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

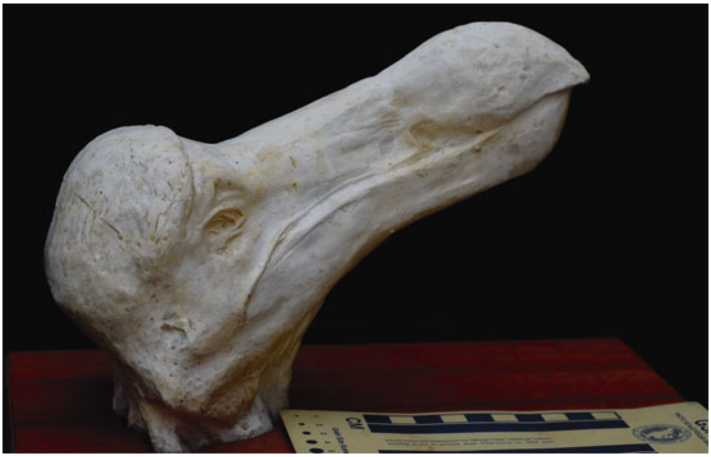

Fig. 2.2 The dodo of Mauritius, which became extinct in the late seventeenth century, is an icon of extinction in modern conservation biology and was also widely cited as a case of human caused extinction from the eighteenth century onwards. In his discussion of the extinction of the dodo in volume two 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'après 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

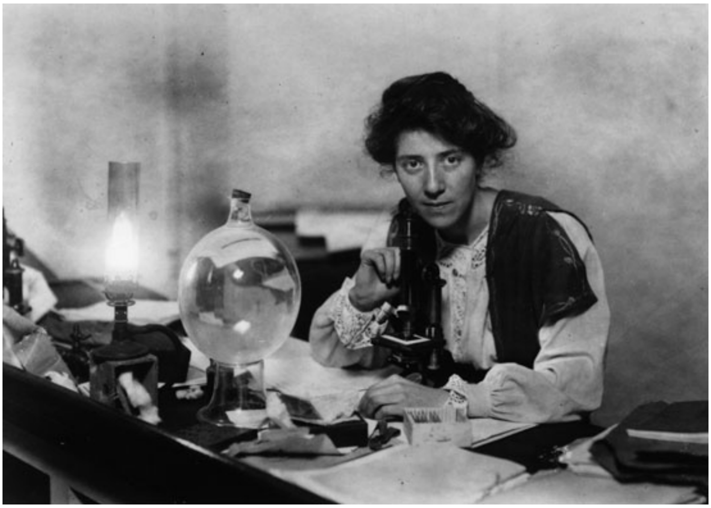

Fig. 2.5 Marie Stopes, age 24, at her microscope. The photograph may have been taken in Munich during her Ph.D. work (Chaloner 2005) (Source: Wikipedia, photo provided by Marie Stopes International for use in publications that further understanding of Dr. Marie Stopes work)

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.

2.6 The Bigger Picture: The Growing Split Between Ecology and Paleontology

All four of my brief historical vignettes show savants (or 'scientist' in the case of Stopes) mixing biology and geology in their attempt to understand the world. In doing so, they address important ecological ideas such as the existence of natural extinction, the role of climate in species distributions in both time and space, and early ideas on the ecological niche.

The rise of the term 'scientist' happened during the nineteenth century and was in part due to the increasingly fragmented nature of science. As science became larger and subdivided into a range of disciplines many perceived the need for a more general term for the practitioners of all these diverse subject areas – leading to William Whewell coining the term 'scientist' at the 1833 meeting of the British Association for the Advancement of Science (Fara 2009). The term 'science' itself was also undergoing change at this time, slowly narrowing to include only what we now call the sciences – rather than being a general term for most types of knowledge. Certainly Whewell himself was concerned that the growing specialisation in science would lead to an unfortunate narrowness with even eminent scientists no longer able to comprehend more than a small fraction of the whole field (Fara 2009). These are concerns that still trouble many philosophers (e.g., Midgley 1989). The vignettes I have chosen to use in this chapter illustrate the fragmenting of this larger picture. From Leonardo to Stopes, these savants studied an increasingly smaller fraction of what we would now call biology and geology.

2.7 The Bigger Picture: Does Earth Systems Science Provide a Model for Modern Savants?

Trying to understand a complex system such as the Earth from the perspective of just a single scientific discipline will most likely not be successful. An acknowledgement of this has led to the rise of 'Earth Systems Science' in the later twentieth century – a term that appears to have been coined at NASA during the 1980s (Wilkinson 2006). In an editorial essay in *Science* the ecologist John Lawton (2001, p. 1965) describes how to address the challenges of understanding the Earth system, and its response to human driven changes, 'we need to study not only the processes which go on in each component (traditionally the realms of oceanography, atmospheric physics, and ecology, to name but three), but also the interactions *between* these components'. He goes on to point out that life (hence ecology) is central to this question, writing, 'James Lovelock's penetrating insights that a planet with abundant life will have an atmosphere shifted into extreme thermodynamic disequilibrium, and that Earth is habitable because of complex linkages and feedbacks between the atmosphere, oceans, land, and biosphere, were major stepping-stones in the emergence of this new science' (Fig. 2.6).

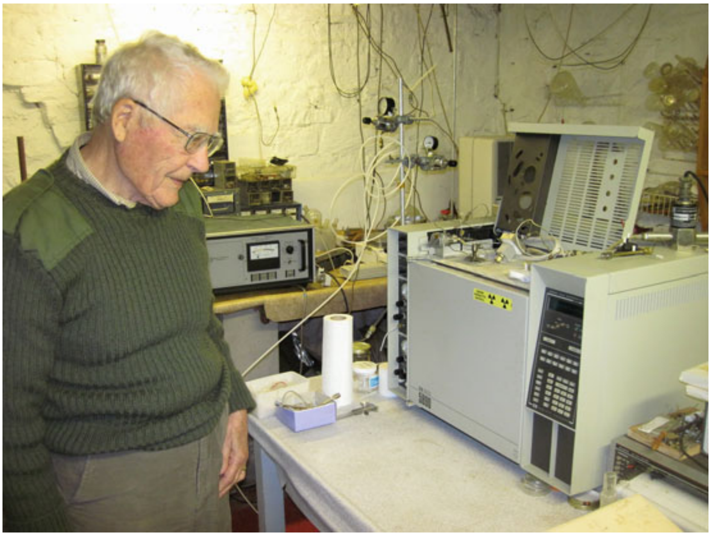

Fig. 2.6 James Lovelock (1919–) photographed in his lab in 2011 with a 1980s HP gas chromatograph – he was an advisor to Hewlett Packard on gas chromatography and used this technique in a number of groundbreaking studies of atmospheric chemistry studying an atmosphere in 'extreme thermodynamic disequilibrium' due to the presence of life. His concept of Gaia stresses the role of life as part of a single-coupled system, from which can emerge the sustained self-regulation of the Earth's climate and chemistry at a habitable state for whatever is the current biota (Lovelock 2003. Photo: Dave Wilkinson)

The approach to Earth systems science taken by some of the best textbooks (e.g., Kump et al. 2010) is reminiscent of the wide range of ideas utilized by Lyell. The key difference is that Lyell was writing before the major scientific disciplines had hardened into the modern discrete entities, while now people have to make a deliberate effort to unite separate disciplines in an attempt to better understand the whole Earth. It is interesting in the context of this historical chapter that several historians with an interest in eighteenth and nineteenth century geology and biology (e.g., Bowler 1992; Oldroyd 1996) were favorably disposed to Lovelock's ideas on Gaia even at a time when much of the scientific establishment was still hostile – seeing in these ideas a return to some of the ways of thinking which they were familiar with from the eighteenth and nineteenth century. Clearly as the other savants described in this chapter illustrate the earth sciences played an often-overlooked role in the early history of ecological ideas.

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