Methods; Vertebrate Functional Morphology and Physiology

Figure 5  Comparison of average confidence interval (CI) size obtained by collecting more replicate samples versus larger replicate samples at different levels of total sampling effort. Results are shown for four species with different average abundances sampled from a patchy distribution. Reproduced from Bennington and Rutherford (1999), with permission from The Society for Sedimentary Geology.
Key Methodological Issues

Key methodological issues in paleoecology relate to sampling effort and the counting of individuals. Variation in sample volume and replication can affect our ability to detect biological pattern. Replicate cores or bulk samples of equal volume both increase our inferential power to detect taxonomic differences and ameliorate artificial variation among samples (e.g. due to unequal sampling, small-scale patchiness or postmortem transport; Foote and Miller, 2007; Figure 5).

When samples cannot be removed from the host sediment due to lithification, or where the spatial arrangement of fossils is expected to reflect true biological distributions, further sampling methods include transect and quadrat-based in situ censuses akin to those of neontological ecology (Foote and Miller, 2007).

The wide range of preservational modes assures that no method for extracting, identifying and even counting fossils can be standard across all study systems: choice in methodology is largely dictated by the nature of the target sediments (e.g. loose matrix/unlithified versus indurated bedrock/lithified). An alternative approach is to standardize effort by the number of specimens identified in a sample. This technique is often employed when counting pollen grains or microfossils to make data collection logistically feasible and subsequent analysis more comparable across studies (Faegri and Iversen, 1989). Another approach is to standardize metrics of interest (e.g. taxonomic richness) by the number of individuals counted after data collection has been completed. This is typically done through a statistical procedure called rarefaction, which estimates the number of species that would have been found if a smaller number of individuals had been sampled (Raup, 1975; Gotelli and Colwell, 2001). Finally, given a documented decrease in the number of lithified fossil-bearing rock units through time, recent studies have demonstrated the importance of taking rock quality, abundance and lithification state into account when reconstructing patterns of ancient diversity through time (Peters and Foote, 2001; Hendy, 2009; Sessa et al., 2009).

Once samples are collected, it is remarkable how difficult the seemingly simple process of counting individuals can be. Specimens typically consist of disarticulated and disassociated elements, potentially derived from the same individual depending on various factors important in the entombment process such as the speed of burial (Badgley, 1986). Bivalves, for example, have two valves (left and right). Thus, at a minimum the true number of individuals in a sample equals the more frequent of the two valve sides. This metric is known as the ‘Minimum Number of Individuals’ (MNI). In contrast, the ‘Number of Identified Specimens’ (NISP) considers each valve and every shell fragment a separate individual, thus providing a maximum bound on the number of individuals in a sample. Over 100 such counting metrics exist for the increased ‘complexity’ introduced by the vertebrate skeleton (summarized in Lyman, 1994b). Additional information such as an element’s age and size can also be incorporated into metrics such as MNI, making estimates increasingly accurate.

In summary, the fossil record is a unique and highly valuable archive of ecological information on ancient communities. Much effort in the last half century has been dedicated to understanding and quantifying potential biasing factors such that we now have high confidence in the quality of this ecological information and thus our paleoecological reconstructions. The paleoecological research of the future will benefit much from replicated sampling protocols, sample standardization, as well as consistency in and the explicit description of the sampling and counting methodologies that are employed to tabulate primary data.

References


Further Reading


