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Julien Louys *Editor*

Paleontology in Ecology and Conservation

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Foreword

Paleontology is no longer about just the biggest or oldest specimen. The science has come of age in the respect that now abundant fossils of many kinds of plants and animals have been recovered, identified, and cataloged in massive, easily accessible databases such that community attributes and dynamics can be traced through hundreds, thousands, and millions of years. Even a decade ago, the prevailing wisdom about fossil accumulations was that they were hopelessly biased, to the extent that it would be difficult to ever meaningfully compare fossil communities to modern ones. That has luckily proved not to be the case.

Meticulous work, much of it accomplished in the past 10 years, compared the samples obtained from modern communities by zoologists and botanists, with samples of long-dead communities mined from the fossil record, and revealed something surprising. In many situations, fossil samples provide as good, or even better, representation of the community as the modern samples do. This was long known in the paleobotanical world through much research that compared fossil pollen in Quaternary lake deposits with modern surface samples; in the mid-1990s, the fidelity of the fossil record was also demonstrated for certain kinds of terrestrial and near-shore marine deposits. In short, it became apparent that for several kinds of communities, such ecologically important metrics as species composition, trophic structure, abundance, and even genetic diversity could be tracked through hundreds, thousands, and (excepting genetic information) millions of years.

The timing could not have been better. Also emerging through the 1990s was another scientific revelation: that human activities were changing the Earth more and faster in one generation than had ever been seen in human history – or prehistory. In 1950, there were about 2.5 billion people in the world; that number has nearly tripled today. Correspondingly, transformation of natural landscapes for human use increased, intensifying fragmentation of natural habitats. Greenhouse gases, emitted into the atmosphere from ever-growing use of fossil fuels, rose to some 35% above normal levels, rapidly warming the planet and causing other climatic disruptions, and also changing ocean chemistry towards the more acid end of the scale. Agricultural runoff and other pollutants began to create vast dead zones offshore. Invasive species increasingly are creating novel species assemblages. The net effect is that biological systems are now being squeezed from both the bottom up by humanity's direct transformations of ecosystems, and from the top down by indirect, global-scale forcings, like changes in atmospheric and ocean chemistry, which emerge from myriad human activities. This pressure on biological systems seemingly will not be relieved any time soon: if anything, it is intensifying.

As a result, conservation biologists are faced with new problems about how to manage ecosystems that have long acted, and in the case of about 12% of Earth's lands, have been intentionally set aside as areas to nurture biodiversity, save species at risk of extinction, or preserve special landscapes and ecosystems. For example, in the USA, Glacier National Park is anticipated to witness melting of all its glaciers, and Joshua Tree National Park is projected to have a climate unsuitable for Joshua trees. A key issue is that the baseline of normal that land-managers have traditionally used – like presence of a particular species or assemblage of species that characterized a given area when it was first preserved – is no longer sufficient, because the climatic conditions, dispersal routes, and interacting species are no longer the same.

In a similar vein, ecologists are faced with a problem when they try to assess ecological impacts or understand ecological processes, even in remote places that do not exhibit direct signs of people. How much observed change is too much? When can we say that human activities have pushed a given ecosystem outside its normal range of variation? Do the ecological processes we observe and experiment with today represent ecological signal or noise, in terms of what holds ecosystems together over the longer term?

That is where paleontology comes into the picture for conservation biology and ecology. Ecosystems do not arise overnight, their species are not fixed in place, and they exhibit some natural range of variation that can only be adequately measured over at least centuries and millennia. As land managers find it increasingly necessary to manage for healthy ecosystem processes rather than specific species, and as ecologists try to assess the extent of change natural ecosystems are exhibiting and understand the processes at work, this deeper time perspective has become essential. Paleontology now affords the opportunity to define metrics that reflect ecological structure and function, and trace how those metrics vary over timescales much longer than just a few human generations. And importantly in a world where species will be forced to move rapidly to different parts of the globe, reshuffling species compositions we tend to think of as the "normal" ones, paleontology is developing ataxic ways to characterize ecosystems. Thus, it becomes possible not only to know if a certain species has existed at a certain rank-order abundance in a given ecosystem through long time periods, it also becomes possible to characterize the range of normal for features such as species richness, evenness, distribution of species through size and trophic classes, and structure of food webs. These same traits can then be assessed in systems today, and monitored into the future to manage ecological health in specified regions, provide a barometer of change by which to assess the biological impacts of human activities, and uncover ecological principles that only become apparent at long time scales.

The merger of paleontology with conservation biology and ecology is not yet complete, but it is well on its way. The papers in this volume nicely illustrate many of the areas where contributions are now being made, and also highlight where next steps will prove useful. As more and more such studies accumulate, paleontology is destined to move from the realm of simply interpreting the past, to helping to forecast and manage the future.

Anthony D. Barnosky
Elizabeth A. Hadly

Contents

Chapter 1
Paleontology in Ecology and Conservation: An Introduction

Julien Louys

Abstract Paleontology is the study of past life. The geological record preserves the history of individual organisms, populations, communities, ecosystems and earth systems through millions of years. It is a unique resource for understanding the dynamics that have shaped our current biota, and developing evidence-based models that will allow us to predict how organisms will respond to future changes to habitat, climate and the anthropogenic manipulation of communities and ecosystems. This book provides examples of the use of paleontological data in ecology and conservation science and illustrates how the addition of data from the fossil record can lead to novel insights and developments. It examines possible future directions in paleoecology and conservation paleobiology.

Keywords Paleontology • Ecology • Conservation • Paleoecology • Conservation paleobiology

1.1 Introduction

Traditionally, paleontologists have been seen as explorers, excavators, morphologists, and systematists. Their role has been seen as one of digging up fossils, describing them, and working out their relationships. Increasingly, paleontology has served as a critical tool for understanding the evolution of life, with fossils forming the basis of understanding phenotypic change through time, serving as markers in molecular clocks and allowing researchers to resolve the origins of major clades. However, understanding the process of evolution requires knowledge of the environments in which evolution takes place, and this knowledge has been the purview of paleoecologists. Using sophisticated techniques such as stable isotope analyses,

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sedimentology, autecology and synecology, paleoecologists have provided paleontologists with the environmental background that shaped and ultimately drove the evolution of the organisms under study.

Perhaps less well recognized by the general scientific community are the contributions that paleoecologists have made to ecology. The lack of synergy between paleoecologists on one side, and ecologists on the other (Birks 1996; McGlone 1996; Louys et al. 2009), has resulted in the parallel development of two bodies of research: one focused on deep time (i.e. centennial to millennial timescales) and the other on near time (i.e. seasonal to decadal time-scales). However, as Wilkinson discusses in this volume (Wilkinson 2012), the dichotomy between deep and near time is a relatively recent division, and is associated with the break up of the study of natural systems into distinct divisions (scientific disciplines). Most early scientists (or savants as they termed themselves) made no distinction between studying biological phenomena in the geological record and in the modern world.

Although modern ecology has been conducted almost entirely independently of paleoecology, several individuals and research groups have attempted to bridge these two disciplines. Wilkinson discusses the research of Marie Stopes, arguably one of the first paleontologists (in the modern sense of the word) who made contributions to modern ecology in the early twentieth century. However, as Wilkinson argues, these insights were not recognized by ecologists of the day, and were independently formulated several years later. More recently in the 1970s, marine paleoecologists began a process of understanding paleontological sequences in terms of ecological processes (e.g., Walker and Alberstadt 1975; Bretsky and Bretsky 1975; Walker and Parker 1976). However, as Bennington and Aronson (2012) argue, this work was ultimately compromised when it was realized that the different scales at which modern ecology and paleoecology operate meant that ecological processes and dynamics, as described by neoecologists, were not directly transferable to paleontological sequences.

This disparity of scale is one of the main reasons why there has not been a greater integration between neoecological and paleoecological studies. The three dimensions over which paleoecology spans are the spatial, the temporal and the taxonomic. Two chapters (Bennington and Aronson 2012; Louys et al. 2012) discuss these dimensions in some detail. Bennington and Aronson review the scale of long-term (in a neoecological sense) vertebrate, invertebrate and botanical studies from around the world, and compare these to the scales at which paleontological studies of those organisms are conducted. They find some areas of fundamental differences, however they also identify areas of fruitful overlap.

Louys et al. (2012) take this one step further, and discuss how ecological data can be collected in order for it to be comparable to paleontological data and in order to facilitate the examination of ecological theories in deep time. They argue that testing of ecological theories in deep time is essential to determining whether these theories are truly general, or simply an artifact of observing modern phenomena. They provide examples of the ways in which paleontology has influenced modern ecology in the past, and advocate a much closer association between these two fields in the future.

Interestingly, one of the primary means of comparing communities and ecosystems across large temporal scales (taxon-free analysis) is also the means of comparing these entities across large spatial scales. Taxon-free studies are focused on morphological traits, ecological niches or functional groups as opposed to taxonomic groups. Although there are inherent phylogenetic controls over the acquisition of particular traits during an organism's evolution, and the ecological niches or functional groups that organism will occupy, they explicitly preserve the evidence of how that organism or community interacts with its environment. And because these taxon-free variables can be identified either through time or across different biogeographical regions (i.e., space), this methodological approach is a critical tool for the examination of ecological principles that cross taxonomic boundaries.

An excellent example of such a study is the chapter by Lawing et al. (2012). These authors examine three morphological traits in the North American snake metacommunity ("ecometrics"), and are able to demonstrate that these traits are significantly correlated with certain environmental variables. While the principal employment of such a study will probably be for the reconstruction of paleo-environments, extending such a study in geological time allows researchers to examine how the distribution of these traits have shifted over time, and hence how they might be expected to change in light of predicted habitat alterations and climate change (Polly et al. 2011). In their chapter Lawing et al. (2012) use the correlations to determine whether environmental changes in protected areas are reflected in snake biometrics, and find that the major biome shifts observed in those areas are predicted from the snake communities. This study highlights the conservation potential of ecomorphological approaches to the fossil record.

The conservation approach espoused by this study is an example of the surge of paleontological studies and data addressing conservation science that has emerged over the last 20 years or so, such that the need for paleontological perspectives to conservation issues is becoming widely acknowledged by both scientists and policy makers alike. This is in marked contrast to the paleontological contributions to modern ecology discussed above. This surge has resulted from the understanding that only the fossil record can provide the deep time perspective of ecosystem processes such as ecological succession, migration, adaptation, microevolution, and extinction, processes that can't be observed or predicted from neontological studies (Vegas-Villarrúbia et al. 2011).

Paleobotanists Margaret B. Davis and Brian Huntley, and vertebrate paleontologists Michael Archer, Suzanne Hand and Henk Godthelp, in the late 1980s and early 1990s, were some of the first to directly advocate for the consideration of paleontological information in conservation science (Archer et al. 1991; Davis 1989, 1991; Huntley 1990, 1991). Since then, many government and international organizations have either used paleoecological data in their reports or directly advocated their inclusion in conservation studies (e.g., Houghton et al. 1990; Alverson et al. 2003; Flessa et al. 2005; Parry et al. 2007; Solomon et al. 2007).

Moreover, the use of paleontological data for informing conservation issues has been embraced by paleontologists in many different sub-disciplines including geology, micropaleontology, palynology, paleobotany and vertebrate paleontology, so much so that 'conservation paleobiology' can be considered a separate field of its own (Dietl and Flessa 2010).

The principal aims in this nascent field are to determine baselines of natural variability in ecosystems, the identification of vulnerable species in critical need of protection and to determine the nature of biotic responses to climate change (Dietl and Flessa 2009, 2010). The conservation paleobiology chapters presented in this volume span all three of these aims.

Behrensmeyer and Miller (2012) review the contributions to ecology that can and have been acquired from the study of the paleontological subfield of taphonomy; that is the study of the processes through which biological material is incorporated into the geological record. Because this field of study specifically targets the time period between modern ecological studies and paleontological ones, it can provide unique insight into both these disciplines. The guidelines for future taphonomic research provided by these authors are an invaluable resource for the future exploration of the intersection between modern ecology, taphonomy and paleontology.

Pardi and Smith (2012) discuss species' reactions to past climate change, particularly in the late Quaternary, in order to provide reliable predictions of species' responses to human-induced global warming. They describe and provide examples of the three types of reactions that have been experienced by species in the past; namely adaptation, relocation and extirpation/extinction. They focus on the late Quaternary small mammal communities from North America, which are some of the most well-studied and best-poised paleontological collections with which to understand ecosystem responses to climate change.

Lyman (2012) presents a discussion on understanding background fluctuations in biodiversity and argues that the bottom-up processes of climate change can be distinguished from top-down processes such as anthropogentic impacts on ecosystems. Like Pardi and Smith, he also focuses on the small mammal faunas of North America. Lyman introduces the term paleozoology, which refers to the study of both faunal paleontology and zooarcheology. One important implication of his chapter is that he demonstrates that the zooarcheological record can also be used to determine natural ecosystem baselines, albeit with some caveats.

Price (2012) examines the long-term trends in koala (phascolarctid) diversity through deep time. He finds that there has been a steady decline in the number of both species and genera of koalas since the Oligo-Miocene, such that this once more diverse family is currently only represented by a single species. He highlights the conservation importance of such a trend by comparing it with that of the Tasmanian wolf. This marsupial also showed a downward trend in phylogenetic diversity throughout the last 25 million years, such that it was represented by only a single species in the Holocene, and eventually it became extinct in the early twentieth century. Price (2012) discusses some of the conservation implications of such observations.

Zimov et al. (2012) present a detailed look at the effects of global warming on the frozen soils of northern Siberia. The thawing of these soils, they argue, will release huge amounts of carbon and methane into the atmosphere. Zimov et al. further contend that the only way this can be prevented is through a rewilding program, which would seek to return this region to biodiversity levels present during the Pleistocene. They present evidence to suggest that the extinction of the megafauna in Siberia was the result of human overhunting, and advocate that returning the steppe to former biodiversity levels will return that ecosystem to health and prevent the thawing of the soils.

Louys (2012a) examines the zoogeographic history of large-bodied mammals in Southeast Asia in order to determine if any distribution patterns are indicative of extinction risk. His study finds that many extinct and critically endangered species experience widespread distributions until the Holocene, where they become very restricted in range or extinct. Endangered species experiencing the same pattern include the giant panda, the tiger and the Malayan tapir, suggesting that these species are at critical risk of extinction. Louys argues that conservation efforts for the tapir, an animal whose conservation priority is not as well recognized as the panda or tiger, needs to be increased.

Finally, Faith (2012) examines the historical and paleozoological record of South Africa's Cape Floristic Region (CFR). He demonstrates that the roan antelope was a part of that ecosystem well into historical times, and because of this argues that it should be re-introduced and be made part of conservation plans for the CFR. In this chapter, Faith successfully highlights the relationships between ecology, historical biology and paleontology.

This book therefore presents a series of reviews, new analyses and case studies that demonstrate how paleontology has been included in ecological and conservation studies, and highlights the unique insights that can be gained from such inclusions. In the final chapter (Louys 2012b) I suggest some theoretical avenues where such collaborative efforts might be successfully pursued in the future. Ultimately, it is hoped that this book highlights the critical deep time contributions that paleontology can make to ecology and conservation science, and engenders greater dialogue between the practitioners of these fields.

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Chapter 2
Paleontology and Ecology: Their Common Origins and Later Split

David M. Wilkinson

> *'Why run the Earth and life sciences together? I would ask, why have they been torn apart by the ruthless dissection of science into separate and blinkered disciplines.'*
>
> *James Lovelock (1995)*

Abstract Today paleontology and ecology exist as separate disciplines, however for much of the history of research on these topics that was not the case. The splitting of 'science' into multiple discrete disciplines is mainly a product of the nineteenth century – when both paleontology and ecology acquired their names. To provide a historical background to the interrelationship between these two areas I consider four illustrative figures from the sixteenth century to the early twentieth century and discuss the extent to which these two areas of science interacted in their attempts to understand the world. I suggest that the rise of Earth Systems Science in the final few decades of the twentieth century shows one way of returning to a less compartmentalized approach to studying the Earth and illustrates the advantages to be gained from breaking down the boundaries between traditional late nineteenth and twentieth century scientific disciplines. I argue that the more geological aspects of natural history have often been overlooked by historians looking for the origins of the ideas that were to help form academic ecology during the twentieth century. Many key ecological ideas can be found in the work of the 'earth scientists' discussed in this chapter. For example fossil data was required to establish the fact of natural species extinction – an important ecological idea.

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2.1 Introduction

There are many ways of writing the history of science: there can be Marxist perspectives, feminist ones, even post-feminist ones or determinedly Post Modernist interpretations (Bowler and Morus 2005; Fara 2009). Perhaps one of the most obvious distinctions in this area of historical study is between the histories of science as written by scientists, and those written by historians or other social scientists. Scientists writing as amateur historians classically tend to focus on elucidating the origins of ideas currently considered correct in their area of study and so ignore much of the history of science that hasn't contributed to modern textbooks. This interpretation of the past in the context of the present is seen as a classic error by most historians – referred to as a Whig-interpretation of history after an influential book of 1968 by the historian Herbert Butterfield (Harrison 1987). However as Winsor (2001) has argued, science historians may overplay this distinction in an attempt to distinguish themselves from those scientists who write history. In this essay I take a Whiggish approach, in-so-far-as I am selecting vignettes from the history of paleontology and ecology that may help provide a context for thinking about how these subjects interact in today's science. This is not surprising as I write as a scientist interested in history – not an academically trained historian – and I write primarily for a science readership interested in the interactions between the study of fossils and the biodiversity we see around us.

It is worth noting that referring to 'ecology' or 'paleontology' in several of these vignettes is anachronistic. Ecology as a named subject came into existence in the second half of the nineteenth century, however, as this chapter illustrates academic discussion of topics now considered 'ecological' has had a longer history than the term coined in 1866 by Haekel (McIntosh 1985). Many 'ecological' ideas were widely discussed before this, especially by savants who would now tend to be described as primarily geographers or earth scientists (Bowler 1992; Bowler and Morus 2005; Rudwick 2005; Wilkinson 2002). Martin Rudwick's (2005) preferred term 'savants' is better for describing many of the people than 'scientists' which would be anachronistic as the term first started to be used in 1833, and it was the early twentieth century before it became fully accepted by most people. Many of these savants would have described themselves as either natural philosophers or naturalists (Fara 2009).

Paleontology is also a nineteenth century term which was originally used by many – such as William Whewell – to cover the study of anything that survived from the distant geological past; not just the remains of living organisms (Rudwick 2008). So the key words in this chapter's title would only have started to make sense to a reader from around the mid nineteenth century onwards – around the time that science was breaking up into separate distinct disciplines and the savants were turning into 'scientists'.

Fig. 2.1 Leonardo da Vinci depicted in a panel on the 1872 monument to Leonardo by Pietro Magi in the Piazza della Scala, Milan, Italy. The panels depict him as the archetypal Renaissance man by illustrating some of the many disciplines that he mastered: painting, sculpting, engineering and architecture. Paleontology and the other 'modern' sciences were not included in this nineteenth century celebration of his cultural importance (Photo: Dave Wilkinson)

2.2 Vignette 1: Leonardo da Vinci

Probably the earliest surviving detailed descriptions of the nature of fossils by a savant are the notes made by the artist and polymath Leonardo da Vinci (Fig. 2.1) around the start of the sixteenth century (Scott 2001). He described his ideas on the nature of fossils in notebooks that were later to become known as the Codex Leicester. At a time when many people either did not believe that fossils were the remains of once living organisms or considered them remnants of the biblical flood, Leonardo put forward a series of arguments to show their biological nature which were strikingly modern in their mix of observation and logical analysis – 'killer arguments' in the view of the art historian and Leonardo expert Martin Kemp (2004). Many of Leonardo's arguments were ones that we now consider ecological (or taphonomic) in nature. For example he pointed out that in rocks where both valves of a bivalve mollusc remain together then the animal must have lived where it was fossilised and not been transported from a distance (for example by The Flood) and that one could also find other deposits dominated by broken shells, exactly as one finds on a modern beach. He also drew attention to rocks where one could see trace fossils of marine organisms preserved on bedding plains – also showing that this was a fossilised marine community and not material washed in from another place. In addition he pointed out that such shells were only found in rocks that appeared to have an aquatic origin and were thus an appropriate habitat for the molluscs to live in (Gould 1998).

Leonardo's views on the nature of fossils are remarkably modern looking – although made in the context of late medieval theoretical ideas of The Flood and of Neoplatonic philosophy (Gould 1998). Yet, these ideas remained hidden in his unpublished notes, which were only translated and decoded in the nineteenth century. This was long after the real nature of fossils had been settled and so his ideas had no influence on the development of paleontology (Gould 1998; Kemp 2004). In the context of this chapter it is important to note that he was applying what we would now call ecology to help understand fossils, rather than using fossils to inform ecological ideas.

2.3 Vignette 2: Georges Cuvier

The influence of geological research has had at least one very obvious effect on ecological ideas; namely the concept of extinction. Briefly, the history of natural extinction is as follows. By the second half of the eighteenth century it was clear that fossils were the remains of former organisms, and it was also clear the some of these fossils appeared to be of life forms not known to be living in the modern world. It was recognised at the time that there were three main potential explanations for this: (1) these species were truly extinct; (2) they were still alive in under-explored parts of the world; or (3) they had changed (we would now say evolved) into the species we see today. The big difficulty was that many of the commonest and most well known fossils were of marine invertebrates, and it was very difficult to rule out their continued survival in the poorly known deep oceans (Rudwick 2005). By this time the fact of human-caused extinction was reasonably well established – interestingly one of the examples used to illustrate this in the late eighteenth and early nineteenth centuries was that of the dodo *Raphus cucullatus*, still a classic of conservation biology texts (Fig. 2.2). The big question was could *natural* extinction happen, without the intervention of humans? The reality of this was eventually established by vertebrate paleontologists, such as Georges Cuvier (1769–1832; Fig. 2.3) around the end of the eighteenth century. While it was plausible that many apparently extinct marine invertebrates could still exist somewhere on Earth, this was very unlikely to be the case for the large, apparently extinct terrestrial vertebrates that Cuvier and others were describing (Rudwick 2005). Archibald Geikie (1897, p. 212) described Cuvier's conclusions in his classic late nineteenth century history of geology; writing Cuvier was 'thus enabled to announce the important conclusion that the globe was once peopled by vertebrate animals which, in the course of the revolutions of its surface, have entirely disappeared.' So the idea of natural extinction, often

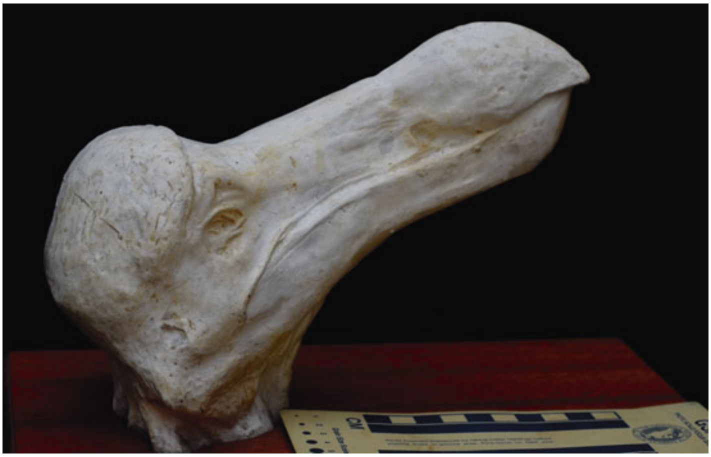

Fig. 2.2 The dodo of Mauritius, which became extinct in the late seventeenth century, is an icon of extinction in modern conservation biology and was also widely cited as a case of human caused extinction from the eighteenth century onwards. In his discussion of the extinction of the dodo in volume two of his *Principles of Geology*, Charles Lyell (1832, footnote on p. 151) writes that ‘the death of a *species* is so remarkable an event in natural history, that it deserves commemoration’. The photograph shows a plaster cast of a dodo head from a mould made before the head’s partial dissection in the 1840s (Photo: Dave Wilkinson)

assumed to be due to repeated global catastrophes, was established by what we would now call Earth Scientists over 50 years before the science of ecology got its name. By the time Geikie was writing this had become well-established scientific ‘fact’ and was seen as a great step forward in our understanding of the history of life on Earth.

However, it would be wrong to classify Cuvier as just a paleontologist or Earth scientist. As Geikie (1897, p. 211) pointed out: ‘Cuvier’s splendid career belongs mainly to the history of biology’; and Ernst Mayr (1982, p. 460) described Cuvier as ‘first and foremost a zoologist’. Aside from his paleontological work – both on extinct vertebrates and the use of fossils in stratigraphy (Rudwick 2005) – Cuvier carried out major work on modern organisms. This work was mainly in comparative anatomy and taxonomy, with perhaps his greatest work being *Régne Animal Distribué d’aprės son Organisation* (‘The animal kingdom arranged according to its organisation’; first edition 1817) a publication which tried to provide a natural classification for all animals and that has been described as no less important that Linnaeus’s *Systema Naturae* (Taquet 2007). Although Cuvier did not really work on ecological questions, other than extinction, his demonstration of natural extinction is clearly important for ecology. In addition, although Cuvier was obviously unusually talented and hard working, his ability to contribute to both state-of-the-art biology and earth science was less unusual in the late eighteenth and early nineteenth centuries than by the standards of the twentieth or twenty-first centuries.

Fig. 2.3 A statue of George Cuvier (1769–1832) situated in Montbéliard where he was born. Now in eastern France, at the time of his birth it was a francophone enclave belonging to the duchy of Württemberg (Rudwick 2005) (Photo: Dave Wilkinson)

2.4 Vignette 3: Charles Lyell

Cuvier's personal extinction coincided with the publication of 'one of the most significant works in the history of the Earth sciences' (Rudwick 1998, p. 3) by Charles Lyell (1797–1875; Fig. 2.4), namely his *Principles of geology* – published in three volumes between 1830 and 1833. The second volume of this (Lyell 1832) is the most 'biological' in content and has been discussed in some detail in several papers in ecology journals for its early discussion of 'ecological' ideas (Wool 2001; Wilkinson 2002; Bueno-Hernández and Llorente-Bousquerts 2006). Indeed I have previously written that a modern subtitle for volume two could be 'Ecology and biogeography, a paleontological perspective' (Wilkinson 2002). The book went through 12 editions during Lyell's life and changed markedly in character as it did so (Rudwick 1998) – here I discuss the 'ecological' content of the first edition (see Wilkinson 2002 for a more detailed discussion).

To a modern reader the word 'Principles' in the title makes it sound like it was intended as an introductory textbook, however the early nineteenth century reader was intended to draw comparisons with Isaac Newton's *Principia* so the word

Fig. 2.4 Charles Lyell (From Judd (1910). Author's collection)

signalled substantial theoretical ambitions on Lyell's part (Rudwick 1998). Many of the ideas were not originated by Lyell – what was largely new was the theoretical approach which he illustrated with a range of existing data and ideas. His key theoretical approach was an extreme version of uniformitarianism which claimed that the causes of geological change observed acting today were completely adequate to explain past changes and *that these causes had always acted at the currently observed rates*. It is the final italicised section of this that was almost unique to Lyell (Gould 1987; Rudwick 1998).

A range of ecological ideas are apparent in volume two of Lyell's Principles (Wilkinson 2002), for example the idea of habitat (called station in the nineteenth century) being distinct from the idea of geographical range (habitation in the terminology of the time). The basic idea of carrying capacity is illustrated in a thought experiment where he suggests that 'if we enclose a park, and stock it with as many deer as herbage will support, we cannot add sheep without lessening the number of deer' (Lyell 1832, p. 142) – this also suggests that he did not understand the concept we now call the ecological niche (Wilkinson 2002). He also realised the potential for disturbance, due to herbivory, to increase plant species richness – an idea that was already widespread at the time he was writing and would be formulated into the Intermediate Disturbance Hypothesis during the 1970s (Wilkinson 1999). In addition he discussed both 'natural' climate-driven (see below) and recent human-caused extinctions, such as the dodo (Fig. 2.2).

One of the oddest ideas in *Principles* – both to modern readers and readers at the time (Gould 1987) – was the suggestion that because species were perfectly adapted to current climatic conditions (this is basically an ecological idea), then if climatic conditions were to return to those of the Mesozoic then the Mesozoic fauna would also return, as they were the correct species for those conditions. So ‘huge iguanodon might reappear in the woods and the ichthyosaur in the sea’ (Lyell 1830, p. 123). Lyell never specified in print by what mechanism he thought the ichthyosaur and iguanodon might reappear, however he told his friends that he thought it was by some unspecified natural processes (Rudwick 1998). This idea is arguably the most extreme version of climatic determinism in the history of ecology or biogeography (Wilkinson 2002).

In the context of both this chapter and this book the most noteworthy point is that Lyell is not discussing biological and geological ideas as separate. The discussion is not interdisciplinary in the modern sense, as Lyell does not appear to see these various ideas as coming from different disciplines (modern day biology and geology). The extent to which one of the key geological documents of the early nineteenth century is full of ‘ecological’ ideas may surprise many modern ecologists.

2.5 Vignette 4: Marie Stopes

Today Marie Stopes (1880–1958; Fig. 2.5) is most widely known as the author of a highly influential sex manual and later as an important campaigner for contraception. However, earlier in her career she was ‘among the leading half-dozen British paleobotanists of her time’ (Chaloner 2005, p. 127). In addition she was also a prolific playwright and poet (Hall 1977). The peak of her paleontological career was between 1903 and 1935 and specifically focused on early flowering plants and the paleobotany of the coal measures (Chaloner 2005). Her most important work focused on the structure and evolutionary relationships of fossil plants, however in this chapter I focus on her more minor contributions to ecology, and in particular her attempts to use paleontological data to understand gymnosperm ecology. Stopes published one paper on straight plant ecology – studying plant succession in a dried up riverbed in southern England (Stopes 1903). In addition she made (in passing!) novel ecological suggestions about the idea of ecological niches in a chapter of a small popular book she wrote on botany (Stopes no date).

The first biologist to use the word niche in an ecological context appears to have been the geneticist Roswell Johnson, who used the term in 1910 in a discussion of the role of geographical isolation in the formation of new species. He never developed the idea and most ecology textbooks name Joseph Grinnell as the originator of the term, which he used in several papers published between 1913 and 1917. He appears to have visualised a niche as an abstract space in the environment, which could be either filled or empty, although he never formally

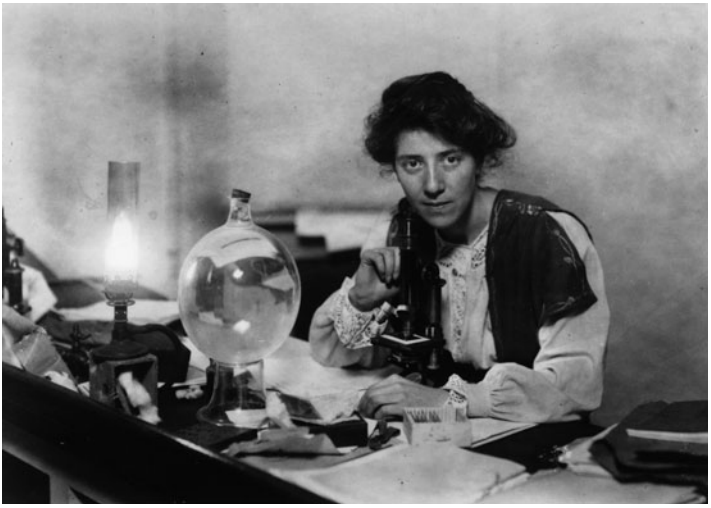

Fig. 2.5 Marie Stopes, age 24, at her microscope. The photograph may have been taken in Munich during her Ph.D. work (Chaloner 2005) (Source: Wikipedia, photo provided by Marie Stopes International for use in publications that further understanding of Dr. Marie Stopes work)

defined it or clearly differentiated it from the concept of habitat (Cox 1980). The first fully worked out niche concept is usually attributed to Charles Elton. In his earlier writings he used the term in a similar way to Grinnell, however in his famous textbook *Animal Ecology* (Elton 1927) he described what has become known as the Eltonian niche. He wrote (Elton 1927, pp. 63–64) that it is 'convenient to have some term to describe the status of an animal in the community, to indicate what it is *doing* and not merely what it looks like' and he suggested the term was niche. On the following page of his book he illustrates this idea with an often-quoted example, which now has a rather quaint period charm to it. 'When an ecologist says, "there goes a badger" he should include in his thoughts some definite idea of the animal's place in the community to which it belongs, just as if he had said, "there goes the vicar"'.

In her short popular book *Botany. The modern study of plants* (Stopes no date, p. 51) Marie Stopes wrote that 'groups of quite dissimilar plants growing together form the communities. . . they correspond to a city among men where there is room for a certain number of tanners and bakers and post men, but where, if the community is to succeed, the types must not all be adapted to the same trade nor exactly to the same environment'. This clearly has much in common with Elton's 'there goes the vicar', although without the use of the term niche. As with Roswell Johnson's first use of niche, she appears not to have realised the importance of the idea and didn't develop it further – or indeed in her case use the technical term 'niche'. But this is clearly the same basic idea that is usually attributed to Elton, but apparently being suggested some years earlier. This makes the date of Stopes' book an interesting question. The standard checklist of her writings (Eaton and

Warnick 1977) suggests 1919. When I previously briefly drew attention to these Eltonian-like ideas I cited this date but suggested it may have been published a few years earlier than that – based on an advertisements at the back of the book (Wilkinson 2005). In fact the book came out as part of a series called ‘The people’s books’ and Peter Bowler (2009) has shown in his account of science popularisation in early twentieth century Britain that Stopes’ volume came out in 1912, with a reprint in 1919. These books were heavily marketed and sold well (Bowler 2009) – and were presumably widely read. So during the first few decades of the twentieth century both Stopes and Elton were, perhaps unsurprisingly, making use of analogies with human society to help explain how an organism fits into its ecological community. In the context of this chapter the interesting thing is we have a paleontologist suggesting what was to become an important idea in ecology – before its traditional invention by an ecologist 15 years later.

Stopes’ short paper on ‘*The “xerophytic” character of the gymnosperms*’ (Stopes 1907) differs from all the work so far described in this chapter in that it applies paleontological data to an ecological problem. She pointed out that most living conifers are xerophytic (drought adapted) and this seemed strange given many live in areas of the world with high rainfall – such as in mountains and at high latitude. She describes the conventional – late nineteenth century – explanation as being due to an evolutionary hangover. Conifers being ‘descended from plants which had grown under conditions demanding special protection, and many of them have retained the ancestral character’ (Stopes 1907, p. 46). She goes on to use fossil evidence to suggest this is wrong, pointing out that when the environments of Tertiary conifers are reconstructed from other plants growing alongside them ‘we find many forms resembling our Maples, Beeches and Magnolias, which do not predispose any excessively xerophytic character in the environment (Stopes 1907, p. 47). As an alternative explanation she then goes on to suggest that the nature of gymnosperm plant anatomy may limit the amount of water that can be transported up to the leaves, and so this means that for large plants in this group water shortage is an unavoidable problem – even in soils which have plenty of available water.

The interesting thing about these arguments, in the context of this book, is that Stopes uses paleontological arguments to falsify a biological theory, and then uses data from modern botany to suggest an explanation that applies to fossils as well as modern plants. So her short paper is a mix of plant anatomy, ecology and paleontology. This mix was neither typical of most papers of the time nor indeed typical of most of Stopes’ own papers. Many later ecologists would argue that she had underestimated the water stress that these trees can be under – because freezing of soil water can have important effects in winter, and this along with the difficulty in growing new leaves from scratch in a limited growing season explains the nature of the leaves of many conifers (Colinvaux 1978). However, Stopes’ early work shows the benefits of combining ecological and paleontological ideas in understanding plant ecology.