SYNOPSIS

In this chapter, we examine some of the approaches and data used to reconstruct terrestrial ecosystem change. Research employing these methods comes under the auspice of ecological biogeography, which is concerned with the factors that have led to the current distribution of plants on the landscape. Palaeoecology is the field of biogeography that utilizes environmental proxy data to investigate the response of species, populations, communities and ecosystems to past environmental change. Palaeoecological research usually concerns ecosystem dynamics during the Quaternary period (the last 2.58 million years), and in particular over the last 21,000 years, which includes the last glacial maximum (LGM) and the Holocene (the current interglacial period that began 11,700 years ago). Environmental proxy data are sensitive to ecosystem change at particular temporal and spatial scales and describe aspects of the environment to which the organism or physical property is sensitive. We outline the approaches taken to reconstruct terrestrial ecosystem change and review some of the common proxy data used to reconstruct past terrestrial ecosystem change, including tree rings, pollen, plant macrofossils, packrat middens, and charcoal and dung fungal spores, as well as supporting palaeolimnological information from diatoms, chironomids, and lake-sediment lithology, geochemistry and mineralogy. Proxy records can be used alone, but fuller understanding is achieved by combining and comparing multiple proxy data from single or groups of sites. Alternatively, developing geographic networks of records from a single proxy type, such as charcoal or pollen data, provides insights about patterns of environmental change over broad spatial scales.

This chapter is organized into the following sections:

- Introduction
- Palaeoecological approaches and data
- Types of proxy data in palaeoecological studies
- Multi-proxy records and global syntheses
- Conclusion

22.1 Introduction

The present is considered key to understanding the past, but historical and prehistorical data conversely play a critical role in informing both the present and the future. The past provides
information on the historical range of variability, improves understanding of the natural and anthropogenic legacies that shape the present landscape, and reveals the sensitivity of ecosystems to a range of environmental conditions. Knowledge of the past comes from many sources. Real-time and near real-time data are acquired from field and remote instruments; aerial photography and satellites provide information about the past few decades. Historical data come from centuries of human observation and measurement. Information about the period before observational and instrumental data is obtained from environmental proxy evidence, such as those preserved in tree rings and lake sediments (Figure 22.1).

Palaeoecology is the field of biogeography that utilizes such proxy data to investigate the response of species, populations, communities and ecosystems to past environmental change. The field is multidisciplinary, drawing on techniques from biogeography, palaeontology, geochemistry, and archaeology in order to reconstruct past environmental conditions, biotic responses, and climate and nonclimatic forcings. While palaeoecology has been applied to marine settings and even the cryosphere, our focus is on examining reconstructions of the terrestrial biosphere.

Most palaeoecological research concerns ecosystem dynamics during the Quaternary period (the last 2.58 million years), when vast ice sheets cyclically expanded and contracted in response to small variations in the configurations of the Earth’s orbit around the sun and the internal feedbacks those variations precipitated (Figure 22.2). Of this body of literature, most attention is given to the last 21,000 years of history, starting with the time of the last glacial maximum (LGM) and extending through the current interglacial period, the Holocene, which began 11,700 years ago. In this chapter, we describe some of the types of data used in terrestrial palaeoecology. Our examples come from work in which we have been involved and published studies that we admire for their detail or approach. Our coverage of this topic is not meant to be comprehensive in concept or geography, and for that we refer to other helpful references.

**Figure 22.1** Temporal and spatial scales of proxy data discussed in text. The primary scale that these proxy data operate at is shown with solid lines. The dashed lines indicate scales that can be achieved in certain unique cases.
Palaeoecological approaches and data draw on a variety of datasets that, because of their sensitivity to climate or environment, can be used as evidence of past environmental conditions. Such proxy data can be temporally discontinuous information, as in the case of plant remains preserved in packrat middens or fossil vertebrates, providing a ‘snapshot’ of conditions and biota during a particular period. Ideally, they are continuous or nearly-continuous time series, such as tree-ring records or lake-sediment profiles, in order to examine ecological change on fine temporal scales. Some stratigraphic proxy data span hundreds of thousands to millions of years, as in the case of trace atmospheric gas records entombed in Antarctic ice cores or foraminiferal data from long marine cores, whereas other time series offer seasonal to annual resolution for the last few centuries, such as tree-ring data.

Palaeoecological studies that describe vegetation history generally span centuries to millennia and utilize fossil pollen, plant macrofossils and other plant remains. Chronologies for such records come from incremental age models, such as counting annually laminated lake sediments, or from radiometric dating methods, primarily radiocarbon ($^{14}$C) dating of terrestrial organic remains and lead-210 ($^{210}$Pb) dating of recent sediments. Radiocarbon dating is by far the most widely used technique for developing late-Quaternary chronologies, and age determinations are made on small fragments of terrestrial plants, charcoal particles, and sometimes on organic lake sediments. Calibrated radiocarbon years incorporate the effect of variations in radiocarbon production in the atmosphere, the impact of climate cycles, storage in different...
carbon reservoirs, and the effects of human activity. Age models are mathematical constructs that use a sequence of individual dates from a sedimentary record to develop an interpolated chronology for the entire time series. The veracity of radiometric dates and the age model can sometimes be determined by comparison with independent time-stratigraphic markers, such as a volcanic tephra of known age, the presence of pollen from an non-native plant species with a known invasion history, variations in palaeomagnetic field strength that have been dated elsewhere, or other historic events with a detectable signature.

Historical sciences, like palaeoecology, often answer questions through an iterative process of testing multiple working hypotheses. Plausible hypotheses (explanations) are formulated at the outset of the study, and the data are used to evaluate the merits of each hypothesis and reject those that do not stand up to scrutiny. Some hypotheses are rejected outright, others are modified in light of new discoveries, and new hypotheses emerge during the course of an investigation. In the case of vegetation history, research and testable hypotheses have focused on reconstructing ancient ecosystems (including the individuals, populations, and communities therein) and their response to past changes in climate, disturbances, and human activity. The motivation is that understanding past ecological interactions will provide insight into those occurring at present and likely in the future. Broad-scale investigations are often concerned with understanding the hierarchy of climatic and nonclimatic drivers that have shaped ecosystems along a variety of spatial and temporal scales.

Sediment cores from natural lakes and wetlands are the best source of information on the history of terrestrial environments. Fossils, geochemistry and other proxy data preserved in the layers of sediment provide a record of conditions in the watershed through time. Such records begin when the lake was first formed, and they end with the uppermost layer deposited in the current year. Most natural lakes and wetlands were created by ice recessional processes following the LGM, but lakes can also be formed following volcanic eruptions or as a result of fluvial processes, landslides, and coastal aggradation. Boreal wetlands are features of deglaciation but wetlands can also be formed by coastal, fluvial and other geomorphic processes that dam waterways or impound natural springs. Selection of a lake or wetland site for study is based on decisions about whether the vegetation, geological substrate, and climate of the location are representative of a particular region. A good research question in palaeoecology has importance beyond the boundaries of the study or site (i.e. it is one that addresses a timely scientific question or that proposes to look at old findings with a new, possibly transformative approach). In addition, such a research question can be answered by thoughtful selection of study sites, critical examination of multiple palaeoecological proxy, and a plan for using site results to gain broader inference.

### 22.3 Types of Proxy Data in Palaeoecological Studies

In this section, we discuss different sources and types of palaeoecological proxy data and provide examples of studies that have employed them. Of particular importance are the temporal and spatial scales that each type of proxy data addresses (Figure 22.1). Temporal scales include annual, decadal, centennial and millennial. Spatial scales range from metres to many hundreds of kilometres.
Proxy Data of Terrestrial Ecological Change

Tree-Ring Data

Most temperate tree species (i.e. those growing between 25–65° latitude) produce annual growth rings. Tree rings can be sampled using a simple coring device that extracts a pencil-width core of wood from the bark to the pith of a tree. Cores are prepared for analysis by simple sanding and polishing procedures. Rings are sequentially counted to provide the age of a tree. The varying width of rings over time provides information about the environmental and climate history of a locale. By analysing the pattern of ring widths, insight can be gained into the conditions under which the tree was subjected over the course of its life. The ring patterns are analogous to barcodes that can be matched to nearby trees. It is by matching or ‘crossdating’ the distinct pattern of ring widths between living and dead trees that a tree-ring chronology can be constructed. Dating by tree rings is called ‘dendrochronology’. Crossdating is a straightforward concept but complicated by differences in growth rates among individual trees, local factors and the occasional problem of missing rings because of poor growing conditions. It is important to sample many trees in an area to overcome these issues.

Dendrochronological data cover a timespan of centuries to millennia at annual-to-interannual resolution. Tree-ring studies have been conducted on six continents. Tree-ring data are utilized to make ecological and climatological inferences about the past. These data have also been used to study the history of fire – this will be discussed later in the chapter.

Dendroecology is the application of tree-ring analysis to ecological questions. One major area of research in this subdiscipline is forest disturbance dynamics. This research area seeks to reconstruct and understand forest dynamics as driven by external disturbances both biotic (e.g. insect outbreaks) and abiotic (e.g. fire, flood, windthrow). Investigations often focus on identifying the timing and spatial extent of tree-growth releases or suppressions and cohort establishment events.

Dendroclimatology is the study of past climate using tree-ring data. Climate records are developed by comparing ring-width patterns with modern climate data to build a calibration function. The instrument-based calibration is then used to convert the tree-ring record from the earlier, pre-observational period and estimate variations of the climate variable back in time. A major strength of tree-ring climate proxy data is that reconstructions can be replicated across large spatial networks. The North American Drought Atlas contains a 2005-year-long record of yearly drought estimated from 835 tree-ring chronologies (Cook et al., 2004; http://iridl.ldeo.columbia.edu/SOURCES/.LDEO/.TRI/.NADA2004/pdsiatlashtml/pdsiviewmaps.html). These data show that long-lived severe droughts have been a feature of the North American climate for centuries and had negative consequences for some pre-industrial societies (e.g. Stahle et al., 1998; Munoz et al., 2014).

Pollen Data

The assemblages of pollen grains in lake, wetland and bog sediments preserve the record of past vegetation and data derived from pollen studies can be used to provide an indication of the response of vegetation to climate and environmental changes as
well as to human impacts over thousands of years. Pollen is produced by angiosperms (flowering plants) and gymnosperms (seed-producing plants), and not surprisingly, wind-pollinated species that produce a lot of pollen each year are more abundant in the sediments than insect-pollinated species. Pollen falls on the surface of a body of water and becomes incorporated in the sediment and cores can be extracted from the sediment accumulated at the bottom of a lake, wetland or bog. The temporal scale of a pollen record depends on how fast sediment accumulates in a lake or wetland basin. Typically records of vegetation change derived from pollen analysis have centennial-scale resolution. However, greater temporal resolution can often be achieved if the research questions require it. The spatial resolution of pollen records varies from site to site and is often not well resolved. The size of sample lakes and wetlands strongly influences pollen source area and smaller (< 0.5 ha) sites are preferred to provide vegetation histories at the watershed scale (Ritchie, 1987).

In order to perform pollen analysis, sediment samples are taken at regular intervals in the lake/wetland/bog sediment core, and these samples are treated with a variety of chemicals to remove all the constituents except the pollen grains (see Chapter 21). The residue of pollen is mounted on glass slides and examined under the microscope at magnifications of 400–1000x. Pollen grains (generally between 25-100 microns in size) are identified by comparison with modern reference material and published atlases. Typically, 300–400 pollen grains are tallied for a given sample in the core, and it can take a trained analyst two or three hours or more to ‘count’ a sample. The ability to assign a pollen grain to a particular plant taxon is variable and the taxonomic resolution limits interpretation in some cases. For example, grass pollen cannot be identified below the taxonomic level of family (Poaceae), so it is not possible to determine whether the grass pollen comes from alpine, steppe or riparian species. Most pollen grains are securely identified to the level of genus or family but species identifications are often inferred by phytogeography. The presence of seeds, needles and other plant remains in the core also provides species identifications in cases where pollen cannot. A typical pollen record from temperate latitudes will include about 50 different pollen types from trees, shrubs and aquatic plants.

Pollen counts at each level in the sediment core are converted to percentages and accumulation rates, and changes in the proportion of different taxa through time are the basis for interpreting past vegetation. Because pollen does not have 1:1 relationship with the plants that produce it, modern studies are used to interpret past pollen assemblages. Modern pollen information comes from the surface sediments of lakes or pollen traps set out by researchers. The number and quality of surface pollen studies vary from place to place. In North America and Europe hundreds of surface samples have been collected and provide excellent calibration for the interpretation of pollen data through time (www.neotomadb.org).

As an example of the application of pollen data to understand past vegetation and climate, Williams et al. (2006) produced a synthesis of the late-Quaternary vegetation history in northern and eastern North America, examining changes across different levels of ecological organization from individual taxa to biomes. Broad-scale features of vegetation history emerged by comparing the records from multiple sites, and these could be compared with site-specific features that described local responses at individual sites. Different aspects of past vegetation dynamics were revealed by individual pollen time series, pollen maps, dissimilarity measures and estimates of temporal rates...
of vegetation change. The synthesis suggested that distribution and composition of vegetation were relatively stable during the LGM and during the mid- to late Holocene (last 6000 years). This stability was in contrast to the rapid changes that occurred during the late-glacial period to early Holocene transition (14,000–6000 years ago) and in the last 500 years. The history of particular pollen types suggested that the dominant tree species behaved independent of each other in their response to past climate change, and shifts in range were attributed to changes in regional moisture patterns, causing west-to-east responses and changes in temperature evidenced by south-to-north shifts. Some of the common plant communities today developed in the early Holocene, but there are also vegetation types common to the late-glacial period (e.g., *Picea–Cyperaceae–Fraxinus–Ostrya/Carpinus*) that no longer exist. The study is an excellent example of how vegetation changes across multiple spatial and temporal scales and the use of pollen data to reconstruct the distribution, composition and structure of plant communities over time.

**Plant Macrofossils**

Macroscopic remains of plants, including seeds, leaves, needles and fruits, can be found in most deposits suitable for pollen analysis (Birks, 2013). The best sites for these types of records are wetland sites or the littoral margins of lakes within steep catchments, where the opportunity for slopewash or stream input to deliver organic detritus is increased. Species identifications provided by these remains complement pollen-based interpretations by providing greater taxonomic resolution and also confirming the local presence of particular plants (unlike their pollen which can be transported long distances). In wetland deposits, the identification of bryophytes has offered useful information on temperature and hydrologic conditions (Mauquoy and van Geel, 2013). While the majority of plant remains in lake sediments are from aquatic taxa, the less common occurrence of terrestrial plant macrofossils has helped resolve important points in vegetation history (Jackson and Weng, 1999).

**Packrat Middens**

In semiarid regions, packrat midden data provide important vegetation information from semi-arid regions where lake-sediment pollen records are rare (Betancourt et al., 1990). The middens of packrats (21 different species of *Neotoma*) and other nest-building mammals are composed of plant material cemented into caves and rock crevices by urine. In dry settings, these nests are preserved for thousands of years, entombing plant remains of past vegetation as a series of cemented layers. The preservation of plants in midden deposits is excellent, and the remains have been used to reconstruct the local plant communities and population dynamics as well as make broader inferences about climate through the analysis of isotopic signatures and stomata density. Vegetation reconstructions depend on understanding the foraging area and dietary preferences of packrats, as well as the factors that may have led to differential preservation of the remains also posing challenges for interpretation (Finley, 1990; Eliás, 2013).

In the American Southwest, plant assemblages in packrat middens that date to the LGM indicate large downslope shifts in the biogeographic range of subalpine conifers,
such as *Pinus longaeva* and *Pinus flexilis*, as a result of cool humid conditions. Midden studies have also been used to trace the migration history of conifer species during the Holocene. A recent study of remains of Utah juniper (*Juniperus osteosperma*) in packrat middens documents its spread into Wyoming and Montana during the Holocene (Lyford et al., 2003). Utah juniper became established first in northeast Utah in the early Holocene about 9000 years ago (Figure 22.3 a–h). In mid-Holocene the species had advanced into central Wyoming and southern Montana.

Because of the wide distribution of packrat middens in the region, it was possible to study the dispersal, landscape structure, and climate variability that governed the spatial and temporal patterns of the juniper establishment (Lyford et al., 2003).

**Fire**

Two forms of primary proxy data have been used to study the history of fire on the landscape: tree-ring data and charcoal particles from lake, bog, small hollow and wetland sediments. Tree-ring data are widely used to reconstruct the timing and occasionally the extent of past fires. Fires that are not severe enough to kill trees often leave distinctive scars that can be used to determine the exact calendar year a fire occurred. These ‘fire scars’ are preserved within tree-ring sequences. Fire-scar chronologies have been compiled at local-to-regional scales in many regions including western North America and southern South America (Swetnam, 2002; Veblen et al., 2003; Falk et al., 2011). The fire-scar network for western North America includes over 800 fire chronologies spanning centuries. This network shows a close correlation between drought years and years with extensive fire activity (Swetnam, 2002). Fire-scar networks can be created and analysed at a range of spatial scales, from trees and stands to subcontinents, revealing different patterns and processes at different scales (Falk et al., 2011). In forests where few fire scars are present, stand-age analysis has been used to reconstruct the dates of past fires. This method requires the dating of a large number of trees in an area in order to determine when even-aged cohorts of trees became established. Pulses of tree regeneration occur after fire and other disturbances such as insect outbreaks, thus determining the age of tree cohorts in a forest allows researchers to determine the timing of forest disturbances.

The fire-scar network in western North America shows that large-scale climate teleconnections strongly influence fire activity on a sub-continental scale. A study by Kitzberger et al. (2007) employed both dendroclimatological methods and a large network of fire-scarred trees in the western United States in order to examine the links between large-scale climate teleconnections and fire activity. Three climate indices – El Nino Southern Oscillation (ENSO), Pacific Decadal Oscillation (PDO), and Atlantic Multidecadal Oscillation (AMO) – were reconstructed using tree-ring chronologies from the US and Mexico in the case of ENSO and PDO, and Finland, France, Italy, Jordan, Norway, Russia, Turkey, and the US in the case of AMO (Kitzberger et al., 2007). The fire-activity record was composed of individual fire chronologies from 238 sample sites. Synchronous fire activity across the sample sites was compared to the climate indices. The study found the warm phase of AMO has synchronized fire activity over multidecadal timescales in the western US for the last 500 years (Figure 22.4; Kitzberger et al., 2007).
Figure 22.3  The location of woodrat-midden records of Utah juniper invasion in Wyoming and adjacent regions. Calibrated dates given in thousands of years before present (ka).

(a) Locations of woodrat-midden study sites (black circles) and modern distribution of Utah juniper (grey circles) in Wyoming and adjacent states. (b) Holocene records of presence (filled circles) and absence (open circles) of Utah juniper macrofossils from woodrat middens at 14 sites. (c) Map of presence (filled circles) and absence (open circles) of Utah juniper macrofossils in woodrat middens dating between 10 and 6 ka. (d) Presence and absence of Utah juniper macrofossils between 6 and 4 ka (e) Presence and absence of Utah juniper between 4 and 3 ka. (f) Presence and absence of Utah juniper between 3 and 2 ka. (g) Presence and absence of Utah juniper between 2 and 1 ka. (h) Number of study sites occupied by Utah juniper as a function of time in the mid-to-late Holocene.

Source: Lyford et al., 2003: 576/7. © 2003 by the Ecological Society of America
The second palaeofire proxy data are the charred pieces of wood, leaves and grass deposited and preserved in anaerobic environments such as bogs, lakes and wetlands (Brown and Power, 2013). The charcoal from sediment cores from these depositional environments is used to reconstruct fire activity over thousands of years. This method of fire-history research is based on extracting the charcoal from contiguous intervals of sediment cores and examining this under the microscope. Generally two different size classes of particles are analysed: microscopic and macroscopic charcoal. Microscopic particles are counted from pollen slides at a magnification of 400x, while macroscopic pieces greater than 125 microns (μm) are isolated from the sediment and analysed at 40x magnification. Microscopic charcoal can travel long distances before settling in a lake, and it is not typically analysed at continuous intervals. Macroscopic charcoal comes from fires within a radius of < 20 km of the lake (Higuera et al., 2009). It is analysed in every sample throughout a core and used to reconstruct local-scale fire episodes (Whitlock and Larson, 2001). Macroscopic charcoal data are converted to charcoal accumulation rates (number of particles cm$^{-2}$ yr$^{-1}$). As with pollen and tree-ring data, modern studies are used to calibrate and inform the interpretation of charcoal abundance in the pre-observational period.

Analysis of charcoal is undertaken in order to determine and describe the fire regime of a particular area of study. A fire regime describes the characteristics of fire (frequency, size and severity) and its role in a particular ecosystem. A suite of climate, fuel, and landscape variables are required for fire to occur and spread, but their relative importance changes across spatial and temporal scales. Recent advances in statistical methods of charcoal analysis have added to our understanding of past fire regime characteristics.
Getting Information from the Past

(e.g. Higuera et al., 2009; Kelly et al., 2011). Figure 22.5 summarizes the most commonly reconstructed fire regime metrics, including charcoal accumulation rates, background charcoal and mean fire return intervals.

In a regional-scale study from the South Island, New Zealand, McWethy et al. (2009) explored changes in fire activity after Polynesians arrived on the island ca. 1280 CE. Prior to this time, New Zealand was uninhabited by humans and fire was

Figure 22.5 Charcoal data from Morris Pond, Utah, USA, over the past 9,000 years. This figure summarizes the typical metrics of a fire regime that charcoal data have been used to reconstruct. The top panel shows the Mean Fire Return Interval (MFRI). This metric reflects the frequency of fire through time at the site. The second panel shows statistically significant peaks in fire activity and the associated magnitude of the peaks. These peaks are interpreted as local (within 1–3 km) fire episodes. Peak magnitude is a measure of the total charcoal deposition for a fire episode and often reflects the type and amount of vegetation that was burned. The bottom panel shows Charcoal Accumulation Rate (CHAR), Background Charcoal (BCHAR), and the regime shift index algorithm (RSI). CHAR is the measure of the number of charcoal particles per cm$^2$ per year. Background charcoal (BCHAR) is the slowly varying trend in CHAR and changes in this metric often represent variability in the abundance of fuel or biomass at the site (for example, forests produce more charcoal than grasslands or tundra). The RSI was used to identify statistically significant changes in BCHAR and delineate fire regime zones. The dashed vertical lines indicate fire regime zones derived RSI.

Source: Morris et al., 2013: 30. © 2012 University of Washington. Published by Elsevier Inc.
infrequent and ecologically insignificant. The approach of this study was to investigate regional trends in biomass burning by reconstructing local-scale fire activity at many watersheds across a climatic gradient from high to low precipitation. The study also examined climate to determine if temperature anomalies may have contributed to flammability in the decades after human arrival. In order to reconstruct watershed-scale fire activity, high-resolution macroscopic charcoal was analysed in continuous samples through the sediment core. Individual records showed very low levels of fire prior to human arrival, a period of high fire activity, representing one to a few fires, followed by low fire activity until the time of European arrival. Comparison of several charcoal records across the South Island revealed the

![Figure 22.6](image)

**Figure 22.6** Local-scale charcoal records from 16 sites on the South Island, New Zealand. Most records have a clear peak in fire activity within 200 years of human arrival, implicating anthropogenic burning as the ignition source of these fire events.

Source: McWethy et al. 2010: 21344. © The National Academy of Sciences of the USA
Getting Information from the Past

regional patterns of fire activity over the last 1,000 years (Figure 22.6). A period of high fire activity lasting a few decades was evident in all but the wettest and highest elevation sites, although the dates of this period varied. This Initial Burning Period marked the arrival of Māori to the island and the rate of deforestation at this time suggests deliberate and targeted use of fires (Perry et al., 2012). Following the Initial Burning Period, Māori maintained low level fires to sustain vital resources. The study found that fires were not associated with anomalous summer temperatures, and thus the influence of climate on the fire activity was negligible. This study is a good example of using charcoal analysis to test hypotheses of the drivers (human vs. climatic) of fire activity.

*Dung Fungal Spores*

Dung fungal spores in lake, bog and wetland sediments are a proxy data source that has rapidly gained use in the last decade (Gill et al., 2013). These fungi are a type of coprophilous fungi that grow on animal dung. They require herbivore digestion to complete their life cycle, producing spores on the dung of mammals. Palaeoenvironmental reconstructions that incorporate dung spore analysis hold promise as a proxy for the presence and perhaps abundance of large herbivores. These animals can have strong effects on ecosystems by maintaining vegetation openness and patchiness, removing material that would otherwise fuel landscape fire, dispersing seeds, and physically disturbing soil and recycling nutrients (Rule et al., 2012).

The dung fungal spores of the genera *Sporormiella*, *Sordaria* and *Podospora* are the three most reliable indicators of large herbivore activity (Baker et al., 2013). The spores are transported to lakes and other depositional environments by slope-wash. The relationship between the amount of dung spores in sediments is influenced by both the abundance of dung in the watershed as well as its distance from the lakeshore. The methodology for quantifying dung spore source area and large herbivore population size is still developing. Reconstruction of herbivore densities has been performed using accumulation rates (number of spores/cm²/year), and percentage in relation to the pollen sum. The use of accumulation rates is thought to be a superior approach as relative percentage does not provide a proxy for herbivory (plant consumption) that is independent from vegetation changes (Baker et al., 2013).

A number of recent palaeoecological studies have used *Sporormiella* spores to investigate the question of the timing and impacts of megafaunal decline (e.g. Robinson et al., 2005; Davis and Shafer, 2006; Gill et al., 2009; Rule et al., 2012). A study from northeast Australia examined the population collapse of megafauna that occurred around 40 thousand years ago shortly after people first arrived on the continent. This study reconstructed vegetation, fire and *Sporormiella* between 3,000 and 130,000 years ago with a special emphasis on the period between 39,000–43,000 (Rule et al., 2012). *Sporormiella* declined markedly between 40–41,000. This decrease was followed by an increase in charcoal and the pollen of grass and sclerophyll shrubs that tolerate frequent fires (Figure 22.7). This transition in vegetation occurred in the absence of major climate perturbations and thus it appears the mass extinction of megafaunal triggered major changes to vegetation and ecosystem functioning.
Figure 22.7  Pollen, charcoal and Sporormiella diagrams for Lynch's Crater. The interval during which Sporormiella declined and charcoal first increased is shaded grey. A large shift in vegetation from a rainforest to sclerophyll assemblage is evident in the millennia following Sporormiella decline and charcoal increase.

Source: Rule et al., 2012: 1484. © Science
Supporting Limnologic Proxy Data

Diatoms

Diatoms are algae in the division Bacillariophyta that occur in almost all aquatic environments (Jones, 2013). The siliceous skeleton or frustule of these microscopic unicellular organisms is identifiable to the species level and provides information on aquatic conditions that can be tied to changes in nutrients, water temperature, pH, and light penetration. Quaternary diatom remains have proven useful as indicators of local limnologic conditions and used to reconstruct past lake-level changes, water chemistry variations, and human disturbances of lake ecosystems. They are found in a wide range of aqueous or subaqueous environments as benthic (bottom dwelling), epiphytic (attached to plants), or planktonic (free-floating) and thus occupy a wide variety of niches. A key issue in diatom analysis is the accuracy with which diatom assemblages in sediments reflect the composition of the source communities and habitats from which they are collected. To this end, most analyses rely on comparison of the composition of assemblages, as well as the physical limitations of indicator taxa (Korhola, 2013).

Diatom analysis has provided perhaps the strongest case for acid rain effects from industrialization. In a classic study, Battarbee et al. (1984) showed that changes in the assemblages of diatoms preserved in lake sediments provided evidence of 19th and 20th lake acidification in northwestern Europe and North America. The strong relationship between diatom occurrence and water pH allows reconstruction of past pH levels with remarkable precision. Although long-term acidification is a natural process for lakes in areas of resistant base-poor bedrock, diatom analyses of sediments spanning the last 150 years indicated rapid and unprecedented acidification.

In studies where diatom records have been developed at several sites, the limnologic reconstructions often show considerable variability that reflects local site-specific variability superimposed on climate change (Fritz and Anderson, 2013). In some cases, the variability is a result of the changes in vegetation, particularly the early colonization of plants following deglaciation and their impact on catchment nitrogen cycling (Fritz et al., 2004). In other locations, the differences reflect the influence of different substrates and the mineralogy of the parent rock on lake nutrients, pH, and water clarity (Bigler et al., 2002).

Chironomids

Diptera: Chironomidae (non-biting midges) are a large taxonomic group of insects that live in most aquatic or semiaquatic habitats during their larval stages (Walker, 2013). The exoskeletal remains that are sloughed during larval molting accumulate in the sediments of lakes, and the well-preserved chitinous head capsules are identifiable to species by comparisons with specimens of extant species. As with diatoms, information on the modern biology and habitat of individual taxa is the basis for environmental reconstructions. Palaeoecological studies have focused on the development of quantitative calibration models (e.g. transfer functions) for the reconstruction of past environmental parameters based on the composition of the chironomid assemblage (Walker, 2013). This calibration is then applied to the time-series of chironomid remains to interpret past conditions. Some of the issues that vex specialists include misinterpreting past assemblages because modern
samples are generally taken in summer (whereas the sedimentary record preserves the year-round assemblage); concerns about taphonomy (processes by which biological material is differentially deposited and preserved) and the redeposition of fossil remains from different locations in the lake, thus misinterpreting the assemblage; differences in taxa abundance related not to the environment but to differences in the duration of larval life cycle and number of generation and larval stages; and differential preservation of more robust head capsules thus distorting the record (Brooks et al., 2010; Velle and Heiri, 2013).

Chironomid records have been studied in a variety of locations to reconstruct climate change, land-use and other human activities. For example, they have been used to examine the ecological consequences of eutrophication of temperate lakes; monitor water pollution related to industrial inputs and airborne pollutants; record acidification trends in lake sediments; and assess changes in water salinity through time. Because air temperature influences processes of emergence, swarming and settling, the statistical correlation between chironomid assemblages and July air temperature is often stronger than that of surface water temperature (Massaferrro et al., 2009). Available records indicate that chironomids can be successfully used to reconstruct temperature changes, especially if chironomid analysis is embedded in multiproxy, or multisite, studies.

**Lithology, Geochemistry and Mineralogy**

Examination of the sediments, independent of their biotic constituents, provides information on the history of the watershed and the lake as an important context for palaeoecological reconstructions. A variety of non-destructive tools, including colour reflectance, digital imaging, radiography and X-ray imaging and CT scanning, are used in initial descriptions (Kemp et al., 2001; Hodder and Gilbert, 2013). Further analysis of the inorganic fraction of sediment, through mineralogical and geochemical analysis, has been used to identify changes in inorganic inputs to the basin that may relate to changes in erosion, windiness, pollution inputs and nutrients (Last, 2001). Variations in the authigenic (locally formed) carbonate content of the sediments can be a good measure of chemistry and pH changes related to water temperature. The organic component of the sediments is produced by different types of biota in the lake and watershed (Meyers and Ishiwatari, 1993). Organic matter in lake sediments comes from the detritus of terrestrial plants to aquatic algae and bacteria, each with different chemical signatures. The original composition of organic matter may be further altered by biotic and abiotic processes, and the degree of alteration also contains important palaeoenvironmental information (e.g. the degree of water-column mixing).

The isotope compositions of authigenic and biogenic carbonates and diatom silica are commonly examined to better understand changes in temperature, precipitation patterns, evaporation and the carbon cycle. Fluctuations in the isotope composition of authigenic or biogenic minerals are mainly a function of long-term changes in the balance between precipitation and evaporation as well as relative contributions between surface water and groundwater. Interpretation of isotope data from the various components within a lake sediment core requires a detailed knowledge and modern calibration of the processes that control and modify the signal; this must be determined for an individual lake system to establish the relationship between the measured signal, the isotopic composition of the host waters, and climate.
22.4 Multi-Proxy Records and Global Syntheses

Comparing multiple proxy data from a single site provides opportunities to reconstruct past environmental change within the whole watershed. A good example of this type of approach comes from Yellowstone National Park where a 9400-year-old core from Crevice Lake was analysed for pollen, charcoal, geochemistry, mineralogy, diatoms and stable isotopes to develop a nuanced understanding of Holocene environmental history (Figure 22.8; Whitlock et al., 2012). The pollen data indicated that the watershed supported a closed Pinus-dominated forest and low fire frequency prior to 8200 (calibrated) calendar years before the present (cal yr BP; where present = CE 1950), followed by open parkland until 2600 cal yr BP, and open mixed-conifer forest thereafter. Charcoal data suggested that fire activity shifted from infrequent stand-replacing fires initially to frequent surface fires in the middle Holocene and stand-replacing events in recent centuries. Low values of $\delta^{18}O$ were evidence of high winter precipitation in the early Holocene, followed by steadily drier conditions after 8500 cal yr BP. Carbonate-rich sediments before 5000 cal yr BP implied warmer summer conditions than after 5000 cal yr BP. High values of molybdenum (Mo), uranium (U), and sulphur (S) indicated anoxic bottom-waters before 8000 cal yr BP, between 4400 and 3900 cal yr BP, and after 2400 cal yr BP. Diatom assemblages suggested well-developed spring conditions and water-column mixing through much of the Holocene, but also revealed a period between 2200 and 800 cal yr BP with strong summer stratification, phosphate limitation, and oxygen-deficient bottom waters. Together, the proxy data implied wet winters, protracted springs, and warm, effectively wet summers in the early Holocene and less snowpack, cool springs, and warm dry summers in the middle Holocene. In the late Holocene, the region experienced extreme changes in winter, spring, and summer conditions, with particularly short springs and dry summers and winters during the Roman Warm Period (~ 2000 cal yr BP) and Medieval Climate Anomaly (1200–800 cal yr BP). Long springs and mild summers occurred during the Little Ice Age (500–100 cal yr BP) and these conditions persist to the present. Although the proxy data indicate effectively wet summer conditions in the early Holocene and drier conditions in the middle and late Holocene, summer conditions were governed by multi-seasonal controls on effective moisture that operated over different time scales.

Whereas multi-proxy comparison allows for in-depth analysis of a single site or a group of nearby sites, combining the records from a single proxy such as charcoal or pollen data affords the opportunity to reconstruct palaeoenvironmental history over a very large spatial scale. Continental- to global-scale syntheses of late glacial and Holocene fire activity and vegetation distribution have been compiled and are the subject of ongoing research. Global-scale syntheses of fire activity have been compiled and analysed by the Global Palaeofire Working Group (www.gpwg.org; Daniau et al., 2012). The Global Charcoal Database (GCD v2) contains almost 700 sedimentary charcoal records from six continents (Figure 22.9). The general global pattern of biomass burning over the last 21,000 years shows a widespread increase associated with the transition from cold glacial to warm Holocene climates (Figure 22.10; Power et al., 2008; Daniau et al., 2012; Marlon et al., 2013). The influence of temperature on fire activity at this large scale is pervasive.
**Figure 22.8** The summary of the environmental proxy at Crevice Lake over the last 9400 cal yr BP plotted with July and January insolation anomalies.

Getting Information from the Past

The Palaeovegetation Mapping Project (known as BIOME 6000: Prentice and Webb, 1998) was developed to create fully-documented pollen and plant macrofossil data sets for 6750 and 21,000 cal yr BP, and to construct global maps of biomes for these time periods based on plant functional types and biomes. The BIOME 6000 database is publicly available and updated with new datasets (www.bridge.bris.ac.uk/resources/Databases/BIOMES_data). The most recent version of the BIOME 6000 database (v4.2) has records for 11,166 modern sites, 1794 sites at 6750 cal yr BP, and 318 sites at 21,000 cal yr BP (Figure 22.11). Palaeovegetation datasets have been utilized to train and test palaeovegetation models (Figure 22.12; Kaplan et al., 2003; Prentice et al., 2011; Levavasseur et al., 2012) and to model past climate (Figure 22.13; Cheddadi et al., 1996; Ferrera et al., 1999; Bartlein et al., 2011).

Important conclusions have been drawn from these synthetic efforts. They demonstrate that at a global scale fire is controlled largely by temperature (Marlon et al., 2013). Thus, while prehistoric humans likely influenced fire activity in certain locales, globally climate is the primary control. These syntheses are also important for data-model comparisons. Many vegetation and climate models operate at large spatial scales (for example at 0.5-1.0° grid cells) and in order to make meaningful comparisons, palaeoenvironmental reconstructions need also to be compiled at a large spatial scale. One critique of these global-scale syntheses is that there is an uneven distribution of data with a more dense concentration of sites in North America and Europe than in the other continents, which may skew interpretation. Thus, it is important to support continued palaeoecological studies in Asia, Australia, South America and Africa and incorporate them into global databases.
Figure 22.10  Palaeoclimate records and anthropogenic indicators compared with global biomass burning reconstructed from sedimentary charcoal records. Globally fire was low at the beginning of the Holocene and increased during the Holocene (panel G). This trajectory is consistent with the global increase in temperature through the glacial-interglacial transition (panels A and B).

Source: Marlon et al., 2013: 18. © 2013 Elsevier Ltd.
22.5 Conclusion

The study of terrestrial palaeoecology has seen stimulating developments during recent years and it has become one of the most dynamic areas of biogeographical research. Geographical insights can be achieved by employing the appropriate types of data to answer specific, well-formed research questions. The application of independent dating, multivariate analyses, the establishment of databases, and the increasing quantitative precision of proxy reconstructions have broadened the scope of the discipline and helped extend our understanding of ecosystem dynamics beyond modern observations. Studies range from understanding the selective pressure and genetic make-up of individuals, to reconstructing populations, communities and ecosystems across the entire globe. Many of the proxy data sets allow simultaneous examination at multiple spatial and temporal scales; combinations of data-data, data-model and inter-model comparisons allow better understanding of the hierarchy of biophysical drivers of past ecosystem change.

Proxy data operate at different spatial and temporal scales (Figure 22.1), and while their interpretation is firmly grounded in uniformitarianism, the strongest proxies are those that are well grounded in modern empirical and observational research so that the constraints on present distribution are well understood. This information is essential to calibrate and refine interpretation of the past. With proxy data, there is also the opportunity to explore past conditions that may have no analogue in the present. The examples of novel ecosystems in the past offer some of
the most intriguing areas of research as we explore ecosystem responses in the future under projected climate change.

Most areas of palaeoecology are moving from an inductive data-gathering stage to more deductive approaches that generate and explore testable hypotheses about past environments. Individual records lie at the heart of any interpretation, but data composites and mapped summaries are capturing the dynamics of ecosystem change at broad temporal and spatial scales. Geography, with its interest in pattern and process at different scales, has the capacity to contribute greatly to palaeoecology. Collaborative research

Figure 22.12 A comparison of simulated biome distribution at the last glacial maximum (LGM, 21,000 years ago) by the Land Processes and eXchanges (LPX) model (top panel) with LGM biomes inferred from pollen and plant macrofossil records compiled by the BIOME 6000 project (bottom panel)

and exchange among biogeographers and palaeoecologists, climate and ecosystem modellers, molecular geneticists, archaeologists and historians, and conservation biologists and land-use managers, will continue opening new doors of inquiry and relevance.

**SUMMARY**

- We examine some of the approaches and data used to reconstruct terrestrial ecosystem change. Research employing these methods comes under the auspice of ecological biogeography, which is concerned with the factors that have led to the current distribution of plants on the landscape.
- Palaeoecological research usually concerns ecosystem dynamics during the Quaternary period (the last 2.58 million years), and in particular over the last 21,000 years, which includes the last glacial maximum (LGM) and the Holocene (the current interglacial period that began 11,700 years ago).

**Figure 22.13**  Mean annual precipitation and mean temperature of the warmest month at 6,000 and 21,000 cal yr BP reconstructed from fossil pollen data

*Source: Bartlein et al. 2011: 792–793. © The Author(s) 2010.*
• We outline the approaches taken to reconstruct terrestrial ecosystem change including tree rings, pollen, plant macrofossils, packrat middens, charcoal and dung fungal spores, as well as supporting palaeolimnological information from diatoms, chironomids and lake-sediment lithology, geochemistry and mineralogy.

• Proxy records can be used alone, but fuller understanding is achieved by combining and comparing multiple proxy data from single or groups of sites. Alternatively, developing geographic networks of records from a single proxy type, such as charcoal or pollen data, provides insights about patterns of environmental change over broad spatial scales.

Further Reading

Elias, S.A. and C.J. Mock (2013) *Encyclopedia of Quaternary Science*. This encyclopedia is the most comprehensive and up-to-date overview of Quaternary science available. It contains 357 broad-ranging articles authored by well-respected researchers from around the world.


These reference books detail the most important indicators used by palaeoecologists and palaeolimnologists, including pollen analysis, plant macrofossils, charcoal, diatoms, stable isotopes, geochemistry, lithostratigraphy and mineralogy.


These volumes discuss the approaches by which Quaternary terrestrial environments can be reconstructed from fossils and sediments. They provide in-depth explanation of the methods and assumptions for working with a variety of proxy data.

Note: Full details of the above can be found in the references list below.

References


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Major advances in our understanding of the climate, duration and stratigraphy of Quaternary interglacials have occurred over the decade. This review details palaeoenvironmental evidence contained within British interglacial deposits and
their correlation with interglacial episodes recorded in marine and ice core records, allowing us to understand in greater detail how northwest Europe responded to different periods of climate warming. This information is important to understanding the evolving climate of the Holocene.


A longer-time perspective is needed in order to better understand contemporary and near-future global environments. This progress report reviews how an understanding of environmental dynamics over extended time periods is now incorporated into science dealing with predictions of future climate change by the IPCC consortium, how possible analogues for a warmer future are still vigorously explored and how information on past environments may better inform an understanding of contemporary ecosystem processes and influence the future management of biodiversity in protected areas.


Eastern North American forests have effectively lost two major tree species (American chestnut and American elm) in the last 100 years, and two more, eastern and Carolina hemlock, will be functionally extinct over much of their ranges within a couple of decades. This progress report describes a community-based approach to salvaging palaeoenvironmental archives that could serve as a model for collections from other important species currently threatened by exotic forests pests and pathogens (e.g. whitebark pine, ash). The approach calls for building connections between scientists, students, environmental NGOs, and land managers focused on old-growth forests.