Palaeoecology: Methods

Tara M Smiley, *University of Michigan, Ann Arbor, Michigan, USA*
Rebecca C Terry, *Oregon State University, Corvallis, Oregon, USA*

Based in part on the previous version of this eLS article 'Palaeoecology: Methods' (2009) by Rebecca C Terry.

Advanced article

Article Contents

Online posting date: 16th January 2017

Paleoecology investigates the ecology of extinct organisms in relation to their environments and community assemblages. Major aims of paleoecology include the documentation of taxonomic occurrences and abundances across time and space and the reconstruction of species- to community-level ecological traits. Although methodologically similar to the techniques of neontological ecologists, the discipline is distinct for its deeper temporal perspective capturing long-term processes that shape Earth's ecological patterns. The foundational components of paleoecological research are the study of taphonomy, or the processes by which organic remains become incorporated into the fossil record, and methods that standardise the sampling and counting of individuals and species. The development and integration of a diverse array of paleoecological methods and data have broadened the scope of paleoecology to gain insight into the processes shaping both ancient and modern communities and inform conservation strategies for ecosystems undergoing rapid anthropogenic-driven changes today.

Introduction

Paleoecology can be defined as the study of ancient ecosystems, including the interrelationships among organisms and between organisms and their paleoenvironments in the past. Modern biological patterns are shaped by 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. Three primary goals of paleoecology can be summarised as follows: (1) to reconstruct past environmental conditions, (2) to document the occurrences and abundances of taxa through time and across space and (3) to infer past species and community-level ecology, such as an extinct species' preferred diet or the distribution of ecological traits within a fossil assemblage. This article emphasises the latter two goals, treating fossil data not only as archives of past environments but also as archives of past ecological processes, such as the assembly and maintenance of communities within ecosystems markedly different from today and the evolution of ecological adaptations over geologic timescales. Importantly, paleoecology is uniquely valuable for understanding the long-term effects of climate and environmental change on individual lineages, communities, and ecosystem function. Paleoecological studies are thus directly relevant to the conservation of biodiversity under today's rapidly changing climates and landscapes.

eLS subject area: Ecology

How to cite:
Smiley, Tara M and Terry, Rebecca C (January 2017) Palaeoecology: Methods. In: eLS. John Wiley & Sons, Ltd: Chichester.
DOI: 10.1002/9780470015902.a0003274.pub2

History of Methodological Developments

Patterns of faunal succession in rock sequences have been recognised since the 1700s, most famously through the work of William Smith, commissioned to survey canal excavations across England. Early paleoecological studies were intimately tied with biostratigraphy, the correlation of contemporaneous rock units across space based on 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 recognising distinct paleocommunities in the fossil record (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 began to extend these ecological principles to the fossil record in order 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 spatiotemporal comparisons of systems. Seminal examples include (1) multivariate approaches to documenting taxonomic diversity through time (Sepkoski, 1981), (2) ecospace-utilisation analyses which use natural history information of taxon life

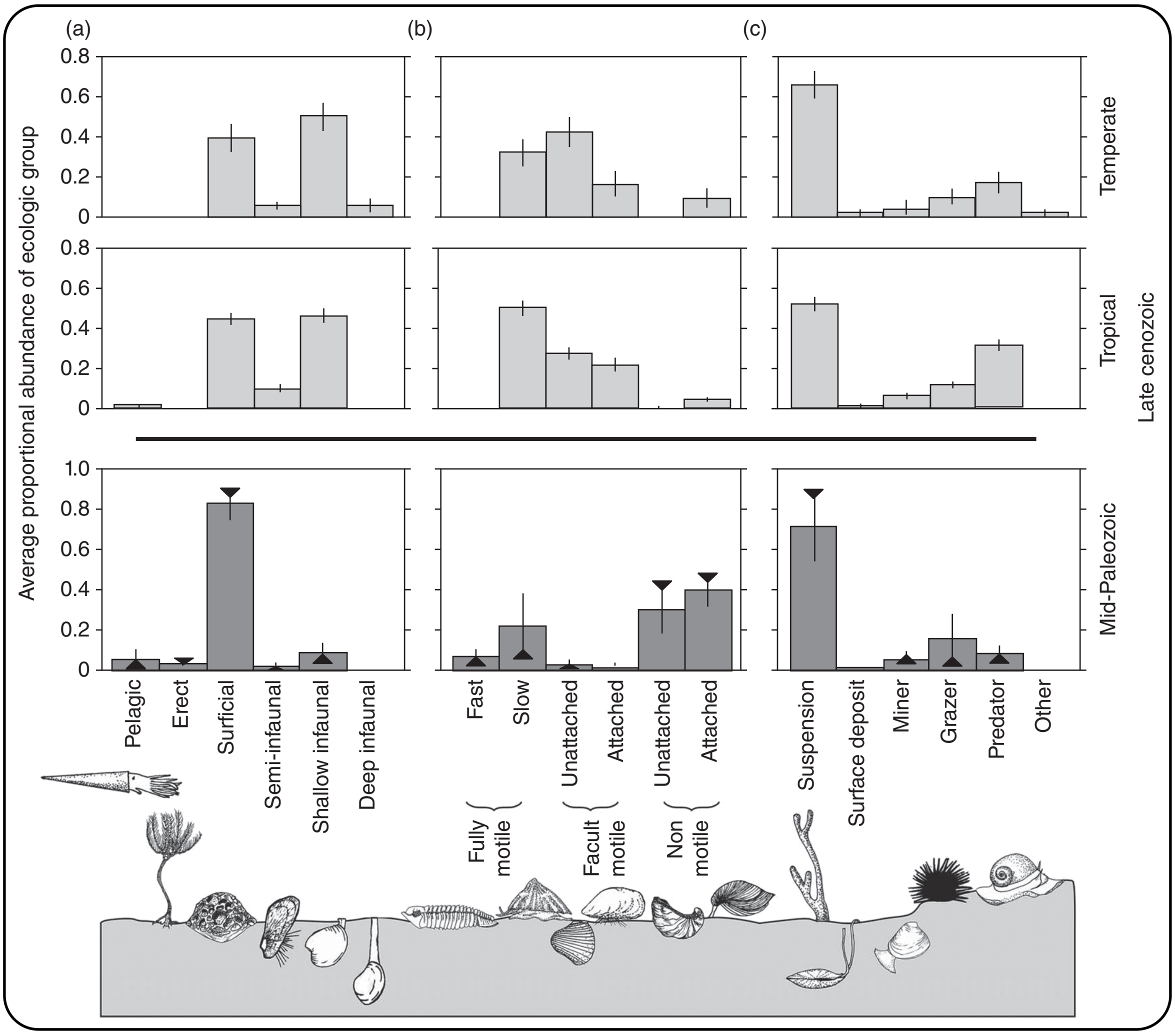

Figure 1 Ecospace utilisation analyses showing the changes in the average relative abundances (based on specimen counts) of tiering (a), motility (b) and feeding types (c) between mid-Paleozoic (461–359 Ma) and late Cenozoic (23–0.01 Ma) fossil assemblages. For the two Cenozoic data sets, the 95% error bars represent simple sampling uncertainty, and they were calculated by a two-stage boostrap 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 disolution 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 with permission from Bush *et al.* (2007) © The Paleontological Society.

histories (inferred from skeletal remains, depositional contexts, and modern analogues) to compare temporally successive faunas (Bambach, 1983; **Figure 1**), (3) reconstruction of vegetation dynamics, paleobiogeography, and nonanalogue climate regimes using pollen cores (Williams and Jackson, 2007; **Figure 2**) and (4) faunal gradient analyses that incorporate spatial dynamics into our understanding of community evolution (Holland and Patzkowsky, 2007). **See also**: **Diversity of Life through Time**; **Geological Time: Dating Techniques**; **Geological Time: Principles**; **History of Ecology**; **Palaeoecology**

A rapidly emerging theme in modern paleoecology is the application of the recent fossil record to the study of human-induced environmental impacts (Jackson, 2007; Kidwell, 2015). The fossil and subfossil records offer unique and unparalleled insights into the functioning of ecological communities before the onset of intense anthropogenic modification (Kidwell and Tomasovych, 2013; Terry and Rowe, 2015). 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. **See also**: **Biological Impacts of Climate Change**

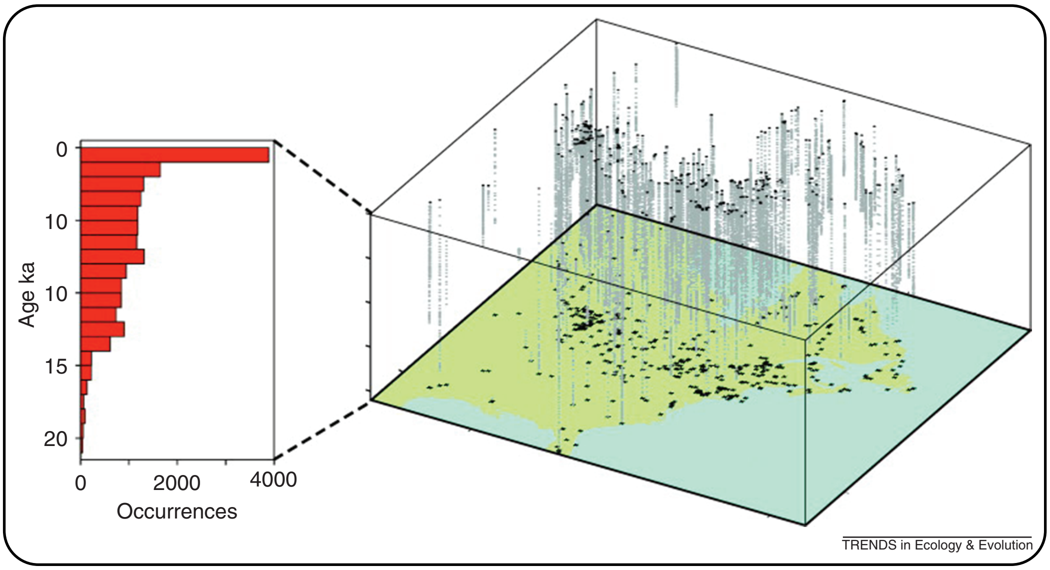

Figure 2 Temporal and spatial distribution of fossil pollen samples over eastern North America. The left plot shows the number of samples per 1000 year time bins over the past 21 000 years. The right plot demonstrates a highly variable 'space–time' cloud of samples (grey dots), with the *z*-axis representing time. Black crosses on the underlying map mark the location of sites and black circles above the map represent 'modern' samples (within the past 150 years). These data have been used to assess vegetation dynamics, including the formation of nonanalogue communities and geographic range shifts, in response to climate change. Paleoecological databases facilitate the collection and analysis of such data sets. Reproduced from Brewer *et al.* (2012) © Elsevier.

Taphonomy and Preservation

Paleoecological data typically consist of temporally and spatially averaged occurrence and abundance records of the skeletal remains of taxa (**Figure 3**). As with surveys in modern systems, data from the fossil record are incomplete and biased. Taphonomy (the study of the fossilisation process) investigates the 'filters' that skeletal remains pass through before being recovered by eager paleontologists: death, decomposition, entombment in sediments, fossilisation and diagenesis (**Figure 4**). **See also**: **Exceptional Preservation**; **Fossils and Fossilisation**

Although taphonomic filters can impact the quality of paleontological information, one of paleoecology's strengths lies in the time and effort that has been devoted to understanding how and why such biases arise and how they might impact analysis and interpretation. For example, we know that marine fossil assemblages typically lack soft-bodied taxa as skeletal hard parts are much more likely to be preserved than soft tissues (Prothero, 1998). Furthermore, differing shell mineral composition (e.g. apatite vs calcite) and life habit (e.g. infaunal vs epifaunal) influence preservation potential across taxa (Foote and Miller, 2007). In terrestrial systems, dense mineralised tissues such as tooth enamel are less prone to postmortem degradation than tissues such as bone (primarily composed of apatite) (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**

Among the approaches developed to account for the effects of averaging and taphonomic filters in the fossil record is 'live–dead analysis'. This is the most direct method for assessing the fidelity of paleoecological data to source communities. The composition of modern 'death assemblages' has been compared to contemporaneous living communities across a wide range of environments (marine to terrestrial) and taxa (marine invertebrates to large-bodied ungulates) revealing remarkably high live–dead agreement within each habitat (Kidwell, 2001; Western and Behrensmeyer, 2009; Terry, 2010). Live-dead analysis of the distributions of trophic guilds, body sizes and population age structures is additionally informative (Miller *et al.*, 2014). 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. In fact, natural averaging can actually be beneficial for understanding ecological dynamics by damping short-term 'noise' for questions posed at longer temporal scales (Terry, 2008; Kidwell and Tomasovych, 2013). Finally, the preservation potential of skeletal remains is variable across different environments. The terrestrial realm is characterised by net sediment erosion, while lakes and seas are characterised by sediment deposition. Thus, terrestrial organisms are more likely to be fossilised if they undergo transport to a subaqueous environment (Lyman, 1994). 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 pack-rats and incorporated into middens, Betancourt *et al.*, 1990; Terry and Rowe, 2015) and tar pits or muddy areas (where animals become trapped in viscous sediments, Friscia *et al.*, 2008). Microfossils, such as rodent teeth and plant phytoliths, can also be

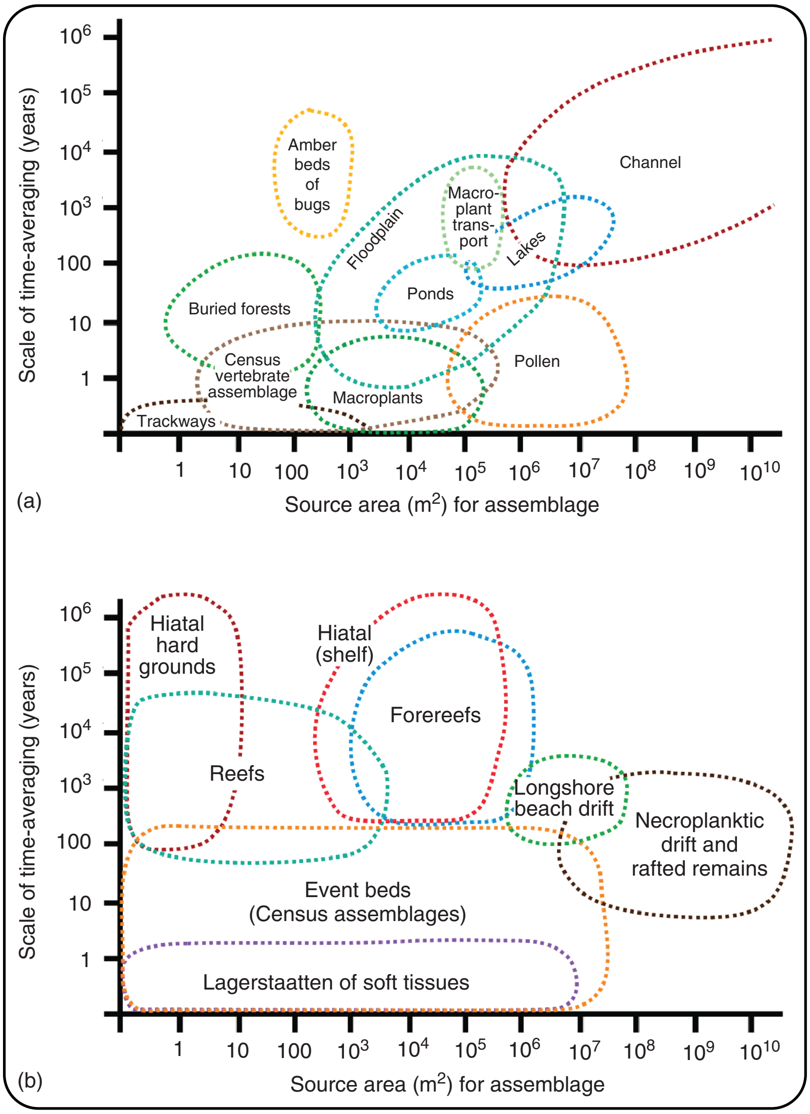

Figure 3 The scales of spatial and temporal averaging in fossil assemblages for different major groups of organisms, in continental (a) and benthic marine (b) depositional settings. Reproduced with permission from Behrensmeyer *et al.* (2000) © The Paleontological Society.

preserved *in situ* in fossil soils, or paleosols, along with corresponding sedimentalogical and paleonenvironmental data (Badgley *et al*., 2008; Strömberg and McInerney, 2011). 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 broader spatiotemporal scales, 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

Several paleoecological methods trace their origin to the application of ecological analyses to fossil data. A persistent issue in both fossil and modern ecological studies is the consistency of data collection and treatment across samples. Taphonomic and preservational filters on paleoecological data present additional challenges and have stimulated the development of methodological and statistical solutions to standardise metrics of interest across samples. One of the most commonly used tools is a 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). Once sample standardisation procedures are applied, ecological metrics

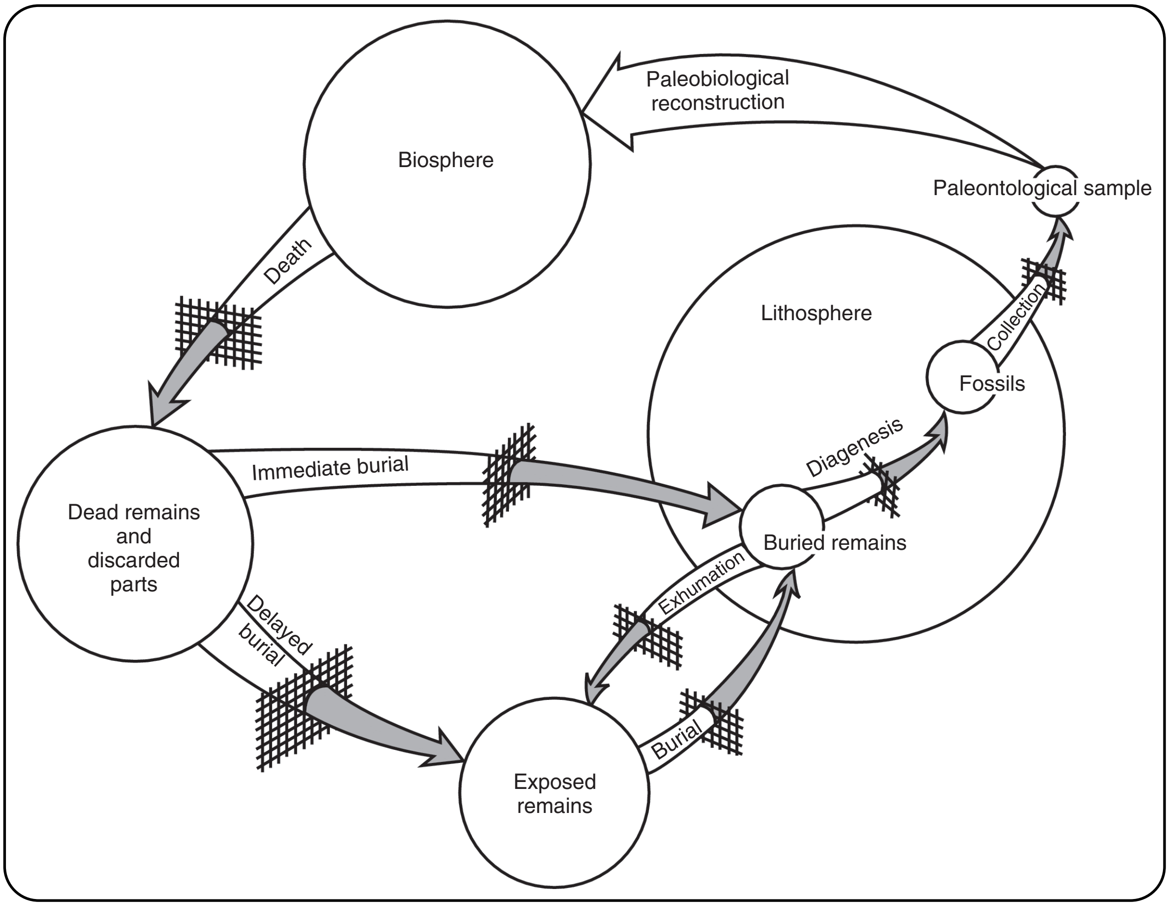

Figure 4 The taphonomic processes and circumstances that, during the fossilisation of organic remains, have potential to modify the original biological signal at different postmortem phases. Reproduced from Behrensmeyer and Kidwell (1985) © The Paleontological Society.

such as species richness and community evenness (the relative abundance 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). 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 using traditional ecological tools, analytical approaches have also been developed specifically for their use in the fossil record (Koch, 2007; Polly *et al*., 2011). These paleoecological tools tend to focus on reconstructing the life histories and ecological interactions of extinct taxa and have since extended into present-day ecological research (**Figures 2** and **5**). For example, body size reflects many ecological aspects of a species biology, plays a major role in community structure and dynamics, and can either be directly measured or, using modern-day calibrations, estimated in the fossil record (Smith *et al*., 2004). Body-size trends across taxa and through time have yielded much insight into the dynamics of extinction and recovery events in the fossil record (Terry and Rowe, 2015; Smith *et al*., 2016). Inferences about the diet and trophic level of extinct organisms can be made using an array of methods, including dental morphology (Damuth and Janis, 2011), the study of abrasion and wear patterns on vertebrate teeth (Mihlbachler *et al*., 2011; Desantis, 2016), and quantitative descriptions of three-dimensional tooth surfaces (Evans *et al*., 2007; **Figure 5**). Geochemical and in particular, carbon, oxygen, and nitrogen isotopic, proxies are now widely used to study diverse paleoecological questions, including temperature and vegetation reconstruction (Badgley *et al*., 2008), life history and physiology (Rountrey *et al*., 2007), dietary and microhabitat preferences (Clementz *et al*., 2003; Koch, 2007), and resource partitioning in the fossil record (Domingo *et al*., 2013). In addition, functional morphological studies of the bones and teeth of both extant and extinct organisms have provided 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**;

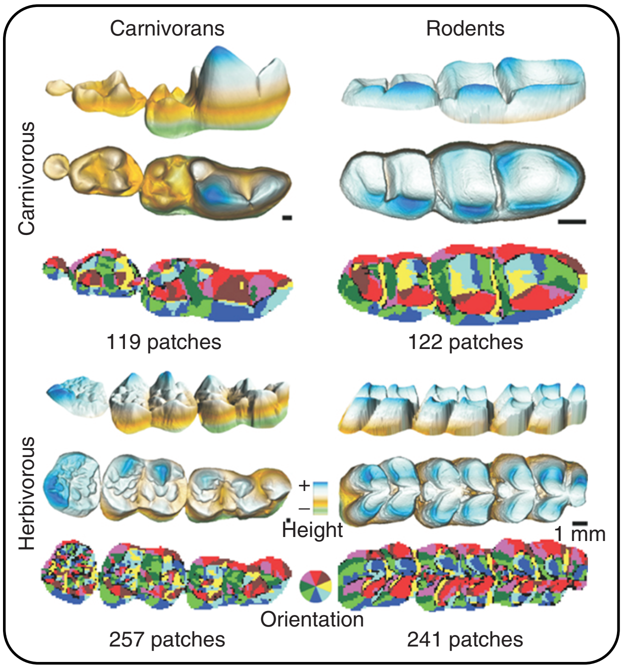

Figure 5 Dental features in relation to diet in two carnivoran species' tooth rows (top left, carnivorous red fox *Vulpes vulpes*; bottom left, herbivorous giant panda *Ailuropoda melanoleuca*) and two rodent species' tooth rows (top right, carnivorous golden-bellied water rat *Hydromys chrysogaster*; bottom right, herbivorous Rothschild's woolly rat *Mallomys rothschildi*). Three-dimensional reconstructions for the buccal–occlusal and occlusal dental surfaces are shown, along with corresponding dental metrics. Crown height and surface curvature metrics, such as orientation patch count (OPC), quantify dental variation across taxa and can be used to distinguish dietary categories among vertebrates. Reproduced with permission from Evans *et al.* (2007) © Nature Publishing Group.

Functional Morphology and Physiology: Comparative Methods; **Stable Isotope Ecology**; **Vertebrate Functional Morphology and Physiology**

Ecological interactions, such as predation and resource competition, can also be inferred from the fossil record. Predation in terrestrial systems can be documented by the breakage patterns of prey skeletal remains in mammals (Faith *et al.*, 2007), as well as by microscopic traces indicating skeletal remains were digested before fossilisation (Rensberger and Krentz, 1988). In marine systems, predation has been studied by tabulating the frequency of drill holes and repair scars (Kowalewski *et al.*, 1998). Species distributions along resource-use (e.g. isotopic) gradients can reflect variation in ecological niche width (i.e. generalist or specialist) and niche overlap among co-occurring taxa and form the basis for inferring resource partitioning (Newsome *et al.*, 2007; Domingo *et al.*, 2013).

Finally, comprehensive, online databases now contain extensive records of fossil occurrences across taxa, through space and over time, and increasingly compile paleoecological data, including number of specimens, body size and trophic category (Brewer *et al.*, 2012; Uhen *et al.*, 2013; **Table 1**). The development of these databases facilitates the investigation of broad-scale questions related to biogeography, macroecology and conservation paleobiology (**Figure 2**). Thus, the integration of diverse datasets across space and time broadens the scope of paleoecological studies beyond individual lineages or fossil assemblages. **See also**: **Macroecology**; **Biogeographical Regions**

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. Now, both traditional and newly developed paleoecological methods are being utilised as a common set of tools to compare paleoecological baselines to ongoing changes in modern communities (Williams and Jackson, 2007; Terry and Rowe, 2015). In order to make paleoecological data useful not only to investigate ecological and environmental processes over a longer time axis but also to better inform conservation efforts, researchers must carefully consider how their samples compare to neoecological samples. The paleoecological record is a vast repository of ecological response to past environmental drivers; therefore, understanding how taphonomic and preservational bias may influence our measures of community composition, structure, and diversity strengthens our ability to apply lessons from the past to better evaluate ongoing and future ecosystem change. The paleoecological research of the future will benefit much from replicated sampling protocols, sample standardisation and consistency in and the explicit description of the sampling and counting methodologies that are employed to tabulate primary data.

Table 1 List of paleoecological and paleoenvironmental databases, compiled by Brewer *et al.* (2012); see publication for the full table, including relevant sources for each database

Database	Datatype	Region	Time period	URL
BugsCEP	Beetles	Global	2 Ma to present	http://bugscep.com/
FaunMap	Mammal fossils	North America	5 Ma to present	http://www.ucmp.berkeley.edu/faunmap
Global Charcoal DB	Paleofire records	Global	22 ka to present	http://www.gpwg.org/
International Tree Ring DB	Tree ring records	Global	Last two millennia	http://www.ncdc.noaa.gov/paleo/treering.html
MioMAP	Mammal fossils	North America	30 Ma to 5 Ma	http://www.ucmp.berkeley.edu/miomap/
MOM v3.3	Mammal body size	Global	60 Ma to 10 Ma	http://www.esapubs.org/archive/ecol/E084/094/
Neogene of the Old World[a]	Mammal fossils	Eurasia	23 Ma to present	http://www.helsinki.fi/science/now
Neotoma	Biological records	Global	2 Ma to present	http://www.neotomadb.org
NOAA Paleoclimate	Paleoclimate data	Global	1 Ma to present	http://www.ncdc.noaa.gov/paleo
Paleobiology DB	All fossil records	Global	542 Ma to present	http://paleodb.org
Pangaea	Paleoenvironmental data	Global	1 Ma to present	http://www.pangaea.de/
PMIP	Paleoclimate simulations	Global	21 ka to present	https://pmip.lsce.ipsl.fr/

Ma, Millions of years ago; ka, thousands of years ago.
[a]Please note, this database is now known as the 'New and Old Worlds' and goes deeper in time than the Neogene and covers a broader geographic region than Eurasia.
Reproduced from Brewer *et al.* (2012) ©Elsevier.

References

Badgley C, Barry JC, Morgan ME, *et al.* (2008) Ecological changes in Miocene mammalian record show impact of prolonged climatic forcing. *Proceedings of the National Academy of Sciences* **105** (34): 12145–12149.

Bambach RK (1983) Ecospace utilization and guilds in marine communities through the Phanerozoic. In: Tevesz MJS and McCall PL (eds) *Biotic Interactions in Recent and Fossil Benthic Communities*, pp. 719–746. New York, NY: Plenum Press.

Behrensmeyer AK and Kidwell SM (1985) Taphonomy's contributions to paleobiology. *Paleobiology* **11**: 105–119.

Behrensmeyer AK, Kidwell SM and Gastaldo RA (2000) Taphonomy and paleobiology. *Paleobiology* **sp26** (4): 103–147.

Betancourt JL, Van Devender TR and Martin PS (eds) (1990) *Packrat Middens: The Last 40 000 Years of Biotic Change*. Tucson, AZ: University of Arizona Press.

Brewer S, Jackson ST and Williams JW (2012) Paleoecoinformatics: applying geohistorical data to ecological questions. *Trends in Ecology & Evolution* **27** (2): 104–112.

Bush AM, Bambach RK and Daley GM (2007) Changes in theoretical ecospace utilization in marine fossil assemblages between the mid-Paleozoic and late Cenozoic. *Paleobiology* **33** (1): 76–97.

Clementz MT, Hoppe KA and Koch PL (2003) A paleoecological paradox: the habitat and dietary preferences of the extinct tethythere, *Desmostylus*, inferred from stable isotope analysis. *Paleobiology* **29**: 506–519.

Damuth J and Janis CM (2011) On the relationship between hypsodonty and feeding ecology in ungulate mammals, and its utility in paleoecology. *Biological Reviews* **86**: 733–758.

DeSantis LRG (2016) Dental microwear textures: reconstructing diets of fossil mammals. *Surface Topography: Metrology and Properties* **4**: 023002.

Domingo MS, Domingo L, Badgley C, *et al.* (2013) Resource partitioning among top predators in a Miocene food web. *Proceedings of the Royal Society B: Biological Sciences* **280**: 20122138.

Evans AR, Wilson GP, Fortelius M and Jernvall J (2007) High-level similarity of dentitions in carnivorans and rodents. *Nature* **445**: 78–81.

Faith JT, Marean CW and Behrensmeyer AK (2007) Carnivore competition, bone destruction, and bone density. *Journal of Archaeological Science* **34**: 2025–2034.

Foote M and Miller AI (2007) *Principles of Paleontology*, 3rd edn. New York, NY: W.H. Freeman and Company.

Friscia AR, Van Valkenburgh B, Spencer L and Harris J (2008) Chronology and spatial distribution of large mammal bones in PIT 91, Rancho La Brea. *Palaios* **23**: 35–42.

Holland SM (1995) The stratigraphic distribution of fossils. *Paleobiology* **21**: 92–109.

Holland SM and Patzkowsky ME (2007) Gradient ecology of a biotic invasion: biofacies of the type Cincinnatian series (Upper Ordovician), Cincinnati, Ohio region, USA. *Palaios* **22**: 392–407.

Jackson ST (ed) (2007) Paleoecology: using the past as a key to the future. *Frontiers in Ecology and the Environment* **5** (4): 455–512.

Kardong KV (2002) *Vertebrates: Comparative Anatomy, Function, Evolution*, 3rd edn. Boston, MA: McGraw Hill.

Kidwell SM (2001) Preservation of species abundance in marine death assemblages. *Science* **294**: 1091–1094.

Kidwell SM and Tomasovych A (2013) Implications of time-averaged death assemblages for ecology and conservation biology. *Annual Review of Ecology, Evolution, and Systematics* **44**: 539–563.

Kidwell SM (2015) Biology in the Anthropocene: challenges and insights from young fossil records. *Proceedings of the National Academy of Sciences* **112**: 4922–4929.

Koch PL (2007) Isotopic study of the biology of modern and fossil vertebrates. *Stable Isotopes in Ecology and Environmental Science* **2**: 99–154.

Kowalewski M, Dulai A and Fürsich FT (1998) A fossil record full of holes: the Phanerozoic history of drilling predation. *Geology* **26** (12): 1091–1094.

Lyman RL (1994) *Vertebrate Taphonomy*. Cambridge, UK: Cambridge University Press.

Mihlbachler MC, Rivals F, Solounias N and Semprebon GM (2011) Dietary change and evolution of horses in North America. *Science* **331**: 1178–1181.

Miller JH, Behrensmeyer AK, Du A, *et al.* (2014) Ecological fidelity of functional traits based on species presence-absence in a modern mammalian bone assemblage (Amboseli, Kenya). *Paleobiology* **40** (4): 560–583.

Newsome SD, Martinez del Rio C, Bearhop S and Phillips DL (2007) A niche for isotopic ecology. *Frontiers in Ecology and the Environment* **5** (8): 429–436.

Peters SE (2004) Evenness of Cambrian-Ordovician benthic marine communities in North America. *Paleobiology* **30**: 325–346.

Polly PD, Eronen JT, Fred M, *et al.* (2011) History matters: ecometrics and integrative climate change biology. *Proceedings of the Royal Society B: Biological Sciences* **278** (1709): 1131–1140.

Prothero DR (1998) *Bringing Fossils to Life*. Boston, MA: WBC/McGraw-Hill.

Raup DM (1975) Taxonomic diversity estimation using rarefaction. *Paleobiology* **1**: 333–342.

Rensberger JM and Krentz HB (1988) Microscopic effects of predator digestion on the surfaces of bones and teeth. *Scanning Microscopy* **2**: 1541–1551.

Rogers RR (1993) Systematic patterns of time-averaging in the terrestrial vertebrate record: a Cretaceous case study. In: Kidwell SM and Behrensmeyer AK (eds) *Taphonomic Approaches to Time Resolution in Fossil Assemblages*. Short Courses in Paleontology, No. 6. Knoxville, TN: The Paleontological Society.

Rountrey AN, Fisher DC, Vartanyan S and Fox DL (2007) Carbon and nitrogen isotope analyses of a juvenile wooly mammoth tusk: evidence of weaning. *Quaternary International* **169**: 166–173.

Sepkoski JJ Jr, (1981) A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology* **7**: 36–53.

Shaw AB (1964) *Time in Stratigraphy*. New York, NY: McGraw-Hill Inc.

Smith FA, Brown JH, Haskell JP, *et al.* (2004) Similarity of mammalian body size across the taxonomic hierarchy and across space and time. *The American Naturalist* **163** (5): 672–691.

Smith FA, Payne JL, Heim NA, *et al.* (2016) Body size evolution across the Geozoic. *Annual Review of Earth and Planetary Sciences* **44**: 523–553.

Stanley SM (1993) *Exploring Earth and Life through Time*. New York, NY: W.H. Freeman and Co.

Strömberg CAE and McInerney FA (2011) The Neogene transition from C_3 to C_4 grasslands in North America: assemblage analysis of fossil phytoliths. *Paleobiology* **37** (1): 50–71.

Terry RC (2008) Modeling the effects of predation, prey cycling, and time averaging on relative abundance in raptor-generated small mammal death assemblages. *Palaios* **23**: 402–410.

Terry RC (2010) On raptors and rodents: testing the ecological and spatiotemporal resolution of cave death assemblages. *Paleobiology* **36** (1): 137–160.

Terry RC and Rowe RJ (2015) Energy flow and functional compensation in Great Basin small mammals under natural and anthropogenic environmental change. *Proceedings of the National Academy of Sciences* **112** (31): 9656–9661.

Uhen MD, Barnosky AD, Bills B, *et al.* (2013) From card catalogs to computers: databases in vertebrate paleontology. *Journal of Vertebrate Paleontology* **33** (1): 13–28.

Valentine JW (1973) *Evolutionary Paleoecology of the Marine Biosphere*. Engelwood Cliffs, NJ: Prentice-Hall.

Western D and Behrensmeyer AK (2009) Bone assemblages track animal community structure over 40 years in an African savanna ecosystem. *Science* **324**: 1061–1064.

Williams JW and Jackson ST (2007) Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* **5** (9): 475–482.

Whittaker RH (1975) *Communities and Ecosystems*, 2nd edn. New York, NY: Macmillan.

Ziegler AM (1965) Silurian marine communities and their environmental significance. *Nature* **207**: 270–272.

Further Reading

Allison PA and Briggs DEG (eds) (1991) *Taphonomy: Releasing the Data Locked in the Fossil Record*. New York, NY: Plenum Press.

Barnosky AD, Hadly EA and Bell CJ (2003) Mammalian response to global warming on varied temporal scales. *Journal of Mammalogy* **84**: 354–368.

Benton MJ (1997) *Vertebrate Paleontology*. London, UK: Chapman and Hall.

Bennington JB and Aronson MFJ (2012) Reconciling scale in paleontological and neontological data: dimensions of time, space, and taxonomy. In: Louys J (ed) *Paleontology in Ecology and Conservation*, pp. 39–67. Berlin: Springer Earth System Sciences.

Dietl GP, Kidwell SM, Brenner M, *et al.* (2015) Conservation paleobiology: leveraging knowledge of the past to inform conservation and restoration. *Annual Review of Earth and Planetary Sciences* **43**: 79–103.

Fritz SA, Schnitzler J, Eronen JT, *et al.* (2013) Diversity in time and space: wanted dead and alive. *Trends in Ecology & Evolution* **28** (9): 509–516.

Kowalewski M and Bambach RK (2003) The limits of paleontological resolution. In: Harries PJ (ed) *High Resolution Approaches in Stratigraphic Paleontology: Topic in Geobiology Series*, pp. 1–48. New York, NY: Plenum Press/Kluwer.

Magurran AE (2004) *Measuring Biological Diversity*. Malden, MA: Blackwell Publishing.

National Research Council (2005) *The Geological Record of Ecological Dynamics*. Washington DC: National Academies Press.

Rogers RR, Eberth DA and Fiorillo AR (2008) *Bonebeds: Genesis, Analysis, and Paleobiological Significance*. Chicago, IL: University of Chicago Press.

