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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

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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 paleoenvironments, 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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Keywords Leonardo da Vinci • Georges Cuvier • Charles Lyell • Marie Stopes • James Lovelock • Ecological niche • Extinction • Gaia

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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Chapter 3
Ecology Needs a Paleontological Perspective

Julien Louys, David M. Wilkinson, and Laura C. Bishop

Abstract General ecological theories have paid scant attention to the information preserved in the fossil record. However, in order for an ecological theory to be truly general, it must hold in any ecosystem at any point in time. Here, we make the case that all modern ecological theories should be tested in geological time. We explore some of the limitations of the fossil record when examined in light of modern ecology. While there are fundamental differences between the way modern ecosystems and fossil ones are studied, we demonstrate that comparisons between the two are not impossible. We present three major research areas where fossil information has been successfully used to inform modern ecological thought; namely community ecology, biogeography and extinction studies. These examples also serve to highlight ecological issues that could not have been conceived purely on the basis of modern data. We advocate a much stronger interaction between modern ecologists and paleontologists in addressing present and future ecological questions.

Keywords Neoecology • Paleoecology • Community ecology • Biogeography • Extinction

3.1 Introduction

A revolution in the study of paleontology occurred during the 1970s, in which paleontology was brought into the fold of modern evolutionary biology (Maynard Smith 1984). Paleontology, as the principle source of observations about how evolution has proceeded, has had a greater input into modern evolutionary theory since then. The field of paleoecology has not had a similar role, despite the recognition that it can

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provide important information for modern ecological theory (Rull 1990, 2010; Beherensmeyer et al. 1992; Jablonski et al. 1996; Allmon and Bottjer 2001; Flessa et al. 2005). This is perhaps surprising as there was a large overlap of interest between many early 'ecologists' and 'earth scientists' at the time when ecology was developing as a discipline (Wilkinson 2012). Ecology, as a named subject, came into existence in the second half of the nineteenth century; however, academic discussion of topics now considered 'ecological' has had a longer history than the term 'ecology'. Indeed many 'ecological' ideas were widely discussed before Haeckel, especially by savants ('scientists' would be anachronistic in this context) who would now tend to be described as primarily geographers or earth scientists (Bowler 1992; Bowler and Morus 2005; Rudwick 2005; Wilkinson 2012). Despite this, temporal concerns did not feature significantly in the early development of the newly named science of ecology. According to Peter Bowler (1992, p. 363); 'There was little attempt at first to study how the ecological balance could shift through time…Most early ecologists simply assumed that the physical environment was stable'. Arguably not that much has changed, as in spite of the growing interest in climate change there are still few paleontological examples in most university level ecology textbooks. This can be best demonstrated by looking at illustrations in such books, which is one approach in determining what a scientist considers important. For example Krebs (2009) is one of the best of the university level ecology text books and 'fossil' organisms hardly feature (either as fossils or reconstructions) in the biota illustrated in the book; the only significant example being the extinctions of the Pleistocene megafauna. One main exception to the lack of fossil-based data in recent ecology textbooks is Colinvaux (1993) who included a whole chapter on paleoecology entitled 'The ecologist's time machine'. This chapter mainly concentrated on Quaternary vegetation history – one of Colinvaux's own research interests.

Based on the way the term is usually applied in the scientific literature, 'paleoecology' can be defined broadly as the study of ancient ecosystems (which carries with it the implication that many important aspects of modern ecology, for example molecular ecology, rarely feature in paleoecological studies). Modern paleoecological studies tend to be more structural than processual. Although some would advocate that "paleoecology" should be distinguished from "environmental reconstruction" (Rull 1990, 2010), we consider both aspects in this paper, although concentrating on paleoecology *sensu stricto*. The most widely applied aim of paleoecology is the reconstruction of past environments (both biotic and abiotic), habitats and ecosystems, in the context of characterising the background for a particular phase or event in the evolutionary past – such as the habitats in which upright bipedal locomotion evolved in hominins (e.g., Elton 2008) or reconstructing past climates often with the intention of informing ideas about climate change and its environmental effects (e.g., Wehrli et al. 2010). In such studies the organisms often stand as proxies for some aspect of the environment that interests the researchers (e.g., extent of forest, summer temperature, or evapotranspiration), rather than as interesting research topics in their own right.

The second, *and more neglected*, aim of paleoecology is the exploration of ecological theory over geological time (Louys et al. 2009b). That is, studying ecological processes described for modern ecosystems over thousands to millions of years, as well as the development of ecological theories explaining processes operating over that timescale. Often referred to as ‘evolutionary paleoecology’ (Valentine 1974; Wing et al. 1992; Allmon and Bottjer 2001), this aim is of critical importance to the study of modern ecology. A truly general ecological theory should hold up over geological time, and one of the few ways to test this is through examination of the fossil record. Examining ecological concepts over geological time has the potential to reveal new patterns not discernable or present in today’s ecosystems, which makes this aspect of paleoecology even more important. It also allows us to explore events not evident today within an ecological framework. The most obvious of these, and the one which has arguably received the most attention in the paleoecological literature, are mass extinction events (more on this below). But other areas, such as the ecological study of disharmonious (or non-analogous) ecosystems may have important implications for the study of modern ecosystems; and indeed the existence of non-analogue vegetation communities in the Quaternary fossil record has affected the way many ecologists view plant communities in modern ecology (Huntley 1996). The contribution of paleoecology to conservation biology is another important function of paleoecology, however this will not be covered here as it has already been widely discussed in the ecological literature (e.g., Archer et al. 1991; Huntley 1991; Birks 1996; Willis et al. 2010; Vegas-Villarrúbia et al. 2011 and the many contributions in this volume). Likewise, temporal predictions derived from ecological theories that could be tested using phylogenetic approaches, such as phylogenetic community ecology, phylogenetic trait reconstruction, molecular dating and phylogeography are not covered herein (but see Webb et al. 2002; Kraft et al. 2007 for examples).

In this chapter we outline some of the potential difficulties associated with trying to use fossil data to test ecological theories and argue that these problems are often surmountable. We necessarily focus on the terrestrial fossil record, as this is our primary area of expertise, however we acknowledge that marine paleoecologists have been at the forefront of the battle to successfully integrate paleontology with ecology since at least the 1970s (e.g., Valentine 1974). We highlight some of the, so far limited, areas where paleontological data has already affected the way ecologists think and suggest additional areas where such data may be crucial in developing ecological science. In brief our key message is that *it is time fossil data played a much larger role in mainstream ecological thinking*. The obverse of this is also true; that ecological theory has a role to play in our study of past ecosystems – however we do not consider this aspect further in this chapter.

3.2 Paleontology: What Can and Can’t We Tell from the Fossil Record?

The fossil record represents an imperfect history of the past. Not everything that once lived will be preserved in the geological record. The preservational issues related to taphonomy (defined below) and paleocommunities are dealt with later in this chapter. In addition to preservational biases that act at the level of the community, physical elements of individual organisms, such as soft body parts are preserved only in exceptional cases. Important features such as muscles, fur, feathers, etc., usually have to be inferred from the preserved hard parts of organisms. Likewise, metabolic characteristics of organisms cannot be directly determined in most cases and are instead inferred. The behavioural characteristics of extinct fossil species are even trickier; in some cases they can be inferred through judicious application of taxonomic and/or anatomical uniformatarianism (e.g., Louys et al. 2009a). This approach can only be confidently applied to extinct taxa that have close extant relatives, and as such its use is rather restricted in deep time. Another potential approach uses trace fossils (called ichnofossils), defined as geological records of past activity or behaviour, such as burrows and feeding signs. These can give insights into past behaviours, including locomotion or predation (e.g., Scott et al. 2004; Skovsted et al. 2007). Taxonomic uniformatarianism has itself a certain (some would say a large) measure of uncertainty. The advent of ancient DNA (aDNA) studies has opened up the possibility of extracting ancient genetic information from extinct species (e.g., Green et al. 2006). This type of data can be used in a number of ecological fields, for example phylogeography. Again, however, the preservation window for aDNA is likely to be quite short and largely restricted to areas of colder latitude and exceptional preservation (Willerslev and Cooper 2005). This means that conventional fossils will continue to play a key role in testing ecological ideas over geological time.

3.2.1 Taphonomy

Taphonomy is the study of the transition of living organisms to the geological record, or from the biosphere to the lithosphere (Lyman 1994). It is the aspect of paleontology that examines all stages affecting preservation and the nature of the material available for paleontological investigation – the death, decay, disarticulation, dispersal, burial, diagenesis (chemical alteration), exposure and recovery of organismal traces in the geological record. Taphonomy deals with aspects of the fossil record critical for the accuracy of paleoecological reconstruction, such as why certain materials are preserved in the fossil record and others are not. Vertebrate faunal remains have been a particular focus for research into taphonomy, partially because these bioclasts are susceptible to peri- and post-mortem damage (and indeed destruction) by potential accumulating agents (Behrensmeyer and Hill 1980; Lyman 1994), along with potentially very important collecting biases. For example collecting bias has lead to an over representation of large-bodied carnivorous dinosaurs being recorded from some North African sites (McGowan and Dyke 2009).

Often, processes in the present are used to examine the factors that may introduce bias in fossil assemblages. In a classical example from the early nineteenth century, for example, William Buckland showed that fossil bones in a cave in northern England were the product of the denning behaviour of extinct hyenas (Rudwick 2005). In a similar vein, the pioneering work of Efremov (1940), Brain (1969), Behrensmeyer (1975), Lyman et al. (1992) and others has been instrumental in distinguishing the causes whereby certain skeletal elements are differentially damaged or deleted from the fossil record and relating this to ecological or environmental factors.

Taphonomic analysis is critical in identifying the biases that may have altered or transformed a particular fossil assemblage relative to the life assemblage from which it was derived; these can affect taxonomic representation or skeletal part abundances, amongst other factors. Thus taphonomic study can help determine whether and how certain assemblages can be compared both with each other, and with the modern biological record.

Another important variable in fossil assemblages is time averaging. Most fossil assemblages accumulated over unknown, and often considerable, lengths of time. Unless the duration of their deposition is taken into account, fossils accumulated over decades to tens of thousands of years or more, during which time environmental variables may have varied considerably, can be anachronistically considered together (e.g., O'Regan and Reynolds 2009). Indeed, Flessa and colleagues (Flessa et al. 1993) have shown that within a single molluscan surface assemblage, shells being incorporated in a bed can have ages of hundreds of years apart.

Furthermore, due to time averaging, individuals within a particular paleocommunity will very rarely have interacted with each other, or been subjected to the same environmental and regional events, even if their respective burials are only separated by a few years. Time averaging is thus particularly worthy of consideration when examining fossil assemblages relative to the biological present. The terrestrial fossil record is highly variable, however, and some assemblages that represent relatively brief or catastrophic events are available as a 'snapshot' of contemporaneous community ecology and structure (e.g., the Laetoli footprint tuffs; Ditchfield and Harrison 2011). Such assemblages are therefore particularly valuable for testing ecological theories in the geological past.

Despite limitations, the conditions and processes affecting the preservation of organisms can often be delimited and categorised (Wing et al. 1992). Assemblages that have undergone similar or identical taphonomic processes (isotaphonomy) can be identified and compared. This facilitates and provides confidence for comparisons between fossil assemblages spanning geographical or temporal boundaries. Furthermore, certain types of community characterisations appear to be fairly resistant to taphonomic change, for example rank-order abundance of dominant forms (Wing et al. 1995). Some fossil communities have been shown to be directly comparable to modern ones under certain taphonomic conditions, for example those recovered from some cave deposits (Hadly 1999). Taphonomic processes can make the comparison of fossil and modern data more difficult but these problems are not insuperable when the appropriate techniques are applied.

3.3 Community and Paleocommunity Ecology

Even amongst neoecologists, the definition of what constitutes an ecological community varies. Most definitions emphasise a collection of taxonomic units in a given place over a given amount of time (e.g. 'An assemblage of species populations that occur together in space and time' Begon et al. 2006, p. 469). Space, time and taxonomic dimensions represent three different scales over which we would argue most biological questions span (Fig. 3.1; see also Bennington and Aronson 2012). Definitions of community by neoecologists vary over the strength of community members' interactions, and range from emphasising strong interactions (e.g., the definitions by Clements (1916) and Elton (1927)), to those suggesting a weak or no real interaction (e.g., Gleason 1926; Hubbell 2001). Other definitions tend to emphasise the importance of environment on community membership (e.g., Emlen 1977; Ricklefs 1990). Clearly the definition of community depends on the questions being asked by ecologists and the data available to them. More importantly, it depends on questions of scale, and most if not all neoecological definitions of community emphasise space and taxonomic identity during a contemporaneous or very short period of time (often constrained by the 3–4 years of a typical Ph.D. study).

The use of neoecologists' definitions of community is problematic for paleoecologists, as individuals (as represented by their fossil remains) found within a single assemblage can rarely be demonstrated to have had direct or even indirect interaction. Rare examples where we may have a snapshot of a once living community include some waterlogged plant communities (e.g., Falcon-Lang et al. 2001) patches of sea floor preserved below microbial mats (e.g., Meyer and Milson 2001), or more recently vegetational and animal assemblages preserved beneath an ashfall tuff (e.g., Miocene forest – Jacobs and Winkler 1992; Jacobs 2002; Kingston et al. 2002). However such situations are very rare. Paleoecologists generally surmount this problem by defining paleocommunities using a measure of (statistical) similarity between assemblages. For example, Bambach and Bennington (1996) define a paleocommunity as a collection of local paleocommunities that are not statistically significantly different from one another. In turn, they define a local paleocommunity as the "assemblage collectible from a single bed at one outcrop" (Bambach and Bennington 1996, p. 125). This is an approach similar to that used by many modern plant ecologists when they are attempting to compare plant communities at different locations – if the species mix at the two sites is similar enough, they are classified as the same community (e.g., Rodwell 1991). Other paleocommunity definitions (summarised in Miller 2001) also emphasise issues of scale, and are generally hierarchical in nature (see Fig. 3.1).

Because the definitions of community used by paleoecologists and neoecologists differ over issues of scale, datasets from both fields are rarely immediately comparable (Bennington et al. 2009). An important exception is studies involving coral reef communities, where there are directly observable relationships between fossil and modern faunas (e.g., Pandolfi and Jackson 2006). Despite this, paleoecologists work under the assumption that fossil communities reflect real ecological entities, and accurately provide an indication of the ecosystem of the geological period under examination. This assumption would seem to be borne out by the often high degree of fidelity between environmental reconstructions made on the basis of communities and other paleoecological proxies such as stable isotope geochemistry, sedimentology and geomorphology (e.g., Louys and Meijaard 2010).

One way in which paleoecologists compensate for the vagaries of the fossil record is by using binary models; i.e. presence/absence of particular taxa versus

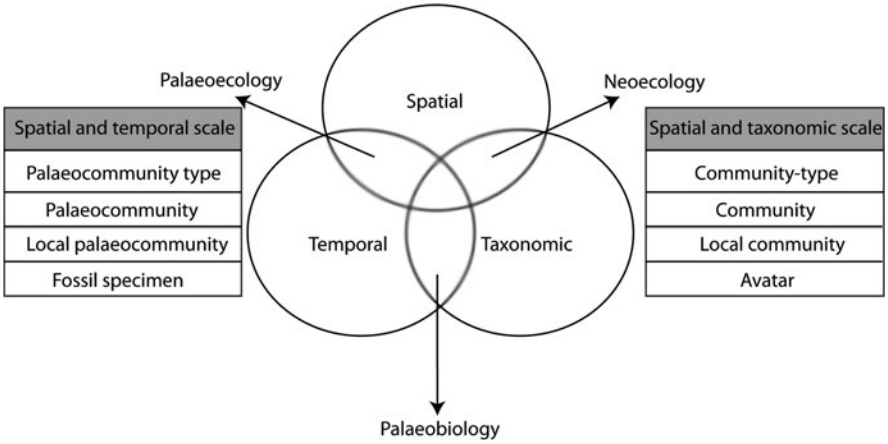

Fig. 3.1 A conceptual representation of the three scales over which biological communities can be defined and interact. Neoecological definitions of community largely span spatial and taxonomic scales, while paleontological definitions largely cover spatial and temporal scales. In the intersection of the dimensions, communities can be defined in a hierarchical fashion: in this figure we have shown the hierarchical definition of Bambach and Bennington (1996; 'avatar' refers to individuals from a species that directly participate in the dynamics of the community). The 'fuzzy' lines in the Venn diagram represent the less than clear-cut intersections between these three dimensions

their proportional abundance. Moreover, outside the recent geological past (i.e., the Quaternary) many paleontological analyses are carried out at higher taxonomic levels. This is because recording the presence of a given species in the fossil record is more difficult than just documenting the presence of its genus or family. These higher taxa may be made up of many species, and so are more likely to have been sampled by the fossil record. In addition, the presence or absence of higher taxa can be less ambiguous as there is likely to be more agreement amongst paleontologists in assigning a specimen to a genus than to a species (Sherratt and Wilkinson 2009). This reliance on higher taxa may not be as problematic for using fossil data to test ecological ideas as it appears at first. It has been well established in conservation biology that in many cases there is a strong correlation between species richness and higher taxon richness (e.g., Gaston and Williams 1993; Williams and Gaston 1994), a relationship which is even seen in at least one microbial group, in Quaternary fossil data as well as modern data sets (Wilkinson and Davis 2000). So patterns identified for higher taxa in the fossil record are likely to be highly relevant to the species level patterns usually studied by ecologists.

Defining modern communities in terms that can be applied to the fossil record (such as higher taxa) is one way that modern and fossil communities can be compared. However, in rare cases species interactions can be directly observed (for example, preserved frog gut contents in a Lagerstätten deposit (Wuttke and Poschmann 2010)) or at least confidently inferred (i.e. breakage or damage characteristic of particular predators), and these can be used to characterise fossil communities in terms of modern variables. One striking example of the use of such data was the creation of highly resolved fossil food webs for two Cambrian marine deposits (Dunne et al. 2008). The construction of such webs facilitated comparisons of modern and fossil communities, and allowed Dunne and colleagues to test whether a theoretical food web model (the "niche model", Williams and Martinez 2000) fitted empirical data from both modern and fossil communities. In addition to taxonomic characterisations, paleocommunities can be compared to each other and to modern communities by defining them according to ecological variables (e.g., the number of species found within a particular guild or functional group). A representative set of communities defined in this way will form a multidimensional space (ecospace), with each variable representing a different dimension in this space. The position of any given community relative to another in this space provides an indication of how similar these two communities are (Rodríguez 2004). The most common application of this principle can be seen in paleosynecological reconstructions, where the positions of communities from modern habitats, nature reserves and/or biomes are compared to fossil ones. The position of modern communities that are unique to certain habitats types (e.g., grasslands) can be used to define that habitat type, thereby allowing classification of fossil sites (e.g., Reed 1997, 1998; Mendoza et al. 2005; Louys and Meijaard 2010).

In addition, this methodology can also be used to examine changes in community structure through time (e.g., Rodríguez 2004, 2006; Louys 2011), which should be of particular interest to modern ecologists. For example, a paradigm in community ecology that can only be addressed fully by an examination of the fossil record is that of communities' stasis through time. In other words, do communities have a propensity to change in structure over time (concomitant with, for example, climate change), or do they remain largely constant? The fossil record preserves many instances of disharmonious associations of species. (The term "disharmonious" was first coined by Semken (1974) to describe the association of species which today are allopatric but which were sympatric in the geological past.) In the terrestrial fossil record, disharmonious assemblages are recognised largely from Quaternary deposits, as their identification requires modern representatives to facilitate unambiguous species level identifications. Amongst mammals, disharmonious assemblages have been described for most major landmasses, including North America (Graham and Grimm 1990), Australia (Lundelius 1983; Price and Sobbe 2005) and Southeast Asia (Medway 1972; 1977). Disharmonious assemblages have also been recorded for insects (Zinovjev 2005) and plants (Huntley 1990). They have been used to argue for an individualistic or 'Gleasonian' model of community construction (Graham and Grimm 1990), as different species are inferred to respond independently to changes in biotic or abiotic conditions.

Arguably the longest running ecological field experiment is the Park Grass experiment at Rothamstead in southern England that started in 1856 and is still running (Silvertown et al. 2006) (Fig. 3.2). Therefore any analysis of ideas in community ecology which need testing on a timescale of over 150 years needs to make use of historical or fossil data. To take a final example, one theory of community ecology that has been receiving much attention is neutral theory

Fig. 3.2 The temporal limits of experimental ecology? The Park Grass Experiment at Rothermstead, in southern England, is probably the oldest ecological experiment in existence – although initially started to address agricultural questions. Since 1856 different fertilizer treatments have been applied to plots in a large hay meadow, providing key insights into many aspects of plant ecology (Silvertown et al. 2006). The photograph shows the junction between two plots with a more flower rich plot to the *left*, which has received no fertilizer treatments during the course of the experiment, contrasting with the less colourful heavily fertilized plot to the *right*. Any test of ecological ideas over a longer time scale that Park Grass must rely on historical or paleoecological data. Photo: Dave Wilkinson

(Hubbell 2001). In Hubbell's model, changes in communities through time will take place through stochastic eliminations and replacements, and communities should show a predictable measure of drift. While the disharmonious assemblages of the Quaternary present qualitative support for this idea, quantitative testing of this theory requires an examination of species' distributions not just in space, but also through time (DiMichele et al. 2004). Incorporating fossil data into such analyses suggests community stasis may be greater than that predicted by neutral theory for terrestrial communities (McGill et al. 2005), although this was not found for marine communities (Olszewski and Erwin 2004). The multidisciplinary nature of these studies serve as excellent examples of the level of integration possible between modern and fossil ecology.

3.4 Biogeography and Patterns of Species Distributions

Another ecological question that can only be answered with fossil data relates to the age of biogeographical patterns observed today. To illustrate this we deal with one example here, namely how old is the latitudinal gradient of species richness?

(This question is dealt with only briefly here; for a fuller treatment see Sherratt and Wilkinson (2009)).

There is good evidence from at least some groups that the latitudinal disparity in species richness observed today has had a long geological history (Renema et al. 2008). Angiosperms, for example, seem to show a higher diversity in the tropics compared to high latitudes, a pattern which has become more pronounced over the past few million years (Crame 2001). However one complicating factor in examining this question in the geological record is the extent of what we might consider the tropics. For example, evidence from a number of sources suggests that the world of the Cretaceous (ca 145.5–65.5 million years ago) was much warmer than today's, with forests extending to within 1,000 km of the poles (Beerling 2007). This, along with many similar examples, indicates that the extent of tropical climates have fluctuated in size (and location) over geological time. Furthermore a tendency over recent geological time for higher latitudes to become colder relative to the tropics may have precipitated increased extinctions away from the tropics (e.g., birds; Hawkins et al. 2007), contributing further to the disparity in species richness between high and low latitudes. In contrast to extinction-based hypotheses, the richness of the tropics may have been caused by higher rates of speciation at lower latitudes. Evidence from a number of groups, for example corals, foraminifera and some mammals, suggests that the average age of genera and families decreases with decreasing paleolatitude (Mittelbach et al. 2007). Accordingly geologically younger taxa are found in the tropics, and these show a greater rate of speciation. This theory is further supported by evidence from other fossils, such as bivalves, where it was found that during the last 11 million years 117 genera first appeared in the tropics, compared to only 46 outside the tropics (Jablonski et al. 2006).

The richness of the tropics has also been suggested to result from the persistence of glacial refugia during periods of extensive polar ice sheet cover, a hypothesis based on observations from modern bird distributions (Haffer 1969). Haffer's model posited that during ice ages the Amazon basin would have been characterised by dry conditions, with forests contracting to a series of isolated patches separated by open country. This, he argued, caused forest birds (and by implication other forest adapted species) to become isolated, leading to allopatric speciation and hence causing high species richness in this area. This hypothesis has largely been rejected on the basis of an analysis of fossil pollen data from Amazonian lake sediments where forest was likely to have been absent during full glacial conditions (Colinvaux et al. 1996; Colinvaux and De Oliveira 2000). The pollen data showed that tropical rainforest had occupied the area for the last 170,000 years; there was no evidence of a dry climate dominated by non-forest vegetation, assumed as necessary for allopatric speciation. We do note, however, that this conclusion is as yet based on a limited set of data, and in another part of the tropics (Southeast Asia) multiple sources of evidence suggest that, at least there, habitats alternated between drier and rain forest conditions concomitant with the glacial/interglacial cycles of the Pleistocene (Louys and Meijaard 2010). Similarly, Kingston et al. (2007) found a correlation between paleoenvironment changes in the Kenyan rift valley and astronomical forcing factors. Haffer's hypothesis clearly requires more testing.

The latitudinal gradient in species richness is clearly an important area of ecology (Willig et al. 2003) and, as the discussion above illustrates, paleontological data are crucial to unravelling the mechanisms responsible for it.

3.5 Extinction

One obvious influence of geological research on ecological ideas is the concept of extinction (Wilkinson 2012). The example of extinction is interesting for several reasons. Extinction is a topic which still features prominently in ecology both from the applied point of view in conservation biology (see other chapters in this volume), as well as for its role in explaining patterns in biodiversity – such as its use in the classic MacArthur and Wilson (1967) explanation for island species richness patterns, or the potential role of differential extinction in explaining latitudinal patterns in species richness (as discussed above). Moreover, it is difficult to envisage how the conclusion that natural extinctions can happen could come from anything but fossil data. Modern ecological data would be inadequate to establish the fact of natural extinction in a world heavily modified by humans, where it is nearly impossible to attribute any extinction to entirely non-human causes unambiguously. Fossil data have allowed attempts to quantify natural background rates of extinctions and thus facilitated the identification of apparent mass extinction events (Barnosky et al. 2011).

The idea of mass extinctions is also ecologically interesting – as is the aftermath of such events in the context of global change – and can only be established from fossil data. The interpretation of such events is still debated, but Gould has, somewhat controversially, argued that during the twentieth century it has become apparent that ‘mass extinctions are more *frequent*, more *rapid*, more *extensive in impact*, and more *qualitatively different in effect*’ (Gould 1985, p. 8, author’s italics). Such mass extinctions have both evolutionary and ecological ramifications, producing ‘major restructuring of the biosphere wherein some successful groups are eliminated, allowing previously minor groups to expand and diversify’ (Raup 1994, p. 6,758). In addition, they clearly provide a useful way of studying the ecological response to major changes in the Earths biodiversity and biomass (e.g., Beerling et al. 2001) or the response to major disturbances or unusual geological events (e.g., Louys 2007, 2011).

3.6 Final Comments

In 1981 Andrew Hill asked the question: “Why study paleoecology?” (Hill 1981). We have described here several examples of ecological processes that would be neither predictable nor expected from neoecological observations. Consider two final examples; only fossil evidence, not modern ecology, can tell us that for most of the history of life on Earth *all ecology was microbial* – so any ecological theory which is intended to be broadly applicable should be tested in microbial systems as well as the macrobial ones more characteristic of modern ecological research (Wilkinson 2006). At the largest of spatial and temporal scales the Gaia hypothesis (Lovelock 1979, 2003) suggests a role for life in stabilizing environmental conditions on Earth over geological time spans. This is an idea that has recently attracted interest in the ecological literature – indeed a decade ago one of us published one of the first research papers on Gaia written from an ecological perspective (Wilkinson 1999; see also Free and Barton 2007). Gaia and long-term stability can only be fully tested with geological data. General theories of ecology must take into consideration the fossil record, either explicitly in the formulation of the theory, or else be presented in such a way that will allow testing from the fossil record. This testing will increasingly use data from the numerous paleontology databases that currently exist, allowing the occurrences of fossil species to be plotted both in space and time (Louys 2012). Any ecological theory must be tested in geological time. As far as (paleo) ecology is concerned, the present is not always the key to the past; but the past might well be a better key to the future.

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Chapter 4
Reconciling Scale in Paleontological and Neontological Data: Dimensions of Time, Space, and Taxonomy

J. Bret Bennington and Myla F.J. Aronson

Abstract Conserving biodiversity in the face of expanding human degradation of ecosystems is facilitated by understanding the natural state of communities prior to the impact of anthropogenic disruptions. Reconstructing communities and ecosystems as they existed in the past requires data from the fossil record on their species composition, richness, and abundance. Fossil data are potentially different from data collected from living communities in their spatial, temporal, and taxonomic scales and these differences must be understood so that accurate comparisons can be made between past and present states of living communities. Fifty-four long-term ecological studies of a wide range of taxon groups (mammals, invertebrates, plants, corals) and habitat types (marine, terrestrial, freshwater) were surveyed from the published ecological literature to determine the range of spatial, temporal and taxonomic scales at which data are commonly collected in ecological research. Long-term ecological studies encompass spatial scales from 50 m^2 to 100,000 km^2 and temporal scales from 5 to 100 years. Most studies resolve taxa to the species level and count individuals, although plant and coral studies sometimes quantify species by percent cover. All taxon groups and habitat types were studied across a wide range of spatial and temporal scales. Whether or not data from fossils can be collected and analysed at scales comparable to data from living communities depends on the type of organism, as well as the taphonomic circumstances of preservation, accumulation and deposition. Marine invertebrates can be sampled at comparable spatial and taxonomic scales to living invertebrates, but time averaging degrades the temporal resolution of the fossil deposits. Vertebrate fossils provide data at comparable taxonomic scales with some reduction in spatial and temporal resolution relative to live data. Plant fossils and pollen are capable of being sampled at temporal resolutions comparable to modern

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ecological studies, but pollen data are prone to spatial averaging and have much poorer taxonomic resolution than censuses of living communities. It is important to be mindful of the limitations that scale mismatches produce in the ability to use fossil data to resolve ecological events and to compare the details of ecological composition and structure between the present and the past.

Keywords Spatial scale • Temporal resolution • Taxonomic resolution • Conservation paleobiology • Taphonomy • Conservation biology

4.1 Introduction

The principle focus of conservation biology is the preservation of biological diversity in the face of anthropogenic disturbance (Soulé 1985). Because species exist in nature as members of biological communities and ecosystems, conservation biology is an inherently ecological discipline and species conservation is most effectively accomplished through the preservation or restoration of habitats and multihabitat ecosystems. Kidwell (2009) observes that ecological assessment and habitat restoration at regional scales rely on answers to three basic questions; what is it like now; is it stable; and what is natural? Answering the last two of these three questions requires pristine reference habitats, historical records, and paleontological data. Unfortunately, the remaining regions of habitat left in the world that have not been moderately to severely impacted by human activities are diminishing at a rapid rate (Burnham 2001) and it can be argued that with anthropogenic climate change and alterations in the global nitrogen cycle, there are no ecosystems on earth that have escaped being impacted by humans (Vitousek et al. 1997). This complicates the mission of conservation biology because there may be no remaining examples of a particular disturbed ecosystem in its former unperturbed state. Furthermore, all ecosystems exhibit some direction and rate of natural change through time and in the absence of examples of extant pristine habitat or long-range historical data on ecological parameters it is difficult to assess the current rate and direction of ecosystem changes relative to natural or human influence (Hadly and Barnosky 2009; Magurran et al. 2010; Roche et al. 2011). An additional problem is the “shifting baseline syndrome” (Jackson 1997) whereby ecologists assess the present state of an ecosystem using historical data as a baseline when, in fact, the historical data derived from the ecosystem have been influenced by anthropogenic factors.

If a perturbed modern ecosystem has no modern unperturbed analogue and if insufficient or inadequate historical data exist to document pre-disturbance structure and assess pre-disturbance rates and direction of natural changes, then the only recourse is to look into the past using paleontological data to analyze and reconstruct the state of the ecosystem prior to significant human impact. This is a main focus of conservation paleobiology, a relatively new discipline that can be defined as the "application of paleontological data and analyses to present-day problems related to conservation biology and human-induced environmental change" (Foote and Miller 2007, p. 322). Paleontological data can also provide a means of assessing how much an accepted historical baseline has shifted due to early anthropogenic influence (e.g., Greenstein et al. 1998).

The sedimentary and fossil record encompasses a wide range of information that is relevant to understanding how and why ecosystems have changed in response to anthropogenic disturbances. Such data include information on past community composition, community structure, biomass, ecosystem productivity, organism growth rates and abundance, temperature, salinity, water chemistry, trace metal and trace element abundances, global ice volume, eustatic sea level, and climate (for examples, see Jones et al. 1989; Dunbar and Cole 1993; Hadly 1999; Kowalewski et al. 2000; Markich et al. 2002; Surge et al. 2003; Dettman et al. 2004; Brown et al. 2005; Carré et al. 2005; Edinger et al. 2007; Kidwell 2007; 2009; Terry 2007; Ferguson 2008; Kowalewski 2009; Tomasovych and Kidwell 2009). Because conservation efforts are usually based on maintaining species diversity within functional ecosystems, in this chapter we focus primarily on making comparisons between present and past ecosystems using data on community composition (changes in the identity of species present in the community and their relative abundances), community structure (changes in species richness and species dominance or evenness), and changes in absolute abundance/biomass of species within habitats (Allmon 2009; Kidwell 2009).

Using fossils to extend the modern ecological record into the past would ideally allow one to compare community composition, community structure, and biomass from before and after the onset of anthropogenic disturbance to gain a better understanding of how an ecosystem has been disrupted, to determine the drivers of change, and to assess what steps might be taken to restore the habitat and component species. However, there are critical issues of scale that arise when attempting to draw ecological inferences from paleontological data. As a cautionary example, in the mid-1970s there emerged a research program in paleontology focused on identifying and studying examples of ecological succession in the fossil record (Bretsky and Bretsky 1975; Walker and Alberstadt 1975; Walker and Parker 1976). Eventually, the authors of these studies and others realized that many, if not most, of the published examples of succession in the fossil record were not directly analogous to succession as defined by ecologists. The problem was that the sequence of changes in species composition and abundance observed in fossil assemblages occurred over thousands of years or longer as a result of allochthonous changes in environmental and depositional conditions (Miller III 1986; Walker and Diehl 1986). This is in contrast to succession observed by ecologists on a time scale of years to decades primarily occurring as a result of autochthonous changes in the community brought on by the colonizing species themselves (Connell and Slatyer 1977; Prach and Walker 2011). In most of the paleontological studies, successional changes due to ecological interactions over years and decades were condensed into single fossiliferous horizons and could not be resolved at the temporal scale of the fossil record. The taphonomic circumstances of the formation of these fossil deposits resulted in the time-averaging of the organic remains, reducing the temporal resolution of the fossil samples below that of the time scale of most ecological studies. In these cases, the temporal scale of the fossil data did not match the temporal scale of the ecological process of interest to the researchers. Such mismatches in scale are an inherent problem in efforts to include paleontological data in ecological analyses.

4.1.1 Scale in Paleontological and Ecological Data

The problem with comparing data collected from extant ecosystems to data collected from fossil deposits is that these data commonly encompass different scales (Bennington et al. 2009). In comparing data collected by ecologists from living communities (the living assemblage) to data collected by paleontologists from accumulations of organic remains (the death assemblage), mismatches in scale can potentially occur because of the various taphonomic filters that affect individual organisms as their remains accumulate and become incorporated into a fossil deposit (note: we use the term "fossil" to indicate any dead organic remains, encompassing both Holocene "subfossil" remains and Pleistocene and older fossil remains, *sensu* Kowalewski 2009, p. 3). Decay, as well as biostratinomic (depositional) and diagenetic (post-burial) processes exclude some taxa from the fossil record, disarticulate, sort, and degrade organic remains, transport and space-average remains from different places, and time-average remains by mixing together individuals that lived at different times (for detailed summaries of these processes, see Western 1980; Kidwell and Bosence 1991; Behrensmeyer et al. 2000). Furthermore, deposits of fossils are often discontinuously exposed at the surface with limited areal accessibility for sampling. Taken together, taphonomic and depositional processes affect the temporal, spatial, and taxonomic scale of the data that can be extracted from samples of fossil remains and it is these three aspects of scale that must be considered when comparing and combining fossil and modern ecological data (Fig. 4.1).

4.1.1.1 Spatial Scale

Imagine taking a census of tree species in a forest by counting all of the taxa encountered in a series of 100 m^2 plots. Each plot is a sample unit (also called a statistical observation) and the sample units are combined to generate the statistical sample estimating the taxonomic composition of the forest. There are several levels of spatial scale inherent in this hypothetical study. The total area of the study can be thought of as the region encompassed by the most distant plots. The total area defines the global population that is being sampled in the study. The individual sample units also have a size, in this case the area of the individual plots (100 m^2). Finally, the sample units (plots) are arrayed within the total area of the study at

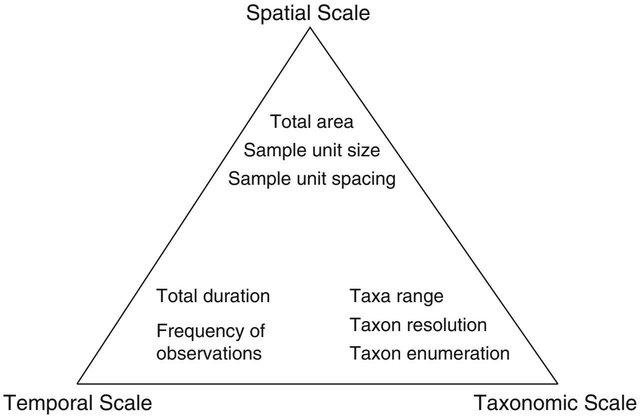

Fig. 4.1 Diagram illustrating the three main elements of scale mismatch and the data entities within each element that might differ between ecological and paleontological studies

some scale and pattern of spacing. This could range from random spacing with varying distances between sample units to an ordered spacing with a set distance between sample units.

The reasons why it is important to reconcile spatial scale in comparing or combining data from the fossil record with ecological data (or when comparing or combining data from multiple studies in general) arise from the patchy distribution of organisms within most ecological communities and from the tendency for habitats to be arrayed along environmental gradients with diffuse boundaries. Consider the ideal case of an ecological community in which all organisms are randomly distributed throughout a physically consistent habitat with well-defined boundaries (Fig. 4.2a). In this case, sampling would be largely scale independent; any distribution and spacing of sample units would yield equivalent data subject only to random variation due to sample size. It would also not matter where within the bounds of the habitat the sample units were collected or whether the entire areal range of the community was sampled, because the data obtained on species richness, species abundance, and individual density would be comparable across all areas of the habitat. However, if the distribution of organisms is patchy (Fig. 4.2b), then the size and spacing of sample units could affect the estimates of ecological parameters if the sample units fail to encompass a representative range of patches (Hairston 1959; Bennington and Rutherford 1999; Buzas 1968). If the boundaries of the community are diffuse (Fig. 4.2c), or if there are gradients in habitat parameters across the areal extent of the community (Fig. 4.2d), then the distribution of and spatial scale at which sample units are collected will affect the statistical estimates of ecological parameters and ecological metrics such as evenness that are derived from richness and abundance (Schreiber and Brauns 2010). Given that many communities are patchy and distributed along environmental gradients (Gaston 2000; Small and McCarthy 2002) and that patchiness and gradients are also found in time-averaged fossil assemblages (Warme 1971;

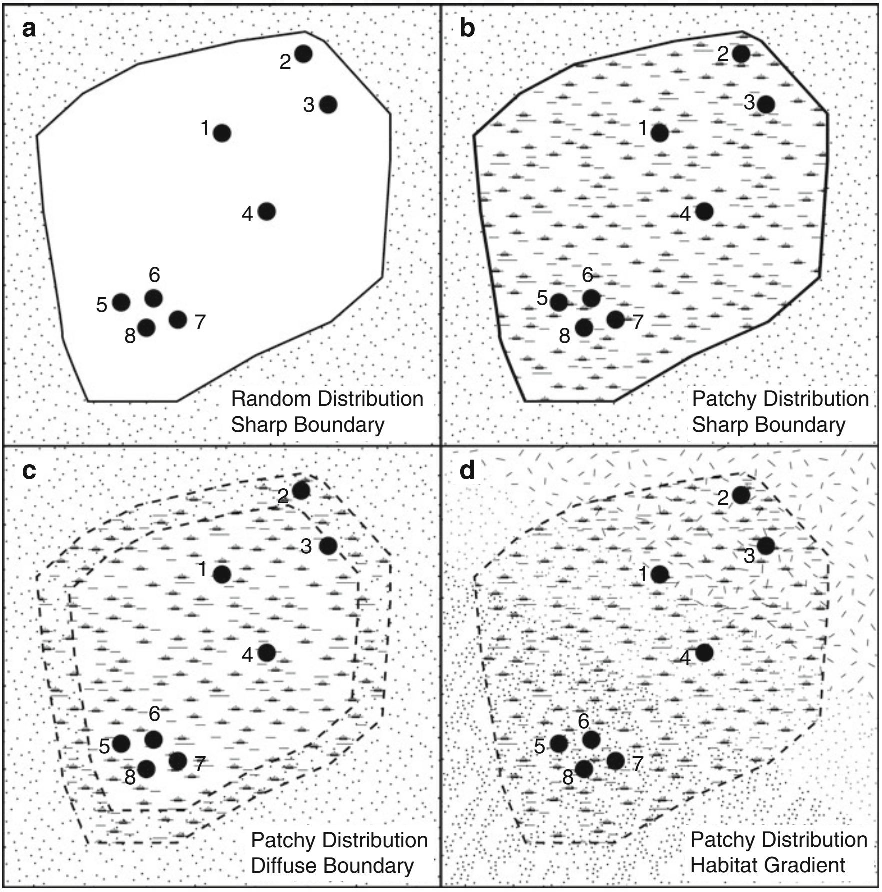

Fig. 4.2 Cartoon showing eight hypothetical sample units distributed in two groupings (SUs 1–4 and SUs 5–8) within a habitat under different conditions of patchiness, habitat boundary, and environmental gradients. (**a**) The ideal situation from the standpoint of sampling. Organisms are randomly distributed throughout a habitat with well-defined boundaries. Spacing and location of sample units is not critical as both sample unit groups will yield equivalent data; (**b**) Organisms are distributed in patches within a habitat with well-defined boundaries (for an example, see Schreiber and Brauns 2010). Sample unit groups will yield equivalent data provided that the spacing and size of sample units encompasses a representative number of different patches; (**c**) Organisms are distributed in patches within a habitat with diffuse boundaries (see Gehlhausen et al. 2000). Sample unit groups will diverge if some sample units are peripheral; (**d**) Organisms are distributed in patches within a habitat encompassing one or more environmental gradients (see Aronson and Galatowitsch 2008). In this case, different spatial distributions of sample units can yield different estimates of species richness and abundance

Miller 1988; Bennington 2003) it is more likely than not that if the spatial scales over which paleontological data are collected diverge significantly from the spatial scales sampled in an ecological analysis of a living community, then the data derived from the fossil record will produce estimates of past ecological parameters for that community that are biased to an unknown degree. For example, space-averaging of fossil data resulting from increasing the area of collection and or number of sampling units tends to increase estimates of species richness (Rosenzweig 1998; Hadly and Maurer 2001), especially if space-averaging results in the mixing of individuals from adjacent communities (Le Fur et al. 2011).

4.1.1.2 Temporal Scale

Now, imagine repeating the census of tree taxa described above every year for 10 years. The total duration of the study provides a measure of the state of the forest averaged over 10 years. The frequency of observations provides an annual resolution to the observed state of the forest and defines the lower limit of our ability to resolve time in the data. One reason why temporal scale is important to quantify for ecological data is because communities are temporally variable. Ecological parameters such as species richness, species composition, and species abundance often fluctuate from year to year due to cycles of reproduction, disease, climate, and the impact of extreme weather events. Repeated sampling of a community through time allows ecologists to obtain a long-term average measure of community composition and to look for trends that might indicate non-cyclical changes outside of the normal temporal variation in ecological parameters. The significance of ecological change observed over time in data collected from a living community might be assessed by looking to fossil data to provide a measure of the temporal variability that existed in a community in the past. However, if the temporal resolution of the data obtained from fossils is significantly less than the temporal resolution of the ecological data they are being compared to, then it will be difficult to assess how variable a community was in the past relative to the present. This is particularly a problem for detecting disturbance events that create short-lived changes in the composition of the living community that may not be preserved in the time-averaged fossil assemblage, complicating the inference of such events as anthropogenic in cause because they are absent from the pre-human fossil assemblage (e.g., recent outbreaks of crown-of-thorns starfish; see Walbran et al. 1989 and response by Pandolfi 1992).

If the goal is to compare the present composition of the community to a previous natural baseline, then some amount of time averaging in the fossil data is acceptable because it averages together normal short-term variation and provides a more complete estimate of total species richness (Hadly 1999). However, too much time averaging introduces the risk of including fossils produced prior to the establishment of the current community (Fig. 4.3), resulting in estimates of past ecological parameters for living communities that are contaminated to an unknown degree by individuals from outside of the community of interest. In the case of both the living and death assemblages, time averaging tends to increase species richness. This has been demonstrated in “live–dead” comparison studies of benthic invertebrates in which the death assemblage richness greatly exceeds the richness in any single census of the live community (Kidwell 2002).

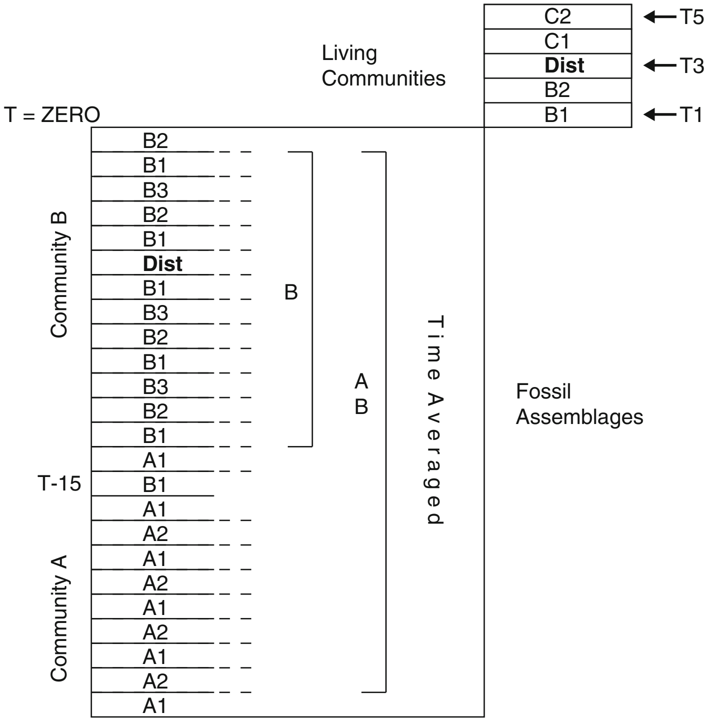

Fig. 4.3 Schematic diagram illustrating differences in temporal scale between living communities and fossil assemblages. A, B, C represent different communities; 1, 2, 3 represent alternate temporal states of the same community. Levels represent equivalent time slices populated by different communities and community states. Living communities can be sampled through time at discrete time slices (e.g. T1, T3, T5). Fossil assemblages might also be sampled at similarly discrete time slices, but more likely the individual remains from multiple time slices have been averaged together through time. The more time incorporated into a time-averaged fossil assemblage, the more likely that the assemblage will mix together individuals from different communities. Short-lived disturbances (**Dist**) observed in the living community may not be recorded in the time-averaged death assemblage if there is insufficient temporal resolution

4.1.1.3 Taxonomic Scale

There are also taxonomic scales inherent in the data collected for our hypothetical study. The range of taxa in the study is defined by the subset of all taxa identified, enumerated, and included in the data. For a census of tree taxa we are deliberately excluding herbaceous and other woody plants such as ferns, forbs, and shrubs, not to mention all of the other forest organisms that live among the trees. Taxon resolution refers to the taxonomic level at which the data are being collected. Are the trees being identified and counted by subspecies, species, genus, or some higher taxonomic category? Another possibility is that individual trees are being assigned to different functional or morphological categories, for example canopy vs. understory, and censused based on those categories. Finally, there is the question of how each taxon is being enumerated. One might be counting individual tree trunks or measuring the area of the crown on each tree. This last aspect of scale is particularly important to be aware of because in many cases organisms are disarticulated in the process of being fossilized so that estimates of the number or density of individuals represented by fossils might be enumerated differently than their living counterparts. This is particularly problematic for counting individuals that have multi-element skeletons in fossil assemblages with disarticulated and broken remains. Data that are collected at one level of taxonomic resolution can be pooled at higher taxonomic levels (for example species abundances could be summed by genus) if there is a scale mismatch between two data sets, however, this usually results in a loss of information.

4.2 Methods

To explore the range of scales inherent in long-term ecological studies, we have quantified and described how ecologists have collected long-term ecological data from a variety of habitats and taxa at the spatial, temporal and taxonomic scales described above. By reviewing the literature on long-term ecological studies we hope to provide a better understanding of how paleontological and ecological data sets can be harmonized to understand changes in biodiversity and ecosystems through time. We chose to focus on long-term ecological studies because of their emphasis on quantifying ecological parameters over an extended period of time to assess changes in communities. Keyword searches were conducted in Academic Search Premier, Google Scholar and PubMed and by examining references in review articles on long-term ecological studies. Search terms used included: "long-term vegetation", "long-term community vegetation", "Long-term mammal community", "long-term marine invertebrate community", "long-term marine invertebrate community mollusc", "long-term coral reef", "long-term community mollusc", "long-term forest change", and "long-term bird community". Most of the search results produced studies of the types of ecological communities that are commonly represented in both the paleontological and ecological literature: coral reefs, benthic invertebrates (marine and freshwater), terrestrial vertebrates (mammals and birds), and terrestrial plant communities (including wetlands). We applied several criteria for choosing the studies used in this review. First, we chose published studies between 1990 and 2011 that examined community patterns over time (5–100 years) at the same individual or multiple sites (no studies based on chronosequences were used). Second, if a search found multiple papers from the same long-term site or sites, the most recent published paper was used. Third, only observational studies were selected, no long-term experimental or continually manipulated studies were examined. However, successional studies were examined if there was no further management or manipulation beyond the original clearing of biota. For each study, we identified variables at the spatial, temporal and taxonomic scales (Fig. 4.1, Table 4.1). In most studies, these variables were clearly defined. However, some variables could not be ascertained in

Table 4.1 Spatial, temporal and taxonomic scale parameters for 54 long-term ecological studies on invertebrate, plant, mammal and bird communities. NS = not stated, Individ = Individual counts

Reference	Habitat	Spatial scale			Temporal scale		Taxonomic scale		
		Total area (km^2)	SU size (m^2)	SU distance	Total duration (yr)	Frequency	Taxa range	Taxon resolution	Enumeration
Addessi (1994)	Intertidal	0.00005	0.2–0.8	1 m	20	2	Marine inverts	Species	Individ
Aronson and Galatowitsch (2008)	Wetlands	69,825	$2{,}000 - 9 \times 10^4$	1–285 km	19	5	Plants	Species	% cover
Augustin et al. (1999)	Coral reef	0.38	5	10 m	24	2	Mollusca	Species	Presence
Balčiauskas (2005)	Multiple	45	125 m transect	5 m	10	3	Small mammals	Species	Individ
Bates et al. (2007)	Western forests	0.018	0.2	NS	13	5	Herbaceous plants	Species	% cover
Bennie et al. (2006)	Grassland	75,710	50	NS	52	2	Plants	Species	% cover
Berumen and Pratchett (2006)	Coral reef	0.00005	10 m transect	NS	24	3	Corals + fish	Species	Individ/% cover
Billet et al. (2001)	Abyssal plain	4,300	6×10^7	None	10	38	Marine inverts	Species	Individ
Bragg and Shelton (2011)	Temperate forest	0.324	1,012	NS	72	11	Trees	Species	Individ
Chapman et al. (2010)	Rainforest	795	Line transects	NS	27	3	Primates	Species	Individ
Chapman et al. (2006)	Temperate forest	17.36	400	124 m	69	2	Trees	Species	Individ
Connell et al. (1997)	Coral reef	1.5	1	800 m	30	16	Corals + macroalgae	Species	Coverage area
Czerepko (2008)	Wetlands	1,300	166	1–10 km	40	3	Plants	Species	% cover
Danby et al. (2011)	Tundra	0.81	0.1	1.5–3 m	42	2	Plants	Species	Individ
Daufresne et al. (2003)	Stream	1.5	7	13 km	29	3.5	Fresh inverts	Genus – family	Individ
Drayton and Primack (1996)	Temperate forest	4	Entire area	None	100	2	Plants	Species	Presence
Elliott et al. (1999)	Temperate forest	21.8	800	200 m	20	2	Trees	Species	Individ
Elmendorf and Harrison (2011)	Grassland	5,484	1	8 m	10	20	Plants	Species	Presence
Feeley et al. (2011)	Rainforest	0.5	1×10^4	Continuous	25	6	Woody plants	Species	Individ
Ilg et al. (2008)	Grassland	0.9	0.1	NS	6	4	Terr. inverts	Species	Individ
Ilg et al. (2008)	Grassland	0.9	100	NS	6	4	Plants	Species	% cover

Kardol et al. (2010)	Temperate forest	0.98	810	NS	40	8	Trees	Species	Individ
Klinger (2006)	Rainforest	350	5,000	125–375 m	5	14	Small mammals	Species	Individ
Laurance et al. (2008)	Rainforest	900	1.5×10^4–5.9×10^6	0.5–5 km	20	2	Nocturnal mammals	Species	Individ
Lawrence et al. (2010)	Stream	40	0.093	NS	20	20	Fresh inverts	Species	Individ
Lwanga et al. (2000)	Rainforest	766	250	NS	23	3	Trees	Species	Individ
Martin (2007)	Riparian	0.22	25 m transect	NS	21	42	Birds	Species	Individ
Martin and Bailey (1999)	Temperate forest	6.07	100	NS	20	2	Trees	Species	Individ
McClanahan et al. (2008)	Coral reef	1,500	10 m transect	NS	15	15	Corals	Genus	Colony size
McEwan and Muller (2006)	Temperate forest	0.52	400	NS	20	2	Trees	Species	Individ
Meiners (2007)	Temperate forest	0.05	1	NS	48	33	Plants	Species	% cover
Moritz et al. (2008)	Multiple	6,356	Transects	NS	92	2	Small mammals	Species	Individ
Munson et al. (2011)	Desert	0.0008	1 m transect	NS	82	9	Plants	Species	Individ
Østbye et al. (2007)	Wetlands	1	Entire area	NA	18	6	Birds	Species	Individ
Pellerin et al. (2008)	Wetlands	50	25	0.5–1 km	34	2	Plants	Species	% cover
Rahlao et al. (2008)	Grassland	0.72	600	NS	68	2	Plants	Species	% cover
Rogers et al. (2008)	Temperate forest	58,695	1	Random	55	2	Plants	Species	Presence
Rooney et al. (2004)	Temperate forest	17,144	400	1–208 km	50	2	Plants	Species	Individ/presence
Sagarin et al. (1999)	Intertidal	0.0001	0.84	1 m	65	2	Marine inverts	Species	Individ
Samonil and Vrska (2008)	Temperate forest	60	25	NS	24	2	Plants	Species	% cover
Schiel et al. (2004)	Intertidal	4	1	3 m	18	94	Marine inverts	Species	Individ/% cover
Schleyer et al. (2008)	Coral reef	0.00007	1	Continuous	13	13	Corals	Genus	% cover
Shenbrot et al. (2010)	Desert	200	1×10^4	400 m–5 km	16	32	Rodents	Species	Individ
Soloman et al. (2010)	Lakes	2,000	0.25	2 m	80	2	Gastropods	Species	Individ
Stearns and Likens (2002)	Boreal forest	0.08	Point quarter	12–12 m	48	4	Trees	Species	Density

(continued)

Table 4.1 (continued)

Reference	Habitat	Spatial scale			Temporal scale		Taxonomic scale		
		Total area (km^2)	SU size (m^2)	SU distance	Total duration (yr)	Frequency	Taxa range	Taxon resolution	Enumeration
Stouffer et al. (2006)	Wetland	0.245	1×10^4–2.1×10^7	NS	22	104	Birds	Species	Individ
Stroh et al. (2008)	Wetland	800	50–150	10 m	15	3	Plants	Species	% cover
Thibault et al. (2010)	Desert	0.2	2,500	NS	28	336	Mammals	Species	Individ
Thibault et al. (2010)	Desert	0.2	0.5	NS	20	40	Plants	Species	Individ
Van der Meij et al. (2009)	Coral reef	1,350	None	NA	70	2	Mollusca	Species	Individ
Vincke et al. (2010)	Steppe	0.25	2,500	Continuous	20	3	Woody plants	Species	Individ
Visser and Sasser (1995)	Temperate forest	0.02	5,000	Continuous	10	4	Trees	Species	Individ
von Oheimb and Brunet (2007)	Temperate forest	0.332	16	50–100 m	67	4	Plants	Species	% cover
Woods (2000)	Temperate forest	25	800	Random	32	4	Woody plants	Species	Individ

some studies and in some cases we used maps within the paper to generate total area encompassed by the study (defined as the region encompassed by the most distant sample plots or sample sites) and sample spacing (range of distances between sample plots or sample sites). If there were no maps within the papers (or map scales were omitted), we used information from reference papers or Google Earth to calculate area and distance. Additionally, if there were differences in sampling design between time periods, we reported the sampling design of the most recent time period. A total of 54 studies are included in this analysis representing a wide variety of taxonomic groups and habitat types (Table 4.1). Studies were categorized by habitat type (coral reef, desert, forest, freshwater aquatic, grassland, marine muddy bottom, marine rocky bottom, rainforest, and wetlands) and taxon group (birds, corals, freshwater invertebrates, mammals, marine invertebrates, terrestrial invertebrates, plants and trees) and analyzed by category.

4.3 Results

The spatial and temporal scales encompassed by the 54 long-term ecological studies identified in our search are summarized in Fig. 4.4 (studies classified by habitat type) and in Fig. 4.5 (studies classified by taxon group). Total duration of studies ranged from 6 to 100 years with most studies occurring over a decadal to multi-decadal scale. The total area encompassed by individual studies was highly variable, ranging from 50 m^2 to 100,000 km^2. There is no apparent segregation by habitat type or taxon group in the area–duration plots, however mammal and plant studies include the largest areas and longest durations, but also include examples of more moderate size and duration. The spatial resolution (sample unit area) and temporal resolution of the studies are plotted by habitat type and taxon group in Fig. 4.6. Again, most habitats and taxa show a wide range of both spatial and temporal resolution. Temporal resolution is a function of both the duration of the study and the frequency at which the living community was sampled. Most studies have temporal resolutions of from 1 to 20 years (annual to decadal sampling). A few studies were conducted over longer time scales from 60 to 100 years. These usually involved an episode of resampling to repeat a former study from early in the twentieth century (e.g., Drayton and Primack 1996; Sagarin et al. 1999; Moritz et al. 2008; Rahlao et al. 2008; Van der Meij et al. 2009). The distance between sampling units (SU Distance, Table 4.1) was not reported in 41% of the studies examined and in an additional 14% of studies sample units were either continuous or not employed (i.e., the entire area was sampled).

A summary of taxonomic scale parameters across the studies we surveyed is shown in Fig. 4.7. In the vast majority of studies organisms were identified to the species level whenever possible, although in some cases taxa were classified at the genus or higher taxonomic level when species identification was impossible or impractical. In a majority of studies organisms were enumerated by counting

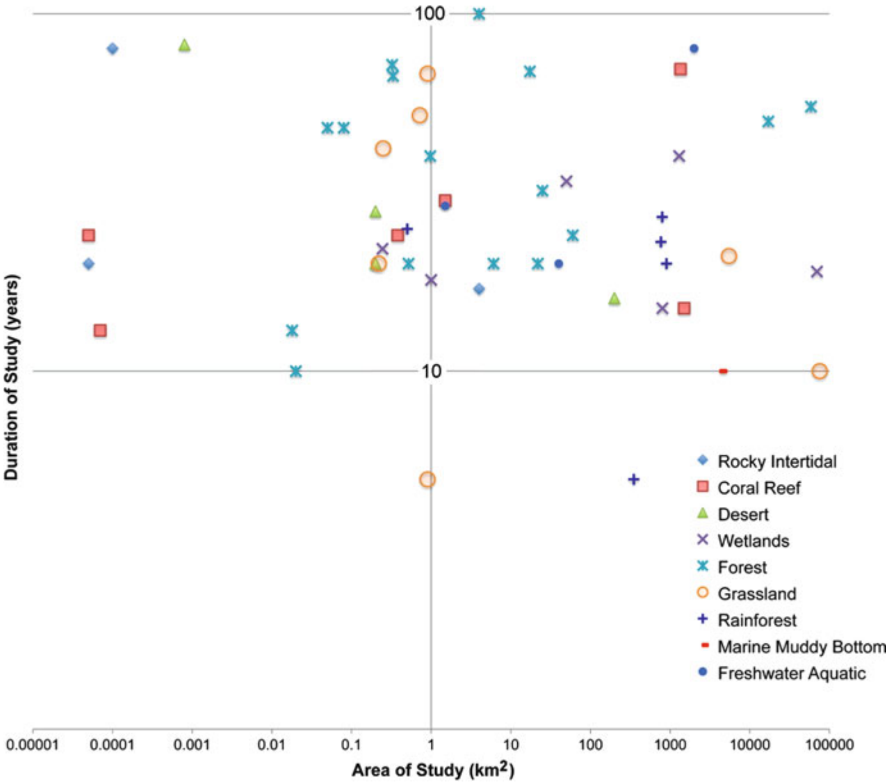

Fig. 4.4 Spatial and temporal scale in 54 long-term ecological studies plotted by habitat type occupied by the community investigated in each study

individuals to obtain species abundance distributions from sample units. In many studies involving corals or plants, taxa were quantified by percent cover, density, or colony size.

4.4 Discussion

Having surveyed and described the spatial, temporal, and taxonomic scales at which ecologists study long-term changes in communities, we can now consider under what circumstances these scales can be matched or approached using data from fossils. Here we discuss the potential for harmonizing scale between living assemblages and death assemblages by major taxonomic group (invertebrates, vertebrates, and plants) and consider examples of how palaeontologists have collected and used fossil data from different habitats to quantify the ecology of

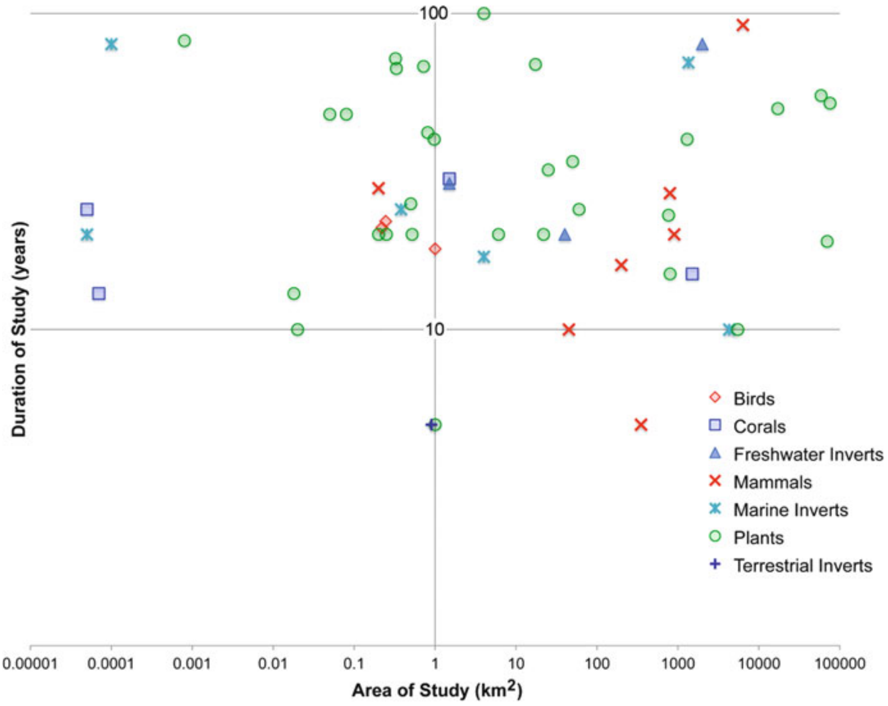

Fig. 4.5 Spatial and temporal scale in 54 long-term ecological studies plotted by taxon group investigated in each study

the recent past. Most ecological studies focus on a subset of related taxa within a habitat. Additionally, different types of organisms vary in their modes of fossil preservation, preservation potential, and susceptibility to different taphonomic filters. Because the goal of conservation paleobiology is to understand the composition and structure of extant ecosystems prior to human disturbance and to determine how modern ecosystems will likely respond to climate change, fossil data from the Late Pleistocene through the Holocene is of primary relevance.

4.4.1 Invertebrates

Given their dominance in modern marine ecosystems and their economic importance, it is not surprising that many ecological studies focus on the coral and molluscan components of marine ecosystems. Aquatic environments, both marine and freshwater, such as bays, continental shelves, carbonate reefs, lakes, and ponds are usually sites of sedimentary deposition over short-term geologic time (these depositional environments may or may not be incorporated into the long-term

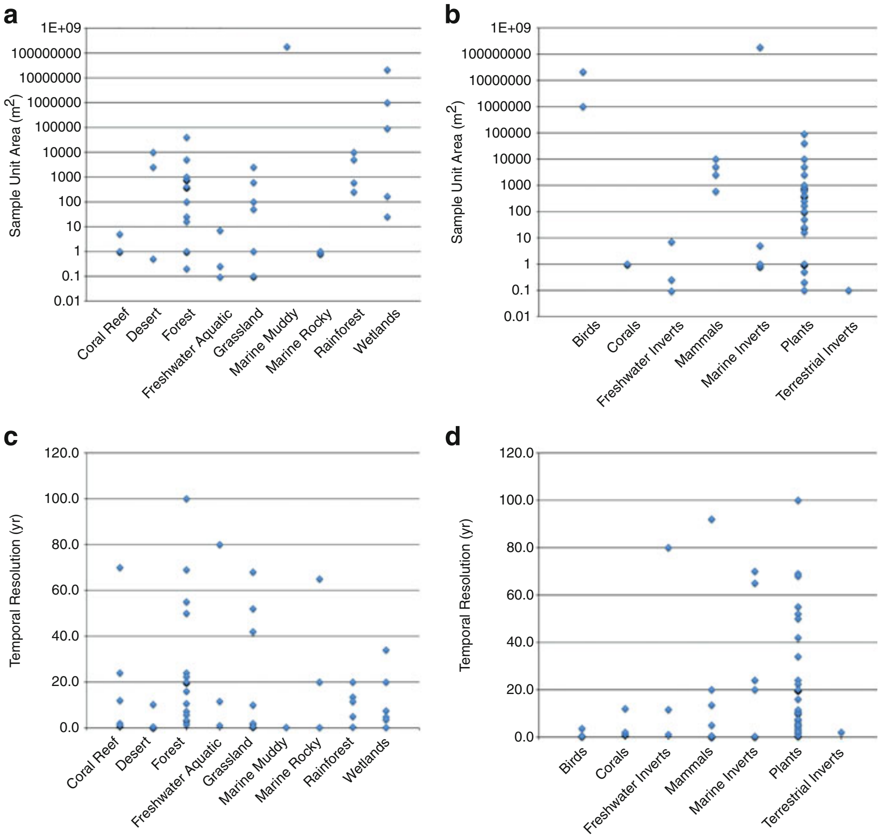

Fig. 4.6 Sample unit size and temporal resolution of 54 long-term ecological studies plotted by habitat type and taxon group investigated in each study. (**a**) Area of sample units used to collect data plotted by habitat type; (**b**) Area of sample units used to collect data plotted by taxon group; (**c**) Temporal resolution of sampling in each study plotted by habitat type; (**d**) Temporal resolution of sampling in each study plotted by taxon group. Studies where sample unit area was not specified or could not be determined from other references are omitted from (**a**) and (**c**)

geologic record, depending on the circumstances of regional tectonics, but they typically accumulate and retain sediments and fossils for thousands to hundreds of thousands of years). As such, aquatic ecosystems have the potential to accumulate fossil remains with the same spatial distribution as the living community, providing perhaps the best opportunity of any set of environments for replicating the spatial scale of sampling of the living community when sampling the death assemblage. Indeed, in studies of benthic invertebrates such as molluscs it is often the case that fossil remains are collected along with the living biota (Kidwell 2009), providing an opportunity to sample the recent past along with the present at the exact same spatial scales. There is a growing body of research describing the detailed taphonomy of marine shelly deposits and the degree of fidelity in species composition,

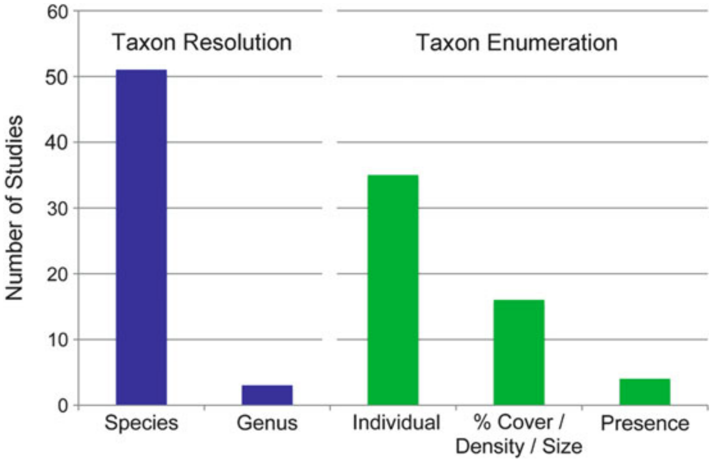

Fig. 4.7 Summary of taxonomic scale parameters across 54 long-term ecological studies

species richness, and abundance between the living community and the death assemblage (Kidwell 2002, 2008). These studies demonstrate that dead shells in open shelf environments record reliable information about the living community from which they derive. In fact, Kidwell (2007, 2009) argues that significant mismatches between the living community and the near surface death assemblage indicate that the living community has been significantly impacted by human activities such as pollution, anthropogenic eutrophication, bottom trawling and dredging, and increased sediment runoff.

In the case of reefs constructed by framework-building corals, which colonise and grow on the remains of previous generations of coral, a detailed record of the coral and associated invertebrate community can be sampled in outcrops or by coring down through the reef at equivalent spatial scales to the living community. In some cases, using these methods, measures of percent cover of both the living and death assemblages are possible. A number of researchers have used the Holocene fossil record of coral reefs to establish a natural baseline for interpreting the ecological status of modern reef communities. For example Aronson and Precht (1997), Aronson et al. (2002), and Greenstein et al. (1998) demonstrate that coral reefs in the Caribbean region are currently undergoing radical shifts in community structure and species dominance that have no preserved analogues in the Pleistocene and Holocene fossil record. In contrast, using similar methods, researchers studying the Holocene history of the Great Barrier Reef have shown no apparent historical change in coral community structure in spite of documented increases in sediment and nutrient influx accompanying European settlement (Perry et al. 2008; Roche et al. 2011).

At the temporal scale, using the invertebrate paleontological record to reconstruct communities is complicated by taphonomy and time-averaging. Fossil shells and coral can be dated using radiocarbon and amino-acid racemization techniques.

This allows both the age and the approximate temporal resolution of fossil assemblages to be determined. The amount of time-averaging in marine fossil deposits depends primarily on the rate of sedimentary deposition and frequency of physical reworking of shells which varies among different environments (Kidwell and Bosence 1991). Measurements of the taphonomic half-life (the time it takes for half of the shells being input from the surface to become permanently buried) from different Holocene shallow-water marine environments show that typical deposits of mollusc shells mix together remains across an average of 90–550 years, depending on the environment, with some shells thousands of years older than others in the same deposit (Meldahl et al. 1997). Clearly, marine fossil assemblages record time at resolutions far longer than those of any ecological study.

Near-surface fossil remains, which have not yet been buried away from the taphonomically active surface environment, are dominated by recently added skeletal material (Kidwell 2002) and preserve a higher resolution record of the recent past. For example, Ferguson and Miller (2007) found that a major change in species dominance in the living benthic mollusc community that occurred over two decades in a carbonate lagoon in St. Croix was preserved in the near-surface death assemblage. However, it is not certain that this change in species abundance will carry through into the longer-term time-averaged fossil assemblage, making it difficult to ascertain for certain whether or not the current shift in species dominance is a result of anthropogenic forcing or is a natural event that has occurred previously in the history of the reef. Similarly, the assumption that recent episodic outbreaks on Indo–Pacific reefs of the crown-of-thorns starfish *Acanthaster* are a result of overfishing of the starfish's molluscan predators has been called into question by the discovery of accumulations of *Acanthaster* skeletal elements in core samples from earlier in the Holocene, suggesting that such outbreaks are part of the natural baseline of the reef community (Walbran et al. 1989). Pandolfi (1992) counters that the temporal resolution and taphonomic circumstances of the fossil *Acanthaster* deposits are poorly constrained, making it impossible to determine whether or not they were produced by population explosions comparable to the modern outbreaks. Again, unless the temporal resolution of the fossil deposit can be determined, it is risky to assume that an event that occurred in ecological time has been recorded in a time-averaged fossil deposit.

Taxonomically, there is little difference in the ability to identify species and enumerate colonies and individuals between living shelled invertebrates such as corals and molluscs and their fossil remains. Because most molluscs have either univalve or bivalve shells it is not difficult to reliably transform counts of valves to counts of whole individuals using the Minimum Number of Individuals (MNI) method (Gilinsky and Bennington 1994) or by simply dividing the number of specimens by the number of valves for each species. However, it is almost impossible to precisely count numbers of individuals for invertebrates such as echinoderms that have complex multielement skeletons, making it difficult to accurately estimate individual abundances or biomass from disarticulated fossil accumulations for these species.

4.4.2 Vertebrates

In spite of the fact that rich accumulations of vertebrate remains are relatively rare in the long-term fossil record, vertebrate fossils, particularly mammals (but also reptiles, amphibians and birds, e.g., Worthy 1997; Steadman 2003), have proven to be very useful for reconstructing communities in the Pleistocene and Holocene. Concentrations of vertebrate remains are often found in caves and rock crevasses where they are left by mammalian and avian carnivores depositing kills and pellets. Remains can also be accumulated in caves by wood rats and porcupines, or through non-biological means such as pitfall traps (Hadly 1999; Schmitt et al. 2002; Hadly and Barnosky 2009; Faith 2011). Bogs, ponds, and swamps also commonly trap and preserve vertebrate remains (e.g. Worthy 1997; Laub 2003).

Vertebrate remains sampled from caves, crevasses, and middens can be compared to remains obtained from modern pellets and scat, as well as to the living fauna to check for biases in the fossil sample. Vertebrate-rich terrestrial deposits occur in a wide range of upland environments distinct from lowland fluvial and alluvial settings, providing information about a wide variety of ecosystems that are less commonly represented in the fossil record. Because terrestrial vertebrate accumulations are distributed sporadically throughout the regions in which they occur, it is difficult to control the locations and spatial scale over which death assemblages are collected. However, sampled localities do provide reliable local censuses of vertebrate diversity and abundance because of the relatively local ranges of the various species of carnivores and wood rats that often act as collection agents (Hadly 1999).

The temporal resolution of Pleistocene to Holocene vertebrate deposits can be assessed by dating multiple specimens within the same layers. In pellets and wood rat middens, organic material associated with the bone accumulations and in the bone can be dated to provide confident chronologies of deposits (Hadly and Barnosky 2009; Jackson et al. 2009). This also allows for temporal correlations to be made between localities, potentially expanding the spatial scale of the data. Individual wood rat middens, for example, represent decades of accumulation (Jackson et al. 2009), providing small samples of vertebrate remains with short temporal resolutions that can be combined to provide a longer-term record. Typical resolutions reported for cave deposits range from hundreds to thousands of years, depending on the age and particular depositional circumstances of the layer (Hadly 1999; Pazonyi 2004).

Taxonomic resolution in the vertebrate fossil record is to the species level in most cases and individual abundances are usually estimated from disarticulated remains using the MNI method (Gilinsky and Bennington 1994). Accurate taxonomic identification of the species represented in these remains is facilitated by the presence of individually unique tooth and skeletal elements and, in certain cases, by the analysis of DNA from bone. There is a bias in cave deposits toward the preservation of small animal species, but they are also good proxies for monitoring ecological stability and health. Small animals provide larger numbers of specimens and therefore better statistical confidence than low numbers of large animal samples, have a greater sensitivity to environmental changes than large animals, and are more easily studied in modern ecosystems (Hadly and Barnosky 2009). Other types of deposits bearing vertebrate fossils, such as fluvial and alluvial sediments, preferentially preserve larger species (e.g., Behrensmeyer et al. 1979) that can result in biased reconstructions of ecological structure from fossil data (Le Fur et al. 2011).

Recent studies that have used vertebrate fossil data to assess changes in ecosystems through the Pleistocene, Holocene and up to the present include analyses of Rocky Mountain mammal communities (Hadly 1996), small mammal communities in the Bonneville Basin, western USA (Schmitt et al. 2002), mammal communities in the Carpathian Basin in Europe (Pazonyi 2004), bird, rodent, and reptile communities on South Island, New Zealand (Worthy 1997) and ungulate communities in South Africa (Faith 2011). In these studies, data were collected at spatial, temporal, and taxonomic scales that allowed for meaningful comparisons with modern living communities and the determination of trends in ecological parameters indicative of climate change and anthropogenic disturbance.

4.4.3 Plants

Pleistocene and Holocene plant communities are preserved primarily as pollen and phytolith plant microfossils recovered from caves, lakes, ponds, and bogs in a wide range of both lowland and upland terrestrial ecosystems. Plant macrofossils, including seeds, needles, twigs, and leaves are also preserved in lake, pond, and marsh sediments, as well as in wood rat middens (McAuliffe and Van Devender 1998; Jackson et al. 2009). The impact and frequency of fire disturbances can be evaluated from soot and charcoal particles preserved in sediments (e.g., Thomas et al. 2001).

Spatial resolution in fossil pollen data is poor relative to ecological data. Because wind is a major pollination vector, pollen data are prone to spatial averaging within an ecosystem, mixing pollen from adjacent habitats and possibly from beyond the bounds of the local community. Additionally, like the spatial resolution in vertebrate deposits, pollen and macrofossil plant deposits are sporadically distributed throughout the landscape and only preserved in the particular habitats mentioned above. However, pollen-bearing deposits can provide well-defined local records of vegetation dynamics resulting from environmental change and species migrations (Foster and Zebryk 1993).

Pollen deposits provide excellent temporal resolution with little time-averaging, in many cases equivalent to the resolution of modern ecological studies. Varved accumulations of lake and pond sediments provide an annual to decadal record of pollen accumulation that can be calibrated using radiocarbon dates (e.g., Brauer et al. 1999; Anderson et al. 2007; Kito and Ohkuro 2011). Plant macrofossil remains may be somewhat more time-averaged, but likely accumulated within decades in a single deposit. Organic material in aquatic deposits and middens can also be radiocarbon dated.

Fine-scale taxonomic resolution is difficult to obtain in plant paleontological studies. Pollen data in particular suffer from poor taxonomic resolution. Many palynomorphs can only be identified to the genus or higher taxonomic level meaning that changes in species composition within genera in an ecosystem might go unrecognized in the fossil record. This is particularly problematic in temperate regions where there are many species in relatively few genera compared to subtropical and tropical habitats where species and genus richness are very high. Plant macrofossils can usually be identified to the species level (Jackson et al. 2009) and can be used to supplement the taxonomic resolution of pollen data if both can be collected together. Additionally, the majority of the pollen record comprises anemophilous (wind pollinated) species (Bush 1995) due to their copious production of light pollen grains. Some taxa are poorly represented in the pollen record, including locally and regionally rare species, species with low pollen production (Foster and Zebryk 1993), and entomophilous species (Bush 1995) that have low dispersal rates due to morphological adaptations to insect-pollination.

Taxonomic enumeration from pollen or macrofossil deposits is also not well defined. It is impossible to count individual plants from pollen or from macrofossil deposits. However, relative taxon abundances can be estimated because pollen species abundances in deposits are closely correlated to the abundances of those species in a habitat and the proximity of the individuals in each species to the site of deposition (Davis 2000). Changes in relative abundance can be assessed from changes in pollen and macrofossil abundance through time, but precise species abundance data is unobtainable.

Overall, it is impossible to sample past plant communities at spatial and taxonomic scales comparable to those at which living plant communities are studied. Nevertheless, the excellent temporal resolution and widespread availability of fossil pollen data from the Pleistocene and Holocene has allowed paleoecologists to analyse broad changes to plant communities in response to climate and anthropogenic disturbance in a wide variety of ecosystems such as arid upland environments (McAuliffe and Van Devender 1998; Thomas et al. 2001), coastal environments (Hashimoto et al. 2006), tropical forests (Lyons-Weiler 1992; Kealhofer and Penny 1998), and temperate uplands (Feurdean and Bennike 2004).

4.5 Summary of Conclusions

Reconstructing communities and ecosystems in the Pleistocene and Holocene using data from the fossil record is critical to understanding how modern communities and ecosystems have been impacted by the expansion of human populations across the globe and how species diversity might best be maintained through ecosystem conservation and restoration. Estimates from the fossil record of species composition, richness, abundance, evenness, and biomass are required for assessing how communities have changed over the last 20,000 years and for understanding the significance of changes occurring now in response a wide range of anthropogenic forcing factors, including pollution, eutrophication, greenhouse gas induced climate change, ocean acidification, habitat destruction, invasive species, and overexploitation of economically valuable species. Drawing reliable conclusions about ecological parameters from fossil data and using fossil data to project community structure and function into the past requires that the various scales at which data are collected and analysed be harmonized between paleontological and ecological investigations. The three most important categories of scale in ecological data are:

- *Spatial scale*: Includes the total area across which data characterizing a community and ecosystem are collected, the size of the sample units that collect the individual entities censused in a study, and the distribution of sample units throughout the area of the study.
- *Temporal scale*: Includes the total duration of time encompassed by the data collected in a study, as well as the frequency of observations made, which together determine the temporal resolution of the data.
- *Taxonomic scale*: Includes the range of taxa included in a study (the subset of all species or other taxa in the community for which data is collected), the taxonomic resolution (the taxonomic level to which individual organisms are identified in a study), and the method by which taxa are enumerated (counted or quantified) in a study.

A survey of 54 long-range ecological studies published in the recent ecological literature indicates the following about scale in ecological research:

- Ecologists commonly focus their research on subsets of similar taxa within a community (e.g., mammals, molluscs, trees, corals) occupying a particular habitat (e.g., forest, rainforest, coral reef, grassland, wetland, stream).
- Most long-term ecological studies collect data at the species level and most enumerate species by counting numbers of individuals. Plant and coral studies sometimes quantify taxa by percent cover.
- Spatial scale in long-term studies is highly variable at all levels from study to study. The total area encompassed by individual studies was highly variable, ranging from 50 m^2 to 100,000 km^2. No taxon group or habitat type is studied only at a particular range of spatial scale.
- Temporal scale in long-term ecological studies ranges from less than a decade to a century. Temporal resolution ranges from annual to centenary. No taxon group or habitat type is studied only at a particular range of temporal scale.

Data from fossils ranging from recently dead to Pleistocene in age can be collected and analysed at scales comparable to data from living communities with some limitations and inherent differences in scale depending on the type of organism and taphonomic details of preservation and circumstances of accumulation and deposition.

- *Invertebrates*: In many cases, marine invertebrate fossils such as molluscs and corals can be collected at spatial scales comparable to their living counterparts because the death assemblage accumulates coincident with the living community. Taxonomic scales are also comparable between live and dead data, as are methods of enumeration. However, time-averaging is common in marine fossils and degrades the temporal resolution of invertebrate fossil deposits. Events that cause large changes in a marine community in ecological time may not be apparent in the time-averaged fossil record.
- *Vertebrates*: Pleistocene and Holocene vertebrates are commonly preserved in caves, crevasses, and wood rat middens in a wide range of terrestrial environments. Taxonomic resolution and enumeration of fossil material are equivalent to live data. Radiocarbon dating can establish the temporal resolution of cave deposits, which is usually from hundreds to thousands of years, although individual wood rat middens are accumulated on a temporal scale of decades. Spatial resolution is constrained by the availability of fossil accumulations, but typical cave deposits reliably record local community composition and abundance of small animals and radiocarbon dating can be used to correlate among different localities to expand the spatial scale of the data.
- *Plants*: Trees and other plants from the Pleistocene and Holocene are commonly represented by deposits of fossil pollen and more rarely by plant macrofossils preserved in swamps, lakes, bogs, and caves, as well as wood rat middens. Pollen deposits can provide excellent temporal resolution when they are deposited annually in varved sediments. Sequences of varved sediments can be calibrated using radiocarbon dates to provide a timeline of plant community composition comparable to data from studies of living flora. The spatial scale at which data can be collected is constrained by the locations and number of deposits containing fossils and fossil pollen, so that sample units and their distribution are unlikely to be comparable between live and dead studies, but the overall area from which the data are collected may be. Pollen data are also prone to spatial averaging, which mixes pollen from local with more distant sources. The greatest mismatch in scale between live and dead plant data is in the taxonomic resolution of pollen and ability to enumerate individuals from pollen and plant macrofossils. Pollen often cannot be assigned to particular plant taxa below the genus level and there is no way to estimate absolute numbers of individuals among different taxa, although relative abundances can be approximated and used to track changes in dominance over time.

Overall, the mismatches in scale between data from living communities and from the fossil record are not insurmountable, although it is important to be aware of the limitations that scale mismatches produce in the ability to resolve ecological events in time and the details of past ecological composition and structure. If ecologists are mindful of these issues of scale in their work and communicate them, paleontologists will be better able to collect data from the fossil record in service of the mission of understanding the history and protecting the future of threatened ecological communities and ecosystems.

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Chapter 5
Building Links Between Ecology and Paleontology Using Taphonomic Studies of Recent Vertebrate Communities

Anna K. Behrensmeyer and Joshua H. Miller

Abstract Ecologists and paleontologists share a common interest in the natural cycles of life and death, but their viewpoints on living organisms and the processes that recycle or preserve their remains are different. The goal of this chapter is to explore the common ground between these fields through taphonomy, the sub-field of paleontology that examines how organisms are preserved as fossils. From studies of recent bone assemblages, taphonomists have assembled information about diversity and abundance, animal behaviour, predator–prey interactions, habitat utilization, mortality (how and where animals die), and nutrient recycling. These studies were initiated to strengthen paleontological understanding of the information content and biases in the fossil record, but the methods and discoveries of taphonomic research in modern ecosystems are also of potential value to ecologists. Both paleontology and ecology would benefit from increased exchange of ideas and perspectives, and this chapter provides examples showing why such exchange is worth pursuing and offers suggestions to encourage future dialogue and collaboration.

Keywords Taphonomy • Vertebrate • Actualistic • Paleoecology • Bone surveys • Diversity • Ecological baselines

5.1 Introduction

Taphonomy focuses on the transition of organic remains from the biosphere to the lithosphere. An important stage of that transition falls squarely in the realm of ecology, specifically the "decomposer" part the natural cycle of life (Fig. 5.1). With an eye

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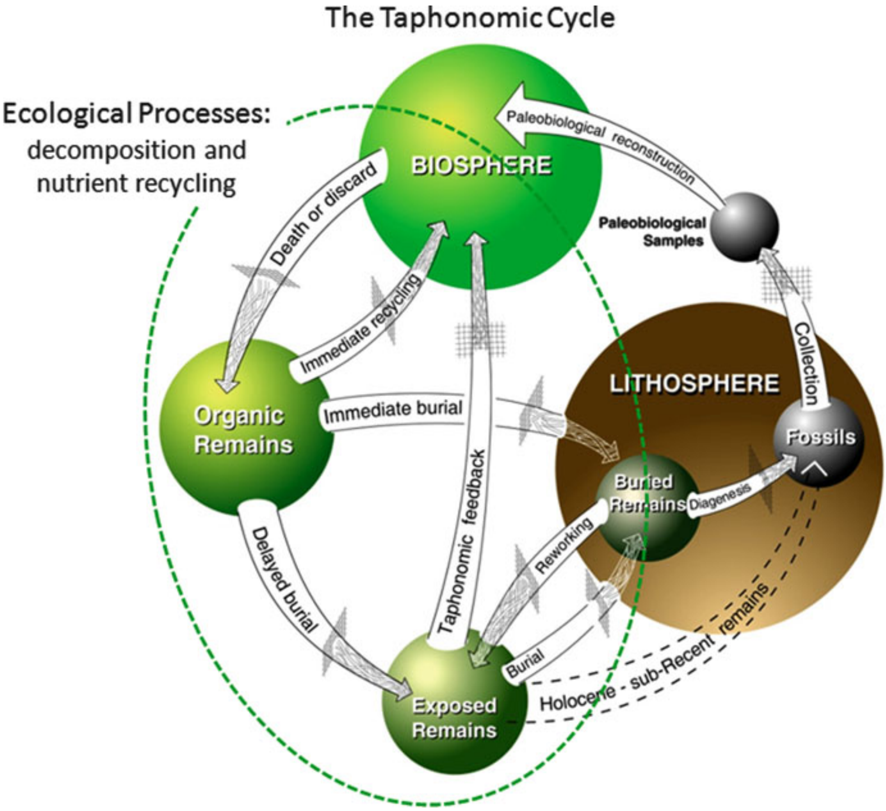

Fig. 5.1 The taphonomic cycle, showing different pathways for dead or discarded organic remains as they are either recycled (destroyed) or survive to go on to the next stage in the transition from biosphere to lithosphere. Filters on the arrows indicate processes that change the biological and ecological information between the different stages. The "decomposer" portion of ecological carbon, nitrogen, and sulphur cycles plays a critical role in determining the nature and effectiveness of these filters (Adapted from Behrensmeyer et al. 2000 Fig. 1)

toward understanding biases in the fossil record, taphonomists investigate biological, chemical and physical processes that either destroy remains or transform them into fossils. While ecologists are aware of the functional significance of bones and teeth, they generally are not informed about taphonomic research and its potential for increased understanding of nutrient recycling. In addition, taphonomists are learning that the remains of the dead can provide a wealth of information about the living, some of which is difficult or even impossible for ecologists to sample from current populations. Recent changes in ecosystems over years to decades can be addressed by studying skeletal remains on the ground surface when live census records are incomplete or absent. This is of great potential importance to conservationists as well as ecologists planning long-term strategies to sustain biodiversity, since time-depth is critical to understanding the historical components of community structure and population dynamics.

In spite of many areas of overlapping interest and research, as well as increasing collaboration on late Pleistocene-Holocene paleoecology, ecologists and paleobiologists continue to occupy mostly separate intellectual arenas. Early naturalists were less constrained by the boundaries of scientific fields and more open to what we would now regard as interdisciplinary leaps of insight (Wilkinson 2012). Charles Darwin noted the potential paleontological significance of recently dead animals when he commented on clusters of guanacos that he thought might have perished in bad weather near a river in Argentina.

> The guanacos appear to have favourite spots for lying down to die. On the banks of the St. Cruz, in certain circumscribed spaces, which were generally bushy, and all near the river, the ground was actually white with bones. On one such spot I counted between ten and twenty heads. I particularly examined the bones; they did not appear, as some scattered ones which I had seen, gnawed or broken, as if dragged together by beasts of prey. The animals in most cases must have crawled, before dying, beneath and amongst the bushes. . . . . I mention these trifling circumstances, because in certain cases they might explain the occurrence of a number of uninjured bones in a cave, or buried under alluvial accumulations; and likewise the cause why certain animals are more commonly embedded than others in sedimentary deposits. (Darwin 1860, p. 168)

The field of taphonomy was named by the Russian paleontologist I. A. Efremov in 1940 (Efremov 1940; see Olson 1980 for a review of its early history). Actualistic study of vertebrate remains was pioneered by Johannes Weigelt, a German paleontologist who surveyed the Gulf Coastal Plain of North America for analogues that would help him interpret fossil vertebrates (Weigelt 1927; translation 1989). The field of "Aktuo-Paleontologie" was further advanced by Wilhelm Schäfer in his comprehensive book on marine ecology and paleoecology (Schäfer 1972). Further advances in actualistic taphonomy (i.e., in modern environments) over recent decades have shown that bone assemblages have much to offer in terms of understanding modern ecosystems. This chapter will provide an overview of information from studies of modern bone assemblages that should be of interest to ecologists as well as to paleobiologists. A thorough treatment of the ecological implications of taphonomic research is not possible within the limits of this chapter. Rather, our goal is to offer examples, commentary, and references that will provide access to the literature and encourage increased exchange among researchers from both fields. We also include an Appendix with guidelines for field surveying of modern bone assemblages.

5.2 Putting the Dead to Work

Using skeletal accumulations to aid understanding of living communities is a relatively new concept for vertebrate ecologists. Karl Flessa of the University of Arizona, Tucson, coined the phrase "Putting the dead to work" for his research on shell beds that record major changes in the ecology of the northern Gulf of California caused by the impact of humans on the flow of the Colorado River

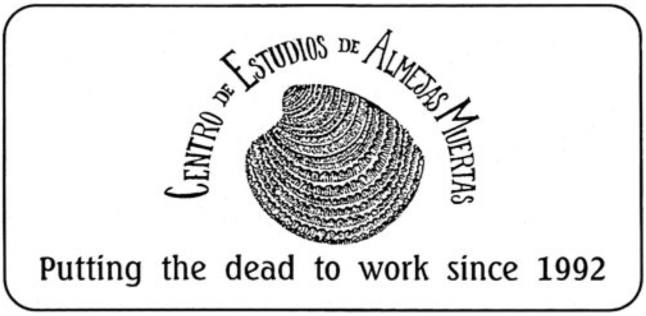

Fig. 5.2 Bumper sticker created by Karl Flessa for his actualistic research project on the invertebrate and vertebrate taphonomy of the Colorado River Delta, Baja, California (Dietl and Flessa 2011)

over the past century (Fig. 5.2) (Dietl and Flessa 2011). Numerous other studies of marine organisms (including "live-dead" research) are being used to document human impact on marine ecosystems (Schöne et al. 2003; Rowell et al. 2008; Flessa 2009; Kidwell 2007, 2009; Kowalewski 2009; Lybolt et al. 2011). This, and earlier research by paleobotanists (Davis 1989, 1991; Huntley 1990, 1991) have established the independent discipline of "Conservation Paleobiology" (Flessa 2002; Dietl and Flessa 2011). The idea of putting the dead to work to increase understanding of recent ecological history and processes applies equally well to vertebrate remains, from small mammals (e.g., Smith et al. 1995; Hadly 1999; Reed et al. 2006; Hadly and Barnosky 2009; Blois et al. 2010; Terry 2010a, b) to large terrestrial mammals (e.g., Lyons and Wagner 2009; Western and Behrensmeyer 2009; Miller 2011a) and marine mammals (e.g., Liebig et al. 2003; Pyenson 2011). Simultaneously, such research informs vertebrate paleontologists about ecological processes that control recycling vs. preservation in the early post-mortem environment and how to interpret information that got through these filters. Understanding the taphonomic impact of early post-mortem ecological processes allows paleobiologists to assess biases in fossil assemblages, providing necessary tools for distinguishing ecological signals contained in these assemblages from overprints and noise imposed by processes that lead to destruction and (sometimes) preservation.

The viewpoints of ecologists and paleontologists on processes that interact with dead organisms are two sides of the same coin. Thus, taphonomy can be a unifying conceptual bridge to bring these fields into closer collaboration and mutual understanding. In an effort to help stimulate this discussion, we will describe a series of topics relating to vertebrate taphonomy and examine their implications from both points of view. We will emphasize what has been learned through recent actualistic studies of bone assemblages, as this provides a readily accessible foundation for increased dialogue between ecologists and paleontologists.

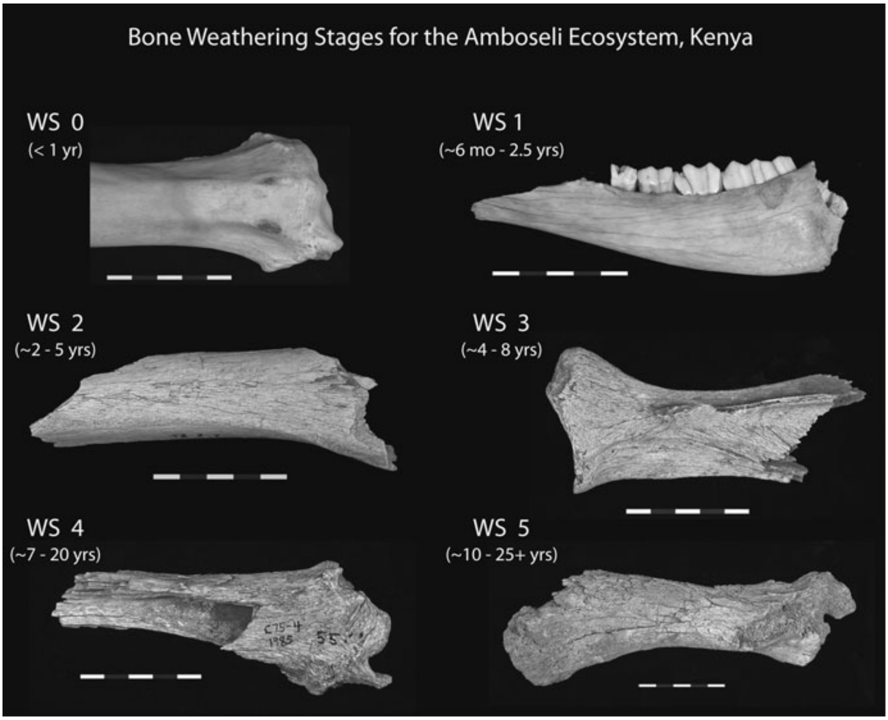

Fig. 5.3 Bones showing the progressive weathering stages: WS 0 (unweathered), WS 1 (fine cracking), WS 2 (flaking of surface bone), WS 3 (revealing fibrous inner bone), WS 4 (spalling and deep cracking), and WS 5 (fragile, degraded, falling apart); see Behrensmeyer 1978 for details and other examples. The approximate years represented by each weathering stage are for bones exposed to full sun on the ground surface in Amboseli's tropical, semi-arid climate (Behrensmeyer and Faith 2006 and Behrensmeyer unpublished data). Scale in centimetres

5.3 Useful Information from Bone Taphonomy

5.3.1 Bone Weathering

Bones on the ground surface weather or decompose at rates that are predictable for a given climate and exposure situation. Sequential weathering stages based on simple morphological criteria can be used to estimate the years since death (Behrensmeyer 1978) (Fig. 5.3). This makes bone weathering stages rough but useful "taphonomic clocks" – a tool that allows ecologists and conservationists to assess change over years to decades in animal populations. The descriptive weathering stages reflect the gradual weakening of bone structural components that are similar across vertebrate classes. Mammals are best known in this respect, but limited research on birds, reptiles, and bony fish indicates that, with some caution, the six-stage weathering classification can also be applied to these groups as well (e.g., Brand et al. 2003; Behrensmeyer et al. 2003).

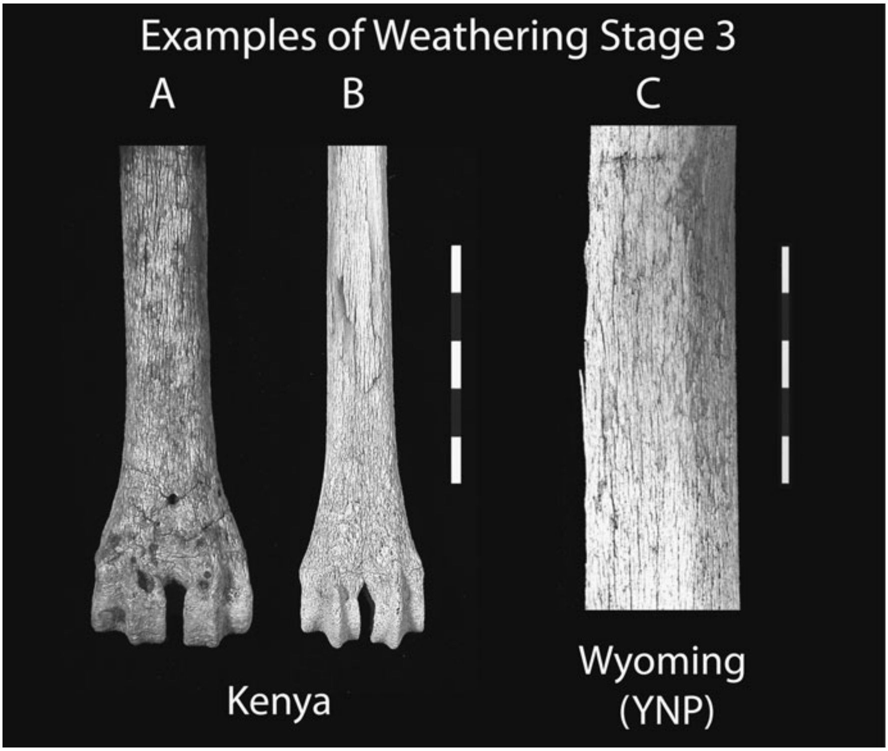

Fig. 5.4 Examples of bones in Weathering Stage 3. (**a**) Fossil artiodactyl metapodial from East Turkana, Kenya (Pleistocene); (**b**) Modern metapodial with WS 3 surface very similar in surface texture to (**a**) note remaining patch of WS 2 on shaft; (**c**) Modern elk metatarsal from the temperate climate of Yellowstone National Park, Wyoming, showing characteristic WS 3 surface texture. Scales in centimetres

Bones weather much faster in tropical environments than in temperate or arctic ones (Andrews 1995; Andrews and Armour-Chelu 1998; Meldgaard 1986; Sutcliff and Blake 2000; Janjua and Rogers 2008; Miller 2009), but the descriptive stages are more-or-less consistent across latitudes (Fig. 5.4). In Amboseli National Park, a semi-arid tropical ecosystem, surface bones are subjected to intense sunlight and seasonal fluctuations in moisture and temperature (Behrensmeyer 1978) (Figs. 5.3 and 5.4). Rates of weathering differ across body size; in medium-sized ungulates (25–200 kg), bones usually proceed to Weathering Stage (WS) 3–4 within 5–10 years. Bones of very large animals (elephants, rhinos) can last in identifiable form for at least 35 years. Weathering of medium to large mammals in the temperate climate of Yellowstone National Park appears to stall at WS 3 (Miller 2009) and bones may survive, without burial, for over a 100 years (Miller 2011a). The effects of relatively consistent moisture and seasonal freezing on bone weathering have yet to be experimentally studied. Variation in the micro-environment of surface bones can greatly affect weathering rates, including the up versus down side (with respect to the substrate) of the same bone. Protection from direct sunlight (and associated UV damage to organic components) slows down the weathering process, while precipitation of salts from the underlying substrate can accelerate weathering (Behrensmeyer 1978).

Paleontologists and archeologists originally studied weathering stages in order to determine natural rates of destruction of bones on land surfaces (Isaac 1967; Behrensmeyer 1978; Lyman 1994). Paleontologists are interested in recognizing pre-burial weathering in fossil bones as evidence of surface exposure prior to burial. Weathering stages can be problematic in fossils because post-burial weathering, diagenetic cracking, and post-exposure damage on outcrop surfaces can cause similar surface damage or obscure original weathering features. In modern bones, however, the descriptive categories have been tested by many different workers, are reproducible, and could be readily adopted by ecologists. Two important caveats regarding the method are: (1) rates of weathering should be calibrated within each study area (not assumed based on other areas), and (2) only exposed (not shaded) bones should be used to calibrate the maximum weathering rates for any given climatic regime.

5.3.2 Natural Bone Concentrations

Bone concentrations in dens, lairs, pellets, or faeces represent a point source of information about species in an ecosystem as well as predator size and behaviour. The remains of small vertebrates accumulated by predators in owl pellets are a relatively faithful sample of prey species within the size range and geographic area accessible to any particular species (Andrews 1990; Reed 2007; Terry 2010a, b). This may also be true for prey species found in other raptor bone concentrations (Stewart et al. 1999; Trepani et al. 2005) or in carnivore faeces but has not been documented as well as for owls. These bone accumulations may be time-averaged over days to decades or even millennia in the case of cave accumulations (Terry 2008; Graham et al. 2011). In situations where bones are exposed to natural weathering, the time-averaging interval should be shorter for small bones than for large ones because of slower destruction rates for the latter. Hyena dens and leopard lairs have received considerable taphonomic attention as analogues for past bone concentrations, both in terms of the species represented and damage patterns displayed by skeletal parts (e.g., Brain 1981; Hill 1989; Pickering et al. 2004; Lansing et al. 2009)

Paleontologists are especially interested in causes of mortality that generate dense bone concentrations – i.e., bonebeds (Rogers et al. 2007). Bonebeds are often sources for more complete anatomical information as well as clues about population demography, herding behaviour and other attributes and vulnerabilities of extinct species. Many bonebeds represent mass mortality events (e.g., Voorhies 1969, 1992), but others are formed through attritional bone accumulation and sedimentary processes or circumstances that concentrate the remains in restricted areas, such as caves and fissures, as well as stratigraphic condensation of reworked skeletal material at sedimentary (sequence) boundaries (Rogers and Kidwell 2000).

Although mass mortality events may be uncommon by ecological standards, they likely contribute a disproportionate amount of information to vertebrate paleontology and paleoecology, mainly because unusual death events overwhelm the recycling capacity of decomposers, resulting in relatively complete specimens. Such events also may be associated with uncommon geological processes (e.g., flooding, volcanic eruptions) leading to rapid burial.

5.3.3 Demographic Information

Ecologists can assess the demography of a standing population of live animals through direct examination of individuals or general categorization of juveniles vs. adults, males and females. Capturing or observing the living is considerably more time and labour intensive than surveying the dead and recording skeletal fusion and dental eruption stages. Many ecologists, of course, are well aware of the value of examining the remains of dead animals for evidence of health issues, predators and age at death, but they generally work with individual species rather than taking a broader approach to learning from multi-species mortality patterns (see Green et al. 1997 for an exception). There is a wealth of information about the living population as well as the dead in skeletal remains and teeth, and this could be a valuable resource for ecologists and conservationists. Under stable conditions of turnover (balanced birth and death rates), the dead provide information on the age structure of the living population (Lyman 1994) and also which age cohorts may be more vulnerable to predation (Behrensmeyer 1993). Live and dead census data for the same community can be compared to look for shifts in the mortality profiles that indicate a species in decline vs. increase (Terry 2010a; Miller 2011a).

5.3.4 Discarded Skeletal Remains

Mammals lose deciduous teeth as they grow, and reptile and fish (e.g., shark) teeth are shed and replaced constantly during life. Cervid antlers are shed and regrown annually, and elephants lose their molars and often parts of their tusks throughout their lives. Broken elephant tusk fragments are an indicator of intra-species conflict and have been linked to population stress, as can happen during times of drought around waterholes (Haynes 1988). Female caribou lose their antlers within days of giving birth, thus concentrations of shed antlers are a taphonomic signature of birthing grounds (Miller 2011b, c). Such accumulations occur in different places in different stages of decomposition (weathering), which can show how calving grounds have shifted over time. Most cervids grow and shed antlers in particular seasons, thus providing evidence for seasonal habitat utilization (Miller 2008). Basal measurements of shed crocodilian teeth can be used to track habitat use by individuals of different size and life stage (Bir et al. 2002). It is important to remember, when considering relative abundance of species in either the actualistic or fossil record, that some species may produce many more preservable parts per individual than others that only lose their hard parts when they die.

5.3.5 Bone Modification

This term refers to many different types of damage that alter bones and bone surfaces, including breakage, tooth and tool marks, insect excavations, etching by acid (gastric and otherwise), trampling, various types of physical abrasion (by wind, water, or sediment), and internal microscopic tunnelling by fungi and bacteria. Many of these modifications represent distinctive signatures of a particular agent or process while others are harder to interpret. Single bones may bear the marks of one or many different types of modification that occurred soon after death, and depending on how long they remain on the surface, can acquire a succession of modification traces. Thus, a single bone may be broken and chewed by carnivores, weathered to WS 1, gnawed by rodents, and have its lower side burrowed into by termites prior to burial. Such features can be used to reconstruct the post-mortem history of a bone or carcass, analogous to a forensic investigation of human remains, and the resulting information is useful to both paleobiologists and ecologists. Early post-mortem surface modification is best recorded on unweathered bones and gradually disappears as the bone is weathered or abraded. In the fossil record, there are added complications: (1) bone modification features may have no modern analogue, representing extinct bone-modifying agents, and (2) burial, diagenesis, and destructive processes that occur as bones are naturally exhumed onto outcrop surfaces or uncovered by excavation can overprint pre-fossilization modification traces. In any quantitative assessment of bone modification on recent or fossil bones, such as the frequency of tooth marks on limb elements, it is critical to control for the specimens, and parts of specimens, that are well-preserved enough to record the presence or absence of such modification (e.g., Marean and Spencer 1991; Blumenschine et al. 1996; Faith 2007; Faith et al. 2007).

Bone breakage imparts distinctive features that can indicate the agent and timing of fracturing. Bones of large animals (e.g., >15 kg) are physically tough and not easily broken; it takes considerable force to fracture an unweathered limb element of a wildebeest or other ungulate. Agencies capable of such force include bone-crushing carnivores, humans with implements, or trampling on a firm substrate. These processes can also preferentially destroy low density limb ends, resulting in characteristic patterns of survival of proximal, distal, and shaft components (e.g., Marean et al. 2004; Faith et al. 2007). Fracture surfaces of fresh bones have distinctive morphologies, such as spiral and saw-toothed patterns resulting from the retained tensile strength of their organic matrix. Once bones are weathered to WS 2 and beyond, bone collagen has decayed to the point where breaks tend to follow cracks and become more stepped (perpendicular to bone fiber direction) and splintered. Contrary to popular belief, fluvial transport generally does not break relatively fresh bones, whatever their size or major taxonomic group (Aslan and Behrensmeyer 1996). However, once weakened by sub-aerial weathering or sub-aquatic decay, transport by wind, water, or mudflow can break bones as well as disperse and abrade them (Behrensmeyer unpublished data).

5.3.6 Footprints and Trackways

Animal tracks are worth including in this overview because they are instantaneous records of animal behaviour and faunal associations, and because they are of interest to both ecologists and paleontologists. Actualistic research on tracks and their taphonomy include both experimental and field studies (e.g., Laporte and Behrensmeyer 1980; Cohen et al. 1991). In modern ecosystems, it is usually not too difficult to identify the track-maker, whereas in the fossil record, tracks are given their own Latin names (ichnotaxa) because of the uncertainties in positively identifying the track-maker. Ecologists value the knowledge of expert trackers in studies of animal behavior, and there have been a number of collaborations between trackers and paleontologists seeking to understand tracks and trails left by extinct species (including early humans) (Hay and Leakey 1982; Leakey and Harris 1987). This is yet another point of contact between ecology and paleontology that could be explored in the future.

5.4 Ecological Information from Dispersed Surface Bones

5.4.1 Species Richness

The most basic measure of diversity is the number of species present in a community – i.e., species richness. Aside from the newly developed method of assessing diversity using aDNA in soils ("metagenomics"; e.g., Poinar et al. 2006), measuring diversity involves counting animal species in a community or ecosystem using systematic visual censuses (air and ground), collecting and trapping, and/or compilation of anecdotal sighting and historical records. Rarely are censuses taken of all vertebrate species in an ecosystem; rather, target groups are usually vertebrate classes, or orders within a single class, such as Mammalia, and often further restricted to size ranges within these (e.g., macro vs. micro-mammals). Taphonomic surveys, in contrast, can theoretically sample the remains of all species dying in an ecosystem, as well as document shed or discarded materials such as eggshells, antlers, tusk fragments, regurgitated pellets and faeces. In recent taphonomic surveys in Africa, species that were unknown from live census data turned up in the bone assemblage, including domestic animals that were illegally brought into national parks to graze (Odock 2011).

There are, of course, limitations on diversity sampling using dead and discarded skeletal remains. These include differential rates of bone recycling (how fast they disappear), their visibility in different types of habitats, and the observer's ability to identify the original owner of any given skeletal part, tooth, or other trace. The latter issue is an obvious dividing line between vertebrate paleontologists and zooarcheologists, with their training in identifying bones and species from fragmentary fossils, and ecologists, who know the living organisms but may have limited expertise in recognizing their internal hard parts. Identification of most vertebrate species using bones and teeth is not difficult, given appropriate training and comparative osteological collections. More problematic is distinguishing species that have very similar skeletal or dental morphology, such as many types of micromammals. Paleobiologists are used to dealing with genera rather than species in assessing diversity, but most ecologists would consider that a serious limitation in building a record of richness for a living community. Bird, reptile, and fish species can also be difficult to distinguish based on isolated bones, although higher taxonomic levels usually are identifiable, depending on the skeletal part.

5.4.2 Species Abundance

Determining species abundances allows many useful characterizations of diversity that are important in population ecology, community structure, and measures of environmental and human impact on vertebrate faunas. Again, ecologists rely on various methods of censusing to assess absolute or relative abundance within particular groups, such as large or small mammals, birds, etc. Taphonomists gather information on the number of individuals of all animals represented in their surveys – referred to as MNI (Minimum Number of Individuals). This number is an estimate rather than a direct count because of the dispersed and taphonomically altered nature of carcass remains on a land surface. There are various approaches to calculating MNI (e.g., Behrensmeyer 1991; Lyman 1994). Also, the relative numbers of MNIs for different species do not provide a snapshot sample comparable to an ecological census, but rather a time-averaged accumulation of dead animals over a period of years to decades. Nevertheless, MNI counts have proved to be a reliable indicator of relative population abundances for small mammals in the Great Basin ecosystem, USA (Terry 2010a, b), and for large mammals in the ecosystems of Amboseli National Park, Kenya (Western and Behrensmeyer 2009) (Fig. 5.5) and Yellowstone National Park, USA (Miller 2011a).

5.4.3 Causes of Mortality

Taphonomic methods could contribute to ecological studies of animal mortality. While ecologists can observe predation and other types of death in their field studies, these events are relatively rare and hard to document. Taphonomists have access to a much larger sample of mortality events and have developed various criteria to determine probable cause of death. Admittedly, this must be inferred from what

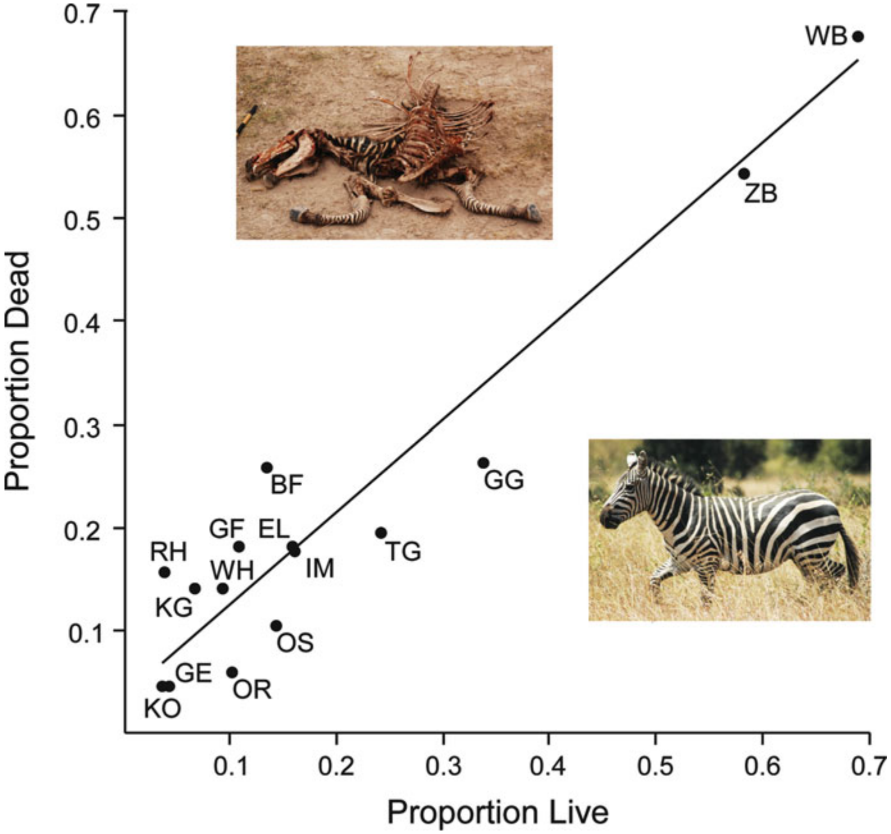

Fig. 5.5 Correlation between live population and carcass abundances for 15 ungulate species >15 kg body weight in Amboseli National Park, Kenya. Coefficient of reduced major axis correlation: $r = 0.9523$, $p < .05$. Totals were summed over the same sampling intervals, 1964–1975 and 1993–2004; N(live) = 169,235 total census counts, N(dead) = total 1,502 carcass MNI. Key to species: *WB* wildebeest, *ZB* zebra, *GG* Grant's Gazelle, *TG* Thompson's Gazelle, *BF* buffalo, *IM* impala, *EL* elephant, *GF* giraffe, *WH* warthog, *KG* kongoni, *RH* Black rhino, *OS* ostrich, *OR* Oryx, *GE* + gerenuk, *KO* waterbuck. (Modified from Western and Behrensmeyer 2009 Fig. 2)

could be termed forensic investigation, but there are clues that can allow a high level of certainty for many carcasses, especially if these are examined early in the post-mortem interval. Thus, in an ecosystem with diverse carnivores (e.g., lion, cheetah, spotted hyenas), a fresh intact carcass indicates death from disease or starvation, while a skeleton with soft tissues removed and intact limb bones is evidence for a felid predator rather than a hyena. When bone-consuming scavengers such as hyenas are abundant and have early access to a carcass, it is often impossible to determine the original predator, although tooth marks and skeletal part survival patterns can provide evidence for the sequence of carcass consumers (e.g., Cleghorn and Marean 2007). As predators, modern humans can leave distinctive marks on bones that are easily interpreted by taphonomists (e.g., knife marks, bullet holes). Criteria have also been proposed to differentiate more subtle damage patterns inflicted by early stone-wielding hominins from those of other meat-eaters (Brain 1981; Blumenschine et al. 1996).

5.4.4 Where Animals Live and Die

There is a recurring story in the popular literature about "elephant graveyards" and other places where animals "go to die." Darwin (1860) even mentions that this was proposed by locals to explain the massed guanaco remains, though he inferred that their deaths occurred during a winter storm. These stories likely originate from observations of real phenomena such as mass mortality events, or attritional bone accumulations around watering holes. Such obvious sites of localized mortality have their own taphonomic stories to tell about the circumstances and the animals involved. However, the spatial patterning of dispersed skeletal remains can provide more general ecological information about places and habitats where animals are dying, the role of predators, and seasonal behaviour patterns in the living populations. The study of surface bones in Amboseli National Park, Kenya, shows that resident species such as impala live and die in the same habitat, but migratory species such as wildebeest have carcass distributions that differ from the spatial patterns recorded in live censuses (Fig. 5.6) (Behrensmeyer et al. 1979; Behrensmeyer and Dechant Boaz 1980). During the dry season when wildebeest are abundant in the Park, they also move into the lush grazing of the swamp habitat by day and out to the plains at night, behaviour that is interpreted as a predator avoidance strategy (D. Western pers. comm.). Carcasses of wildebeest occur in all habitats but are abundant in the swamp edge and the plains, indicating that the bone distribution is skewed toward areas of greater vulnerability to predation (Behrensmeyer et al. 1979). In another actualistic study, bone distributions tracked changes in seasonal landscape use by live elk in Yellowstone National Park, including correctly identifying calving areas and bull elk wintering grounds from concentrations of neonatal skeletons and shed antlers respectively (Miller 2008).

This actualistic research provides vertebrate paleontologists with increased understanding of ecological information recorded by bone accumulations and how this information passes through the initial taphonomic filters leading to the fossil record – particularly for large, mobile animals. The benefit for ecologists is the realization that taphonomic data could provide important evidence for animal populations and their landscape use that may be unavailable from standard censusing methods. While GPS collars on animals provide the opportunity to examine geographic use on ultra-fine time-scales, deployment is often limited to a few individuals within a community, and establishing long-term variability takes many years or decades of study. Aerial surveys have a longer history of legacy data to draw upon, though such surveys primarily reveal diurnal behavior, and reactions to survey aircraft by target species may impact the data. A strength of bone survey

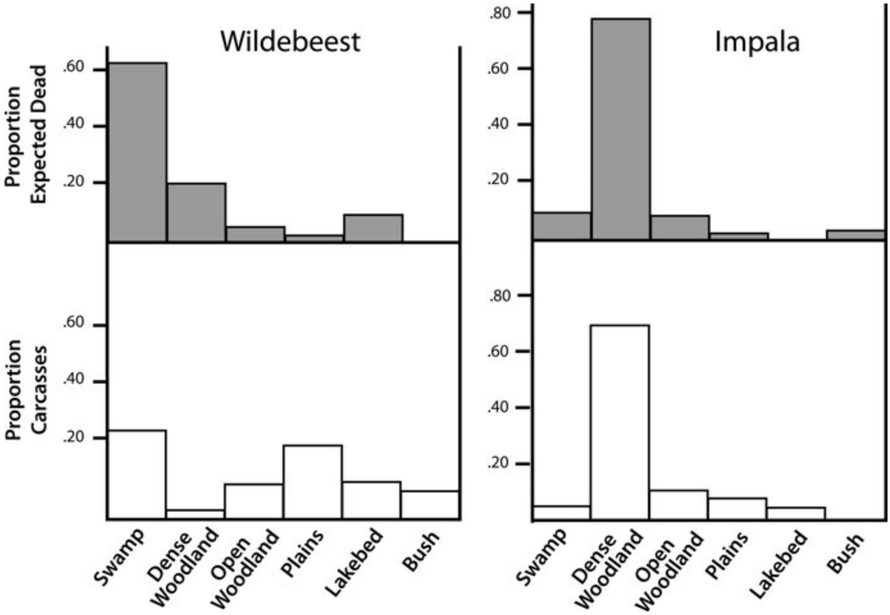

Fig. 5.6 Contrast between the habitat distribution of live populations and skeletal remains of two ungulate species in Amboseli National Park, Kenya. Proportion of expected dead is calculated based on the live population counts in each habitat and the species' annual turnover rate. Proportions of dead are based on MNI in each habitat. Wildebeest migrate out of the basin seasonally and also move between habitats diurnally. Live censuses record high wildebeest abundance in the swamp habitat where they feed during the day. Skeletal remains record relatively high abundance in both the swamp and plains habitats, where predation occurs during the day (swamp) and night (plains). Impala are resident species closely tied to the dense woodland habitat, and this is reflected in the spatial similarity of their live and dead abundances. (Modified from Behrensmeyer et al. 1979 Fig. 5)

data is that it is averaged over many years to decades (or more) of biological input and, thus, may incorporate ecological variability over extended time-scales. Particularly for regions with limited historical data, bone surveys can provide readily accessible baselines on landscape use for comparisons to patterns of live populations.

5.4.5 Carnivore Behavior and Impact on Prey Populations

Bones record various aspects of the interaction of carnivores with prey populations and could be put to work by ecologists as a tool for assessing the impact of predators on their prey. In general, the more complete the utilization of carcasses – how disarticulated and damaged they are – the greater the predator pressure on the prey animals. This has been demonstrated in a long-term taphonomic study in Amboseli

Fig. 5.7 Examples of bone modification from Amboseli National Park, Kenya. *Top row* shows two distal wildebeest humeri with broken shafts; *right-most* has been chewed from the ends. The *lower image* shows a zebra mandible severely reduced by chewing; note scalloped edges and tooth scoring. Damage is attributed to spotted hyenas (*Crocuta crocuta*). These specimens were collected in 2002–2004 when hyena population levels were high and intraspecific competition for carcasses intense

National Park, Kenya, where a marked increase in the population of spotted hyenas (*Crocuta crocuta*) in the 1990s resulted in a ~75% decrease in the number of bones per individual in the surface assemblage (Behrensmeyer 2007; Watts and Holekamp 2008). Many other taphonomic studies have documented the types of damage characteristic of different carnivores (e.g., Brain 1981; Hill and Behrensmeyer 1984; Marean et al. 1992; Pickering et al. 2004), especially their ability to disarticulate, break and consume bones and leave distinctive tooth marks and other surface damage (Fig. 5.7). Bone-consuming specialists such as hyenas leave taphonomic evidence of fluctuations in predator vs. prey populations

(Faith and Behrensmeyer 2006), but this should also be detectable for other types of carnivores. In any given vertebrate community, the pressure for utilizing animal protein should be reflected in the degree of disarticulation and bone scatter from individual carcasses, the survival of more consumable (delicate) bones, and damage to the larger skeletal elements. Of course, this type of evidence also depends on the size ratio of predator to the prey; larger prey animals may suffer little damage, while smaller or juvenile individuals may be completely consumed (although their bones could occur in raptor pellets or mammalian faeces).

Carnivores are relatively rare, often nocturnal, and hard to observe, thus the taphonomic records they leave in the remains of their prey animals could be a valuable addition to ecological methods used for assessing modern carnivore populations. Comparisons of the spatial distribution of skeletal remains with habitat use by the living populations of the same species for the same time period is a potentially powerful tool for examining the role of predation in controlling resource utilization across an ecosystem.

5.4.6 Documenting Ecosystem Stability or Change

Given a sample of surface bones in different weathering stages, it is possible to divide this sample into subsets representing older and younger contributions to the death assemblage. This provides a potentially powerful tool for looking back in time for changes in community structure, species richness, habitat utilization, and predator–prey interactions. Ideally, the years represented by each weathering stage could be calibrated to establish six subsets corresponding to the weathering stages (Fig. 5.3) (Behrensmeyer 1978; Cutler et al. 1999). In reality, however, variability in the time bones spend in any given stage blurs temporal resolution, so that some bones from the same time of death are in WS 1 while others may be in WS 2. On the other hand, there is minimal overlap in years since death (at least for known examples) of WS 0–2 and WS 3–5. Thus, it is advisable to combine the samples into three (WS 0–1, 2–3, 4–5) or two (WS 0–2, 3–5) groups. The latter option provides the highest confidence for separation of older and younger components of the bone assemblage and permits comparisons of species abundances and habitat distributions from different times, usually across years to decades. For the Amboseli bone assemblage, this showed significant change over four decades in the proportions of browsers and mixed-feeders relative to grazers and also shifts in the composition of sub-communities in different habitats (Western and Behrensmeyer 2009).

Many land ecosystems lack reliable records for animal population shifts over the recent past. Ecologists in need of such historical data should consider adopting surveys of surface bones and their weathering stages as a way to “back-census” vertebrate communities. This approach is already being used to aid in conservation assessment in various areas of Kenya (Faith 2008; Odock 2011) and the Arctic National Wildlife Refuge (Miller 2011b, c).

5.4.7 *Nutrient Recycling*

Nutrient recycling provides a unifying concept for ecology and paleontology. What gets recycled in the early post-mortem environment doesn't become part of the fossil record, and what avoids immediate recycling at least has a chance at becoming fossilized. The effectiveness of the decomposer portion of the ecological cycle thus is critical in shaping the fossil record, from the scale of individual organisms to the fauna and flora of an entire biome. From the moment an animal dies, internal and external micro- and macro-organisms compete for the available nutrients, including both soft tissues and mineralized body parts. Ecologists see rapid and efficient recycling of nutrients from dead organisms as an indicator of a healthy, well-balanced ecosystem. Taphonomists see efficient recycling as fatal to any hope of a fossil record and look for circumstances that help organic remains escape the biological processes that have evolved to break down these remains. Such circumstances include mummification in arid environments, rapid permanent burial (e.g., the "Pompeii effect"), oversupply of remains relative to recycling capacity of the local biota, and even pre-burial mineralization (Trueman et al. 2004). Biotic recycling continues in the buried environment (e.g., soil) unless shut down by unfavourable chemical conditions (anoxia, water saturation, deep burial), or stymied by rapid mineralization of hard tissues.

The study of nutrient recycling from large vertebrate carcasses has attracted the interest of ecologists as well as forensic scientists. In one notable example, a study by Bump et al. (2009a, b) used 50 years of data on moose mortality on Isle Royale (Lake Superior, North America) to show how shifting focal areas of wolf predation helped to shape the island's vegetation structure over decades through the fertilizing and other effects of carcass decomposition.

Given the complexity and power of ecological recycling, it may seem surprising that anything survives to become fossilized, but the diversity and richness of the vertebrate fossil record attests to the fact that the recycling filters are imperfect and equilibrium is rarely, if ever, achieved in energy transfer through the natural cycle of life and death. A continuing question for taphonomy, and vertebrate paleontology, is how the record that escaped recycling represents the much greater numbers of organisms that didn't.

5.5 Enhancing Links Between Paleontology and Ecology

5.5.1 *What Taphonomy Could Do for Ecology*

Ecological models of the carbon, nitrogen, and sulfur cycles show "dead organic matter" as a waypoint for nutrients returning to the ecosystem. Through actualistic research on this part of the ecological cycle, taphonomists have learned about a wide array of biological, chemical and physical processes that leave recognizable signatures on bone assemblages. Skeletal remains hold a wealth of information about the vertebrate species inhabiting an ecosystem, age and condition of the animals at death, mortality relative to habitats frequented by the living animals, the predators and scavengers that utilize the carcasses, and rates of return of nutrients to the soil through decomposition. Bones survive long enough on the landscape to provide years to centuries (or more) of historical information on changes in these variables through time. This source of ecological information has been largely unrecognized by ecologists up to now but has great potential as a tool for monitoring and conservation as well as enhanced understanding of the decomposer part of the ecological cycle.

Taphonomic survey methods are logistically easy and inexpensive (Appendix A). Assembling a species list from a taphonomic survey does require at least one team member to have the expertise to correctly identify species in the bone assemblage. This is not as daunting as it might first appear; many taphonomists have learned by doing rather than through formal training, with frequent use of museum osteological collections and reference guides to skeletal parts and species.

5.5.2 What Ecology Could Do for Taphonomy and Paleontology

Paleontologists and taphonomists could learn a great deal from ecologists about controls on nutrient recycling, both on land surfaces and in soils, and how these affect what escapes into the fossil record. Ecologists can also help expand our understanding of animal population movements, predator–prey interactions, and the ecogeographic data contained in bone accumulations. Recent growth in the availability of GIS databases containing information on both predator and prey species provides novel opportunities to examine patterns of multi-species landscape use across decadal timescales. Such data could be integrated with the locations of skeletons relative to habitat boundaries, water sources, etc. to build ecosystem-wide understanding of the spatial data contained in bone accumulations.

Ecologists are often expert modellers, extending their thinking from laboratory experiments and localized field samples to broader hypotheses about ecosystem dynamics. Why not turn this talent toward modelling what taphonomic samples of communities and ecosystems would look like over varying amounts of time, under different conditions of species richness, body size distribution, predator prey interactions, and nutrient recycling efficiency? We know enough about taphonomic processes to provide realistic starting conditions for such models, and paleontologists could then collaborate to test how such models match what they find in both modern bone surveys and the fossil record.

5.6 Conclusion

Paleontologists initiated taphonomic studies of modern ecosystems to better understand what we can and cannot know about extinct ecosystems. Through such research we have learned that ecological insights available in modern bone accumulations can also enhance knowledge of living communities and their recent histories. The growing field of conservation paleobiology will continue to work towards broadening this window in modern ecosystems and contribute to management and conservation goals. At the same time, it is clear that unlocking the full complement of ecological data in actualistic taphonomy will require collaboration with scientists working closely with the living communities.

This overview has highlighted some of the ways that taphonomy can contribute to ecology and conservation. It also has suggested how ecological research could provide unifying ideas and modelling expertise that would be very helpful to taphonomy. Clearly there is great potential for future exchange between these fields of study, which also could draw upon expertise and ideas that have been developing independently in zooarcheology, paleoanthropology, forensics, and even agricultural science and metagenomics. Forging links between ecology and paleontology is an ambitious and daunting task, one that has been slow to gather steam in spite of many good intentions over the past decades. Workshops, symposia, cross-disciplinary publishing, guest lectures, and joint teaching of university courses all could help increase interaction between ecologists and paleontologists. However, since most of us are challenged by excesses of information and limitations of time, we suggest that one of the best ways to synergize increased collaboration in the future would be to plan field projects that bring together paleontologists and ecologists to conduct taphonomic bone surveys, set up bone weathering experiments, or tackle other bone-related studies (e.g., relating to nutrient recycling). Based on our experience working at the intersection of paleontology and ecology, we can virtually guarantee that focusing initially on a joint field project would lead to novel insights, enhanced communication, and new research possibilities for all concerned.

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Chapter 6
Paleoecology in an Era of Climate Change: How the Past Can Provide Insights into the Future

Melissa I. Pardi and Felisa A. Smith

> *'A nation that forgets its past has no future'*
> *Winston Churchill*

Abstract Anthropogenic climate change is the most prominent conservation issue of our time. Expectations are that the Earth's climate will warm ~2.5–6.5° within the next century. The accompanying biological consequences will no doubt be huge. How will the diversity of life on our planet respond to rapid climate change? The best way to predict the future may be to examine the past as biota have experienced numerous episodes of climate fluctuation throughout geologic time. Some of these climatic fluctuations, particularly those of the late Quaternary, have been as rapid as those anticipated by climate warming scenarios. Analysis of the paleontological record can yield valuable information on how past climate change has shaped biodiversity in the past, and provide clues for what we may expect in the future.

Keywords Climate change • Conservation • Paleoecology • Vulnerability • Adaptation • Community dynamics • *Neotoma* • Historic ecology

6.1 Introduction

Climate change is the most pressing environmental problem humans face. Despite nearly unanimous agreement that anthropogenic greenhouse emissions are the ultimate driver of this change (Oreskes 2004), governments have yet to agree on reduction and control measures. Indeed, in the 15 years since the Kyoto protocol was signed there has been little progress made towards measurable reduction in

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global emissions of greenhouse gases; in the US, emissions have actually increased 11% since 1990 (Olivier et al. 2011). Moreover, recent proposals from global powers plan to put off action until the year 2020, exacerbating the problem. The consequence of inaction is that we are now faced with the possibility of more extreme change than previously thought likely (IPCC 2007a). Model predictions had called for a 2.5–6.5°C rise in global temperature by 2100, with some of the uncertainty reflecting the timing of the onset of emission reductions (IPCC 2007a). The failure to enact controls increases the probability that actual change will be toward the larger end of this range (IPCC 2007a).

Recent studies have highlighted the seriousness and immediacy of climate change. The extent of glacial melting observed has far surpassed that predicted (Joughin et al. 2004; Rignot and Kanagaratnam 2006; Luckman et al. 2006; Howat et al. 2007). Glaciers in the Himalayas have shrunk by as much as 20% in the past 30 years (Fujita and Nuimura 2011; Scherler et al. 2011). Polar sea ice has melted at an alarming rate and the vaunted "northern passage" is now a reality. As of 2011, the strait across the North Pole was ice-free for the first time during the summer months. Warming has already lead to perceptible changes in the number of ice free days in the US (NOAA 2001, http://www.publicaffairs.noaa.egov/releases2001/jan01/noaa01008.html). These wholesale environmental changes have already led to a number of demonstrable perturbations in ecosystems (Parmesan and Yohe 2003). Not only have changes in the abundance and distribution of species been noted, but the phenology of flowering and migration has also been altered (Inouye et al. 2000; Niemelä et al. 2001; Patterson and Power 2002; Post and Forchhammer 2002; Walther et al. 2002; Ogutu and Owen-Smith 2003; Parmesan and Yohe 2003; Root et al. 2003; Grayson 2005).

Conservationists face the daunting challenge of understanding and predicting the biotic responses to climate change over a wide variety of spatial and temporal scales. This is complicated by "an uneven understanding of the interlinked temporal and spatial scales of ecosystem responses." (IPCC 2007b, pp. 214). Yet, successful mitigation and conservation efforts hinge on an understanding of likely ecological and/or evolutionary responses to climate, which include the fine details of species interactions as well as community dynamics.

Paleoecologists know that climate change is not new to the earth systems. From the snowball earth of the Proterozoic, to the thermal maximum of the Paleocene-Eocene, to the ice ages of the Pleistocene, climate has dramatically influenced life over the history of the earth. Our present interglacial, the Holocene, is the most recent interglacial in a series of glacial-interglacial cycles that began some 2.58 million years ago. Since then, biota have experienced repeated bouts of warming and cooling with ice sheets advancing and retreating on 40,000- and 100,000-year time scales. Until fairly recently the dominant view has been that these past climate changes occurred gradually in response to natural processes (Imbrie and Imbrie 1979). This made it problematic when extrapolating past ecosystem responses to climate change to the much more rapid changes associated with human global warming. However, recent paleoevidence derived from deep-sea sediments and ice cores suggest that abrupt climate change is not uncommon (Allen and Anderson

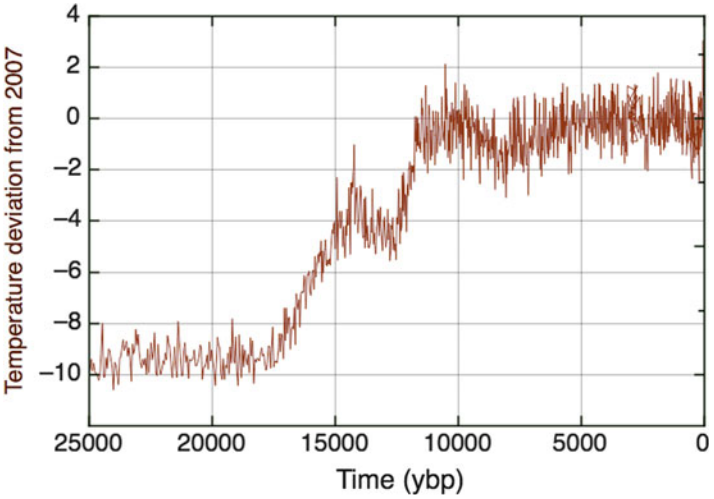

Fig. 6.1 Temperature fluctuations over the late Quaternary. Analysis of $\delta^{18}O$ from occluded air bubbles within highly resolved ice cores drilled in Greenland and the Antarctic provide a historical record of climate over the past 1 Ma. We use ice cores because of their high resolution and long temporal span; admittedly there are substantial differences in location and local climate regimes between Greenland and Antarctica and western North America where our study sites are located. However, our interest is in the relative rates of change over different time periods, not absolute temperature shifts. Data shown here were taken from the EPICA Dome C ice core (EPICA group 2004; Jouzel et al. 2007); patterns are similar with other cores

1993; Dansgaard et al. 1993; Severinghaus et al. 1998; Indermuhle et al. 1999; Alley 2000; Grootes et al. 2001; Martrat et al. 2004; Rial 2004). Indeed, highly resolved ice core records from Greenland and Antarctica reveal more than 20 abrupt shifts in the climate system during the last glacial (Fig. 6.1; Alley 2000) Each oscillation consisted of gradual cooling followed by an abrupt warming; in some cases, such as the Younger Dryas, these shifts exceeded 6–10°C over just a few decades (Alley 2000). Hence, studying the response of biota to climate shifts over the late Quaternary may be the best proxy we have for understanding future responses.

The discipline of paleoecology has become highly relevant for assessing the likely impacts of climate change on ecosystems because it works on scales that are typically larger than those used in classical ecology and more in line with that of climate (Fig. 6.2). For example, given that the average longevity of a mammalian species is around 1–2 million years (Foote and Raup 1996; Alroy 2000; Vrba and DeGusta 2004), it is clear that virtually all extant mammals have experienced multiple episodes of rapid climate change over their “lifetime”. Indeed, all modern taxa in the Northern Hemisphere experienced the severe climate shifts associated with the Younger Dryas cold episode. This particularly severe event must have exerted substantial environmental selective pressure on taxa.

In this chapter, we discuss deep time patterns of biotic responses to climate change. Our emphasis is on the Cenozoic and in particular the late Quaternary

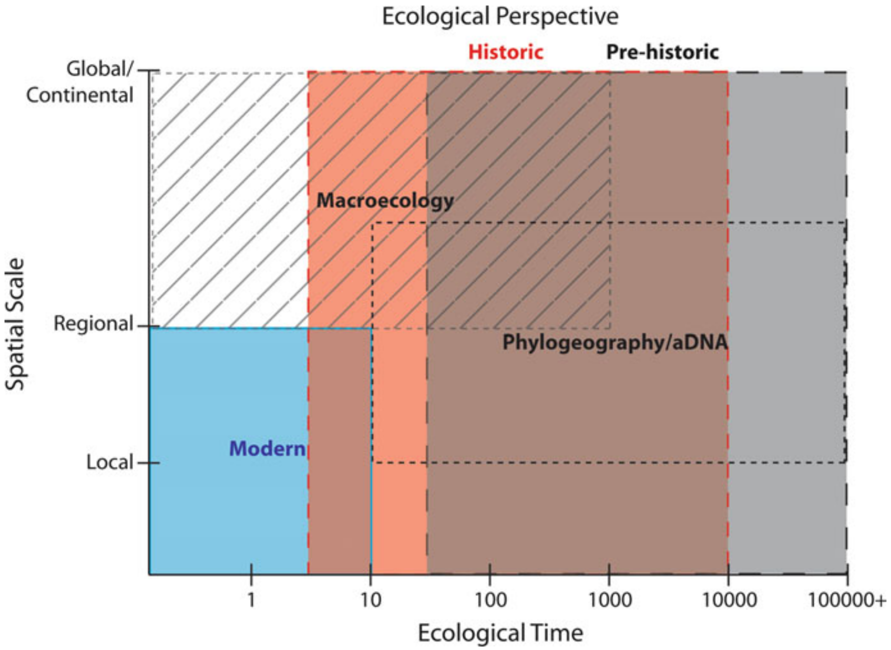

Fig. 6.2 Graphical depiction of the expected spatial and temporal scopes of modern (*blue*), historical (*red*) and paleontological (*gray*) ecological perspectives. Areas of overlap between perspectives represent areas of research that compliment each other, and are areas where modern-, historical-, and paleo-ecologists can work together. Macroecology, phylogeography, and ancient DNA (aDNA) are a few examples of sub-disciplines that overlap these ecological perspectives

because of the exceptionally well preserved and highly resolved fossil and climate record found in this Period. Recent fine-scale paleoclimatic reconstructions developed with pollen, tree ring chronologies, highly-resolved ice cores records, and other proxies have resulted in a new appreciation of how rapidly and frequently late Quaternary climate has changed (e.g., Allen and Anderson 1993; Dansgaard et al. 1993; Bond and Lotti 1995; Dahl-Jensen et al. 1998; Bond et al. 1999; Alley 2000). Thus, the past 40,000 years is arguably the best proxy we have for understanding the influence of anthropogenic climate change on organisms. We address the issue of how resilient ecosystems and species are to climate change. We characterize “resilience” as the ability of ecosystems to “absorb disturbances while retaining the same basic structure and ways of functioning, the capacity for self-organization, and the capacity to adapt to stress and change” (IPCC 2007b, pp. 880). We provide examples of studies that document the ways that species can respond to changing environmental conditions, namely through extinction/extirpation, relocation, and adaptation. Paleoecological work has documented all three of these response types. Thus, our aim is to illustrate the utility of a deep time perspective in studies of anthropogenic climate change.

6.2 Extinction/Extirpation

How resilient *are* ecosystems to environmental change? Critical to this issue is the question of what makes a species vulnerable to extinction, and it is one of the most studied questions in paleontology. It's also a question that has not been completely resolved, and most of the research in this area has focused on marine invertebrates. Still, several of the characteristics that make organisms susceptible to extinction in the fossil record may be the same characteristics predicted to increase vulnerability to future climate change. However, it should be noted that the influence of humans on the extinction process may alter the factors enhancing extinction risk (Finnegan et al. in review).

Extinction selectivity has been the focus of a tremendous amount of research on fossil marine invertebrates (Jablonski 2001, 2005, 2008; Smith and Roy 2006; Payne and Finnegan 2007; Finnegan et al. 2008; Leighton and Schneider 2008; Janevski and Baumiller 2009; Roy et al. 2009). In large part, this is because the marine fossil record is far more complete both in sampling and duration than the terrestrial record. Sepkoski (1992) was the first to assemble a large paleontological database of marine taxa to examine biodiversity over the Phanerozoic; after his death these efforts were expanded and refined (Alroy et al. 2001, 2008; Peters 2004). Such data have allowed examination of patterns of origination and speciation over geologic time. Much focus has gone into characterizing whether extinction risk is dependent on the intensity of extinction; that is, is a mass extinction fundamentally different from background events? This is relevant to anthropogenic climate change, because it is widely believed that this change will herald a sixth mass extinction event, distinct from others in that it is human mediated (Wake and Vrendenburg 2008; Barnosky et al. 2011).

A clear pattern that emerges from the aforementioned analyses on extinction vulnerability is that survivorship is clearly dependent on extinction intensity rather than ecology or life history. The particular traits that offer protection during background extinctions afford little protection during mass extinctions (Jablonski 2005; Payne and Finnegan 2007). For example, the geographic range of marine taxa is positively associated with survivorship during background extinctions, and this relationship is diminished during mass extinctions (Payne and Finnegan 2007). As such, mass extinction events are generally too widespread and too catastrophic to discriminate among species (Raup 1992).

During "normal" or background extinctions, however, several factors have been identified that can either enhance or reduce extinction risk. Low diversity can increase the odds of extinction. Monospecific genera tend to fare worse than more diverse genera with respect to extinctions (Janevski and Baumiller 2009). However being clustered in a clade means that you generally share many of the same traits. If that trait enhances extinction risk, then membership in a diverse clade offers little protection. Thus, even very diverse clades can become extinct at a higher rate than expected from random extinction (Janevski and Baumiller 2009). Large geographic range size also appears to promote survival at the clade level both for background and mass extinctions (Janevski and Baumiller 2009; Payne and Finnegan 2007).

For vertebrates, a common character used to predict extinction risk is body size (Cardillo 2003; Jones et al. 2003; Cardillo et al. 2008). Body size matters because it places constraints on many physiological and ecological traits (Peters 1983; Calder 1983; Brown et al. 2004). For example, the diversity and structure of small mammal montane communities was influenced by climate change more strongly than large-bodied taxa at glacial-interglacial transitions throughout the Pleistocene (Barnosky et al. 2004). Similarly, climate and habitat change at the end of the last glacial has caused modern communities to be relatively less diverse than those recorded from the region before the glacial (Blois et al. 2010).

Extinction risk does not appear to be random, even with regard to mass extinctions (Payne and Finnegan 2007; Janevski and Baumiller 2009). While climate change will affect species globally, regional impacts will be variable, and we can reasonably expect certain taxa to fare better than others based on pre-adaptive traits and their ecology. For example, studies on droughts from past interglacial lacustrine deposits support the prediction that the North American southwest will become more arid with anthropogenic climate change (IPCC 2007b) Huge swaths of forest have burned in recent fires connected to drought. These stands are expected to never return to their pre-burn state, but be replaced with different species (Margolis et al. 2011). Such an ecological filter would open up niches to pre-adapted species, and shape future habitats, speciation patterns, and diversity. Such rapid reorganizations from perturbations have been postulated as one of the reasons that extinctions get so bad (Erwin 2001). This is troubling if, in fact, we are going through a sixth mass extinction.

Ecological filters do not have the same effects across lineages. Whereas climate variability throughout the late Quaternary altered mammal communities substantially (Barnosky et al. 2004; Blois et al. 2010), insect faunas were not impacted in the same way. Indeed, extinction rates in insect faunas have remained relatively low, and species and communities remained fairly constant over the last million years (Coope and Wilkins 1994). Plants also exhibit distinctive patterns brought about by ecological filters. For example, during the Paleocene/Eocene warming, North American paratropical plant communities exhibited only minor changes in diversity (Harrington 2001). Similarly, abrupt climate change during the Pleistocene/Holocene transition did not induce broad plant extinctions in North America, but rather, community assemblages shifted rapidly in response (Jackson and Overpeck 2000; Davis and Shaw 2001; Williams et al. 2001; Williams and Jackson 2007; Shuman et al. 2009). The persistence of plant species during dynamic climate shifts of the late Quaternary occurred through a combination of migration and adaptation (Davis and Shaw 2001).

Ecological filters cull certain taxa, but provide opportunities for diversification and speciation in other lineages. Pre-adaptation for new climate regimes can enable a species to expand into vacated niches after extinctions occur. For example, the extinction rate of horses increased to about three to four times the background level of extinction during the Hemphilian, 6.5–4.5 million years ago (Hulbert 1993).

Increased aridity reduced horse species numbers from their peak (14–20 species) during the middle Miocene, to about three species (Hulbert 1993). However, these surviving species were pre-adapted in that they exhibited extreme hypsodonty and cursorial limb morphology (Hulbert 1993). These adaptations enabled them to survive this ecological filter, and this morphology has persisted in this lineage to the present.

How did past climate change affect extinctions during the most recent deglaciation? Interestingly, the primary response for most taxa appears to be relocation rather than extinction. If we just consider North America, virtually no species under 40 kg went extinct at the end of the Pleistocene (Lyons et al. 2004); however, many species had dramatic shifts in their ranges (Graham et al. 1996; Lyons et al. 2010). Within plants, only one tree species (*Picea critchfieldii*) has been reported as becoming extinct (Jackson and Weng 1999). As a whole, floral communities underwent major range shifts (Davis 1989; Overpeck et al. 1991; Grimm and Jacobson 1992; Williams et al. 2001; Jackson and Williams 2004; Williams and Jackson 2007; Shuman et al. 2009). Although climate change at the end of the last glacial resulted in relatively fewer instances of extinction than migration, we should keep in mind that anthropogenic climate change is happening at a much faster rate than many previous climate shifts, and that it is compounded by human activities.

6.3 Relocation

Given the opportunity, organisms have a tendency to track their preferred habitat as climate changes. The responses of organisms to anthropogenic change have already been observed in many taxa (Parmesan and Yohe 2003). These responses include the poleward tracking of ranges by numerous species of alpine herbs, butterflies, and birds. Changes in phenologies by plants and insects have also been reported, leading to potential mismatches between resources and bird or butterfly migrants (Parmesan and Yohe 2003).

A focus of late Quaternary studies has been documenting range shifts of both plants and animals in response to environmental shifts (Graham et al. 1996; Jackson and Overpeck 2000; Davis and Shaw 2001; Williams and Jackson 2007; Lyons 2003; Blois et al. 2010). The development of several comprehensive databases (e.g., Graham et al. 1994; North American Pollen Database, Grimm2000) has facilitated the analysis of past biotic response to climate. FAUNMAP (http://www.museum.state.il.us/research/faunmap/) is a relational database containing detailed information on mammalian species composition, geological age, and stratigraphy for over 2,900 late Quaternary localities across the United States (Graham et al. 1996). It has been used to examine changes in the distribution of individual species as well as entire community assemblages (Graham et al. 1996; Pardi and Graham in prep). Also of great importance has been the development of various palynological databases, particularly the North American Pollen Database (NAPD) (Grimm 2000, http://www.museum.state.il.us/research/napd/), which includes data from over 800 Quaternary sites across North America. These databases can now be accessed jointly through the Neotoma Paleoecology Database (Neotoma Paleoecology Database 2011, http://www.neotomadb.org). These archives have been instrumental in housing data used to describe Quaternary shifts in floras and faunas (Grimm and Jacobson 1992; Graham et al. 1996; Williams et al. 2001; Williams and Jackson 2007).

Mammal occurrences from the FAUNMAP database are detailed enough that shifts in species ranges can be calculated for various windows of time during the last glacial. For example, range shifts of North American mammals during transitions between pre-glacial, glacial, Holocene, and modern time slices have been examined (Lyons et al. 2010). The difference in range size between the times analyzed and the direction of range centroid movement were then related to ecological parameters. Lyons et al. (2010) compared directional changes in range movement between extinct and extant taxa. Interestingly, there was no distinction found between the direction of range shifts of extinct animals and survivors of the end Pleistocene extinction. There was, however, a weak relationship between the magnitude of the distance moved and body size, with larger mammals exhibiting significantly larger shifts.

Geographic location seems to be important with regard to range changes. During late Quaternary climate change western species consistently moved shorter distances than species in the east, regardless of body size or ecological affinity (Lyons et al. 2010). The implication is that a species living in an area of greater topographic relief does not need to shift its range very much to accommodate climate change. Additionally, mountain ranges may serve as barriers to migration. The results of this study suggest that ecological traits of mammals have a limited impact on a species' capacity to relocate itself in response to climate.

Predicting the movement of montane species in response to climate change will be important for the conservation of those species, particularly those that are already restricted to higher elevations. With increased warming, these taxa will become highly susceptible to local extirpations as habitable areas on mountaintops shrink.

Recent preliminary work of small mammal faunas from cave assemblages in the Black Hills of South Dakota are producing important taxa for understanding the structure and spatiotemporal dynamics of late Pleistocene Northern Great Plains and montane communities (Pardi 2010; Pardi and Graham in prep). These ongoing excavations are producing a mix of plains, boreal forest, and tundra species from the last 20,000 years. Dating of dental elements of specific taxa from various stratigraphic horizons has provided preliminary patterns of the local extirpation of the genus *Dicrostonyx* (collared lemming) around 17,000 year BP, the arrival and loss of the genus *Myodes* (red-backed vole) from lower elevations in the Black Hills around 13,300 year BP, and the arrival of closed environment taxa resembling the morphology of *Microtus ochrogaster* (prairie vole) around 9,500 year BP. Each of these taxa cluster around distinct time intervals, suggesting transitions from one fauna type to the next, as would be expected from progressive climate warming at the end of the Pleistocene (Fig. 6.3). Additional radiocarbon dating of these and other species are expected to clarify this pattern.

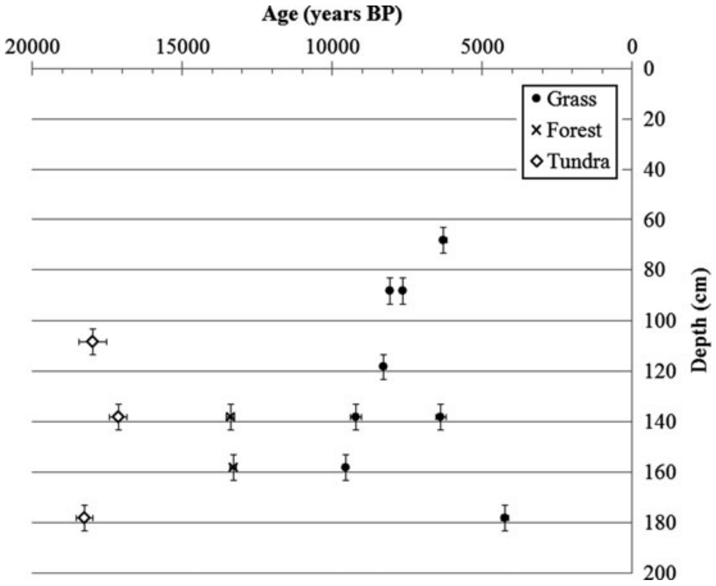

Fig. 6.3 Preliminary pattern of succession of a late Pleistocene fauna from the Black Hills of South Dakota. AMS 14C dates were obtained from individual teeth of tundra (*Dicrostonyx* sp.), closed forest (*Myodes* sp.), and open environment (*Microtus* cf. *ochrogaster*) species from throughout the cave excavation. Overlap of ages within excavation levels indicate significant mixing of strata; however, by dating individual specimens from various levels and stratigraphic types, we have estimated the time intervals of persistence for these taxa. Future dating will refine these ranges for these and other species (Pardi 2010; Pardi and Graham in prep.) Radiocarbon dates were calibrated using Calib 5.0 (Reimer et al. 2004). Median calibrated ages are reported, ± 2 s.d.

Records from the last glacial and the early Holocene are particularly valuable because they allow movements to be observed over long periods of time at the species, population, and community levels. One of the results coming out of recent work on late Quaternary biotas is that species and communities tend to behave in a Gleasonian, or individualistic, manner (Graham et al. 1996; Graham 2005; Semken et al. 2010; Williams et al. 2001; Blois et al. 2010), and that organisms have responded to climate change through both complex species interactions and interacting with their physical environment (Gleason 1926). This contrasts from the more deterministic Clementsian view of succession, where successive communities are very predictable after disturbances (Clements 1916).

It has been suggested that new non-analogue communities have the potential to emerge with future climate change (Jackson and Overpeck 2000; Williams et al. 2001; Graham 2005; Williams and Jackson 2007). A non-analogue association is the past contemporaneous occurrence of species that are geographically isolated from each other in modern faunas. Late Pleistocene faunas from across North America are more taxonomically diverse than Holocene faunas, and many contain non-analogue associations (Graham et al. 1996; Graham 2005; Blois et al. 2010;

Semken et al. 2010; Stafford et al. 2011). Some of these associations occur as a result of taphonomic mixing, but several of these associations have been verified through accelerator mass spectroscopy (AMS) ^{14}C dating (Semken et al. 2010; Stafford et al. 2011). Non-analogue faunas have also been verified on other northern hemisphere continents (Stafford et al. 2011).

If late Pleistocene faunal communities were diverse and novel, it follows that vegetation communities may have been different as well (Graham and Mead 1987; Graham and Grimm 1990; Blois et al. 2010), and non-analogues have indeed been observed in plant communities (Jackson and Overpeck 2000; Williams et al. 2001; Williams and Jackson 2007). Unlike mammal communities, which are simply defined by the co-occurrence of non-analogue species, non-analogue floras are usually defined by the percent composition of different taxa in pollen spectra, often at the genus level. These assemblages are indicative of individualistic responses to, presumably, novel climates (Williams et al. 2001; Williams and Jackson 2007). Interestingly, non-analogue floras and faunas disappear synchronously with the end Pleistocene megafauna extinction, and vertebrate community diversity also decreases after this time (Graham 2005; Blois et al. 2010). The grazing of very large megaherbivores could have kept habitats more open and increased local and regional diversity; however this does not explain non-analogue plant assemblages outright, and the existence of non-analogue climates provides a complimentary explanation (Jackson and Overpeck 2000; Williams et al. 2001).

Dispersal of plants is fundamentally different from that of animals. Range shifts occur through a combination of colonization by propagules and local extirpations, rather than the actual movement of individuals. Can the fossil record tell us how fast plants can respond to rapid climate change? The warming at the end of the Younger Dryas cold interval (~11.5 kyp) occurred extremely quickly, perhaps as quickly as a few decades (Severinghaus et al. 1998; Alley 2000). As measured from Greenland, local temperatures increased by as much as 5–10°C over this brief time (Severinghaus et al. 1998; Alley 2000). In response, there were biome-scale changes in vegetation communities in North America (Overpeck et al. 1991; Shuman et al. 2005, 2009). Dissimilarity analyses of pollen spectra from the northeastern United States show major turnovers in the composition of forests, with the crippling decline of spruce (*Picea*) (Shuman et al. 2009). The spruce species *Picea critchfieldii* was widespread through eastern North America, but went extinct during the last deglaciation (Jackson and Weng 1999).

Rapid climate change during the transition out of the last glacial period influenced the trajectory of Holocene biotic communities. In the northeastern United States, spruce never returned to its pre-Younger Dryas extent, and was replaced almost entirely by pine (*Pinus*), hemlock (*Tsuga*), and beech (*Fagus*) (Shuman et al. 2009). The characteristically diverse spruce and hardwood forests from this region were reduced to marginal environments by the end of the Pleistocene (Jacobson et al. 1987).

The Younger Dryas is, temporally, the closest analog we have to modern anthropogenic climate change. Shifts in community composition such as those seen at the end of this event should evoke a sense of urgency with the prospect of anthropogenically induced climate change. The paleontological record indicates that major community turnovers over large geographic scales can happen within a single human lifetime.

6.4 Adaptation

Most studies of extant organisms overlook the possibility of adaptation to climate change. In general, the assumption appears to be that climate shifts will occur too rapidly for species to respond (Huntly 2007). Yet the literature is replete with examples of rapid evolutionary response to strong selection (Thompson 1998). Is it possible for organisms to adapt? What evidence exists that organisms have adapted to past climate changes? While the paleontological record has always yielded a record of the dynamic nature of animal and plant distributions, more recent work is providing important insights into the evolutionary capability of organisms to respond to environmental perturbations. The most likely and perhaps the easiest way for organisms to adapt to climate change are through changes in body size.

Why body size? Scientists have long known that how animals interact with their environment is strongly influenced by their body size; temperature directly influences the energetic relationships and physiology of animals (Calder 1983; Peters 1983). Indeed, for many taxa the relationship between body mass and temperature is so predictable over time and space that the pattern is known as Bergmann's rule (Bergmann 1847; Rensch 1938; Mayr 1956, 1963). Bergmann's rule is the idea that, for a broadly distributed genus, those species of larger size are found in colder environments, and those of smaller size are found in warmer areas (Bergmann 1849). Although originally formulated in terms of species within a genus, it also holds in terms of populations within a widely dispersed species. The pattern was named after the German physiologist, Carl Bergmann, who was among the first to propose it (Mayr 1956). Among contemporary animals it appears to be generally valid for a solid majority of vertebrates, including birds and mammals; interestingly, it also holds for numerous species of ectotherms, including bacteria, protests, plants, insects, marine organisms, and turtles (Ashton et al. 2000; Millien et al. 2006). In addition to the spatial gradient, Bergmann's rule has been observed in populations over historical and evolutionary time when exposed to varying environmental conditions (Davis 1977, 1981; Purdue 1980; Smith et al. 1995; Smith and Betancourt 1998).

The mechanism underlying Bergmann's rule is often interpreted as a direct physiological response to temperature (Mayr 1956, 1963). As organisms increase in body mass, surface area increases more slowly than volume (surface area α length^2, versus volume α length^3), such that the ratio of S to A scales as $\sim V^{2/3}$. Because heat loss is proportional to surface area, this means that larger animals lose less heat per unit mass than smaller conspecifics. Thus, they have an advantage under cold environmental conditions. Conversely, smaller animals have a greater surface to volume ratio and are more capable of dissipating heat under thermally stressful warm conditions. However, this explanation is not universally accepted (Millien et al. 2006); and several other causal mechanisms have also been proposed for the ecogeographic pattern. These include those invoking gradients in productivity, life history characteristics, development rates and other factors related to thermal characteristics of the environment.

Regardless, Bergmann's rule illustrates the strong selection imposed on organisms by their environment and the potential ability of species to adapt to fluctuating abiotic conditions over evolutionary time. Clearly, the occupation of novel environments, or abrupt shifts in climate or environmental conditions, must radically alter energetic allocation between the essential activities of survival, reproduction and growth. Consequently, it has been argued that morphological shifts in body mass may be the simplest way for animals to respond to environmental change (Barnosky et al. 2003). Whether morphological changes are largely phenotypic or genetically based has not been determined, but considering the high heritability of body mass in many animals, it is likely a combination of the two (Smith et al. 2004).

Paleoecologists have recently been able to document the ability of mammals to adapt to late Quaternary climate perturbations. For example, we have examined the morphological response of *Neotoma* (woodrats) to late Quaternary climate across their geographic range in a number of studies (e.g., Smith et al. 1995; Smith and Betancourt 1998, 2003, 2006; Smith et al. 2009). Our work uses ancient woodrat middens (debris piles) as a source of primary fossil data. Woodrats, or packrats as they are sometimes called, are just that: collectors of material that they deposit in large conspicuous debris piles blocking the entrances to their houses. The materials found within typically consist of plant fragments, fecal pellets, small rocks and other materials gathered by woodrats and held together in an indurated conglomerate of evaporated urine. Middens provide both protection against predators and insulation against thermal extremes. When dens are constructed in rocky outcrops, the protected middens can be preserved for thousands of years and are easily radiocarbon-dated. All woodrat species construct middens to some degree; thus, paleomiddens are ubiquitous across mountainous regions of western North America. A single mountain transect may contain dozens of discrete middens spanning some 30,000 years or more (e.g., Lyford et al. 2003; Jackson et al. 2005; Smith et al. 2009).

Of interest here is that each paleomidden provides an estimate of the population body mass at the time it was deposited. The most abundant component within a midden are fossilized woodrat fecal pellets; the width of these scales robustly with body mass (Smith et al. 1995). Thus, by measuring the hundreds to thousands of pellets within a distinct radiocarbon-dated sample, we can obtain an estimate of the body size of the population of woodrats that produced it. Each midden record also yields plant macrofossils and so we can also obtain information on diet and vegetation communities. In short, we can characterize the morphological and genetic responses (via aDNA) of populations to climate fluctuations over thousands of years.

Our studies clearly demonstrate that woodrat populations readily adapted to the climate changes of the late Quaternary climate by changing body size (Smith et al. 1995; Smith and Betancourt 1998, 2003, 2006; Smith et al. 2009). In most instances, the response is perfectly predicted by Bergmann's rule; woodrats were larger during cold temporal intervals, and smaller during warmer episodes. Interestingly, we find remarkably consistent patterns across the entire distributional range likely reflecting the geographic similarity of environmental fluctuations (Smith and Betancourt 2006). The patterns are somewhat more complicated at geographic range boundaries where animals approach the limit of their physiological and ecological thermal tolerances (Smith and Betancourt 2003). At range edges, high elevation populations demonstrate the predicted Bergmann's rule response, while lower elevation populations are sometimes extirpated if the severity of the environmental shifts is too great.

A strong advantage to working with late Quaternary materials is that study species are extant. Thus, it becomes possible to integrate paleontological work with lab and field studies on contemporary animals. Such work suggests physiological constraints are likely the proximate mechanism underlying the Bergmann's rule cline. Maximum, minimum and lethal environmental temperatures all significantly scale inversely with body mass (Brown 1968; Brown and Lee 1969; Smith et al. 1995; Smith and Charnov 2001). For this small rodent genus, at least, body mass is highly sensitive to temperature. We also know that much of the variation in body size is likely heritable; broad sense heritability estimates exceed 0.8 (Smith and Betancourt 2006).

More recently, we have been able to characterize environmental thresholds that lead to adaption versus extirpation of species. For the past 5 years, we have been investigating the response of *Neotoma* to late Quaternary climate change along a particularly steep elevational and environmental gradient in Death Valley National Park, California. Today, this region of North America is the hottest and driest area in the Western Hemisphere. Temperatures of over 50°C are common during the summer, and temperatures of 57°C have been recorded. However, Death Valley was not always this extreme. During the late Quaternary, for example, much of the valley was covered by pluvial Lake Manly and the climate was about 6–10°C cooler (Van Devender and Spaulding 1979; Thompson et al. 1993; Mensing 2001; Koehler et al. 2005). How did animals respond to the abrupt environmental change from a hospitable habitat to the modern hyper-arid desert?

We have now recovered and analyzed more than 100 paleomiddens from a 1,300 m elevational transect through the Grapevine Mountains on the east side of Death Valley that shed light on this question (Fig. 6.4). Our results document the changing distribution of two woodrat species over the last 32,000 years (Smith et al. 2009). One of these was a large-bodied form, *Neotoma cinerea*, typically found in cooler forested habitat; the other, a small-bodied form, *Neotoma lepida*, characteristic of the Mojave desert (Smith and Betancourt 1998). During the late Pleistocene, only the large-bodied form was present. As climate fluctuated, the animals adapted in situ. Eventually as glaciers retreated and climate warmed, populations both adapted and slowly retreated upslope. By the mid-Holocene, this species was

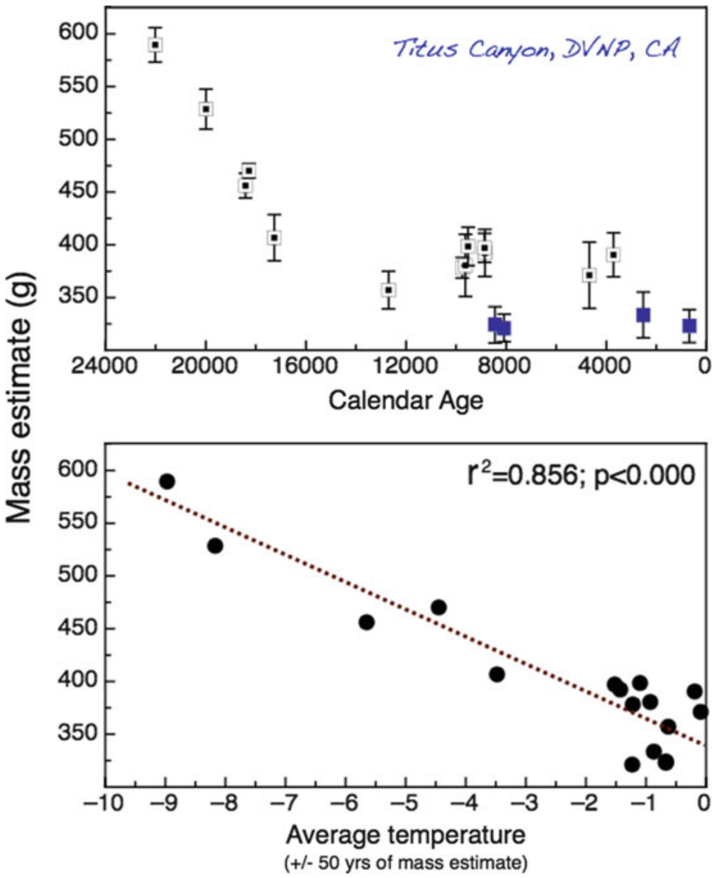

Fig. 6.4 Body mass changes over the last 25,000 years along an elevational transect in Titus Canyon, Death Valley National Park. An additional 50 paleomiddens were collected, but have not yet been radiocarbon-dated. Note the rapid dwarfing of mass that occurs at the terminal Pleistocene as ice sheet retreat and the climate rapidly warms. The relationship between body mass and the temperature at the time of midden deposition is shown in the lower panel. Temperature estimates are taken by averaging Greenland ice core estimates falling within 50 years above and below the radiocarbon date of the paleomidden. Note that the desert woodrat, *Neotoma lepida*, does not enter this canyon until the early Holocene after climate has warmed. The forest/boreal woodrat, *Neotoma cinerea*, is extirpated from this mountain range in the middle Holocene. Legend: Open squares: *Neotoma cinerea*, closed squares: *Neotoma lepida*

completely extirpated on the east side of Death Valley. Although this species was previously unknown from this region before our study, *N. cinerea* was clearly ubiquitous throughout much of the Great Basin during the Pleistocene, with distributions extending down to ~800 m elevation. Moreover, the presence of this species was apparently also tied into the displacement of juniper by almost 1,000 m relative to modern range limits (Smith et al. 2009). In contrast, the smaller-bodied form, *N. lepida*, only appeared in this area in the early Holocene. It too, adapted in situ, but slowly moved upslope in response to cave sites being abandoned by the larger-bodied species. Ultimately, *N. lepida* reached its upper distributional limit at about 1,800 m. Today, no woodrat species occupies the upper reaches of this mountain region. The results from our Death Valley project illustrate in one mountain gradient *all* the potential responses of biota to climate change: adaptation, relocation and vulnerability.

Work on other fossil populations or lineages have also demonstrated the influence of late Quaternary climate shifts on morphology. Martin and Barnosky (1993) related phyletic evolution in late Pliocene and Pleistocene musktrats (*Ondatra* sp) to climate shifts over this period America Examination of a stratigraphic section of endemic diatoms (*Stephanodiscus yellowstonensis*) from a lake in Yellowstone clearly demonstrate an abrupt morphological transition coincident with the retreat of continental glaciers; the authors attributed changes to direction selection caused by the warming climate (Theriot et al. 2006).

While studying the individualist response of species to climate changes requires analysis of single lineages, most paleoecological studies tend to be community based. This is because many fossil localities are excavations from cave or pits, which generally involves the removal and sifting of large quantities of material. These are major undertakings that can take many years to characterize. Some of the most fruitful have come from western North America, where preservation conditions are favorable. In general, an excavation results in a more restricted temporal window but yields much greater sample sizes. For example, work on Lamar Cave, a particularly rich fossil site from northern Yellowstone National Park in Montana, has yielded an exceptional record of small mammal populations over the last 3,200 years. More than 10,500 individual mammal bone fragments have been recovered and identified. This has led to number of studies that have examined species morphology, genetics, and abundance, as well as turnover in the community composition (Hadly 1996, 1997; Hadly et al. 1998). One of the most common elements recovered from Lamar Caver were pocket gophers (*Thomomys talpoides*). Analysis of size-related craniodental characters for these animals has demonstrated both morphological and ecological sensitivity of pocket gophers to the climate shifts of the terminal Holocene (Hadly 1997). Not only do gophers vary in size, decreasing during the warmer conditions of the Medieval Warm Period, but there are also significant changes in abundance related to changes within the vegetative community. Other mammals also demonstrated predictable shifts in abundance that were related to the absence or presence of preferred habitat types (Hadly 1997).

In deeper time, Porcupine Cave in the Rocky Mountains has yielded thousands of mammal fossils that date from 1 Ma to 750 Ka (Barnosky et al. 2003; Barnosky 2004; Barnosky et al. 2004). Analysis using dental morphology of the most commonly recovered mammals from this site illustrates varying adaptive responses that seem to relate to their life history. Little morphological change was observed in marmots (*Marmota* sp.) over glacial–interglacial cycles, which the authors attributed to their fossorial lifestyle. However, sagebrush vole (*Lemmiscus curtatus*), demonstrated substantial variation in dental morphology during the climate changes associated with a glacial–interglacial transition.

Paleoecology studies have also demonstrated that temperature is not always the factor that matters during climatic shifts. For example, in a study of body size variation in California ground squirrels (*Spermophilus beecheyi*), Blois et al. (2008) found that body size of populations was best explained when patterns of precipitation across the spatial gradient were also incorporated into regression models. Comparison of contemporary spatial results with fossils dating from the last glacial maximum suggested a shift towards increased precipitation in modern communities relative to the past (Blois et al. 2008). Similarly, in an early study of morphological change in carnivores, Dayan et al. (1991) found that climate factors were *not* the major determinants of body size fluctuations for many over the late Quaternary. By integrating geographic studies of modern carnivores with the fossil record, they were able to demonstrate the role of competitive interactions in influencing the body size of species. Character displacement, and not temperature or precipitation shifts, was ultimately responsible for producing the patterns observed. The importance of biotic interactions on size patterns, especially combined with climate, has been found elsewhere as well (e.g., Millien-Parra and Loreau 2000; Millien 2004; Millien and Damuth 2004).

The advent of new molecular and geologic tools is changing the field. Increasingly, paleoecologists are focusing on the influence of climate change on the genetics and biodiversity of organisms (Chan et al. 2005; Barnosky 2008). The development of ancient DNA (aDNA), despite its caveats, has revolutionized the ability to examine evolutionary processes (Higuchi et al. 1984; Willerslev et al. 2003; Briggs et al. 2007; Sampietro et al. 2007). These have led to the ability to ask directly how animals have responded to past climatic events. For example, studies of social tuco tucos from a location in South America illustrate a decrease in genetic diversity corresponding to Holocene environmental fluctuations (Chan et al. 2005). In contrast, work on pocket gophers and voles in Yellowstone National Park in Wyoming suggests genetic effects may depend on the ecology of species (Hadly 1996, 1999). While pocket gophers show a decline in genetic diversity during the Medieval Warm Period, voles increase in genetic diversity over this same time period. Other work on aDNA illustrates genetic turnover that is apparently coincident with habitat change. For example, analysis of aDNA from brown bears (*Ursus arctos*) in Beringia suggests population turnover from 60 to 14 ka (Barnes et al. 2002). Similar results are shown for muskox in northern latitudes (MacPhee et al. 2005). As techniques improve and especially, as the resolution of data increases, the integration of aDNA and phylogenetic studies is likely to be of considerable importance towards understanding how animals adapt to shifting environmental conditions.

6.5 Concluding Remarks

The field of paleoecology has been revolutionized in the past few decades by implementing cutting edge technology and techniques that have been “borrowed” from other disciplines. Stable isotopes and dental microwear have been used to tease apart ancient food webs and trophic interactions (Koch et al. 1997; Koch 1998;

MacFadden 2008; DeSantis et al. 2009; Feranec et al. 2010). Sophisticated community models have been used to look at the timing of extinction events with probable causes (Alroy 2001). Radiocarbon dating has so improved in the past decade that past population dynamics can be correlated with very small changes in past climate (Stafford et al. 1991; Stafford et al. 2011). The recent advent of macroecology also provides "a geographic and historical perspective" that may help us understand the likely effects of anthropogenic warming. As an alternative to experimental ecological research, macroecology has been remarkably successful at illuminating large-scale spatial and statistical patterns (Smith et al. 2008). Macroecology has increasingly been effectively used in climate change research (Fisher and Frank 2004; Gaston 2004; Kerr et al. 2007; Kuhn et al. 2008; Pautasso 2007; Tittensor et al. 2007; Webb et al. 2007; White and Kerr 2007; Wilson et al. 2008). Such studies have provided valuable insights into how species are influenced by climate. Less well incorporated thus far, however, is the second perspective, that of time. Macroecology and paleoecology share a lot of common ground, and it is with regard to this historical perspective that paleoecology can greatly contribute (Lyons and Smith 2010).

Future anthropogenic climate change is expected to happen at a rate much faster than most changes over earth history. With the compounding effects of human activities, earth's biota is heading into uncharted territory. Conservationists face the daunting task of trying to predict the actions that would best mediate changes to ecosystems. The window of opportunity to stave off climate change is shrinking (IPCC 2007a), and biotic consequences appear to be imminent. Our best bet is to try and implement conservation efforts synchronously with climate change to help preserve our current biodiversity. The paleoecological literature can provide important insights into patterns of past extinction vulnerability, adaptation, and community dynamics as related to climate change. Paleoecology is an important compliment to current conservation efforts, because of the temporal perspective it provides. To paraphrase Winston Churchill, paleoecology may be the key to the future.

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Chapter 7
The Ecology of Morphology: The Ecometrics of Locomotion and Macroenvironment in North American Snakes

A. Michelle Lawing, Jason J. Head, and P. David Polly

Abstract Morphological traits that have a functional relationship with the environment can be used to study relationships between organisms and environments through time and across space. Dynamics of the trait-environment complex can be studied with ecometrics in individuals, in populations, and in communities. We explored how closely correlated three skeletal traits are with substrate use, and thus macrohabitat, among communities of snakes with the goal of better understanding how climate and macrovegetation might affect snake assemblages. Substrate use explained a large part of the variance in mean length-to-width ratio of vertebrae ($R^2 = 0.66$), PC1 of vertebral shape of a mid trunk vertebra ($R^2 = 0.46$), and relative tail length ($R^2 = 0.71$). Furthermore, mean relative tail length in snake assemblages across North America is strongly associated with ecoregions and vegetation cover ($R^2 = 0.65$ and 0.47, respectively). The close relationship with macrovegetation makes relative tail length a useful tool for predicting how snake assemblages will change as climates and biomes change across space or through time. This "ecometric" approach provides a medium-scale link between data collected from ecological studies over decades to data assembled from the fossil record over thousands, tens of thousands, or even millions of years. We show how historical vegetation changes between the early twentieth and twenty-first centuries at five preserves in North America resulted in ecometric changes that parallel the

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geographic distribution of relative tail length in snake communities across North America.

Keywords Climate • Community morphology • Ecometrics • Ecomorphology • Geographic variation • Paleoenvironment • Serpentes • Taxon-free • Vertebrae

7.1 Introduction

Assessing the impact of climate and habitat change on local communities is often hampered by lack of long-term historical baselines from which to judge changes in habitats and species (Willis et al. 2005; Tingley and Beissinger 2009). To truly understand the dynamics of changing climates, landscapes, and biotas an understanding of patterns is needed at local, landscape, regional and continental geographic scales, as well as seasonal, annual, decadal, millennial, and geological time scales (McGill 2010; Wiens and Bachelet 2010). In this paper we present an ecometric analysis – a broad-scale, community-based functional trait analysis applicable to patterns in modern ecological systems as well as paleontological systems – with the goal of linking patterns on broad geographical scales with patterns relevant to local conservation efforts. Our focus is on North American snakes, a group whose ectothermic physiology links them closely with climate (Webb and Shine 1998; Head et al. 2009), are known to have had pronounced geographical responses to Quaternary climate cycles and that are expected to have large responses to climate change over the next century (Lawing and Polly 2011), shows global signs of population decline (Reading et al. 2010), and whose ecology and conservation are of intense interest (Mullin and Seigel 2009). In our study we use ecometrics as a tool for middle-scale analysis linking continental-scale range and biome data with local historical surveys of changing land cover and species conservation. The same kind of analysis has the potential for quantifying temporal changes using the fossil record and to compare rates and magnitudes of faunal changes observed over the past 50–100 years with changes that occurred with climate cycles during the Quaternary.

Ecomorphology is the study of trait variation within and between species as it relates to climate and environment (Ricklefs and Miles 1994). An analysis of ecomorphological traits at the community level is important for integrating spatial and temporal data to understand biological responses to climate change (Eronen et al. 2010a). Community-wide trait variation that relates to climate and environment is termed community or faunal ecomorphology (Polly 2010). The signature of within species ecomorphology varies greatly between species and is not consistently reliable for inferring changes in the environment (Polly 2003; Barnosky et al. 2004); however, variation in community ecomorphology – which captures the average response of all species in the community – should be a stronger indicator of environment, because it reflects the combination of adaptive responses, dynamic geographic range shifts, and extinction (Polly 2010 and references within).

The quantitative community ecomorphology approach, also known as "ecometrics", models the relationship between trait variation and environment in a taxon-free, trait-based, quantitative and testable manner (reviewed in Eronen et al. (2010a)). The taxon-free nature of ecometrics allows for a systems approach to address the relationship between community structure and environment without having to focus on a limited species group. Even 'taxon-free' ecometric traits, like all morphological traits, have phylogenetic histories as well as environmental correlations (Little et al. 2010), but phylogenetic and environmental correlations are not mutually exclusive (Caumul and Polly 2005). The phylogenetic acquisition of traits may often result from adaptation to new environmental or climatic conditions that today make up the geographic matrix of modern environments and thus are intimately related to contemporary correlations between trait and environment. Environmental controls on the geographic distribution of taxa may result in non-random phylogenetic structure in communities, either mixing unrelated species with different traits or favoring single clades with uniform traits (Kraft et al. 2007; Emerson and Gillespie 2008). Removing the effects of phylogeny will contribute to the identification of the variation in a trait that is not influenced by relatedness, but in cases where environmental sorting is based on traits that are shared phylogenetically (e.g., Jablonski 2008) the uncritical removal of phylogenetic effects risks removing the environmental effects that one is hoping to measure (Kozak et al. 2005; Helmus et al. 2007). Measuring traits instead of species occurrences in a community facilitates more robust quantitative comparisons spatially and temporally (Damuth et al. 1992; Webb et al. 2010). In addition, ecometric models developed with data from the ecological present can be validated with the fossil record and, contrarily, ecometric indices developed with data from the geological past can be validated with the ecological present.

Ecometric tools have been developed for plant and mammal communities. For example, the proportion of untoothed leaf margins in a plant community is positively correlated with mean annual temperature (Wolfe 1979, but see Little et al. 2010), the average tooth crown height in a mammalian herbivore community is a proxy for aridity (Janis and Fortelius 1988; Fortelius et al. 2002) and the average ankle posture in a mammal carnivore community is highly associated with its ecological province, vegetation cover, and mean annual temperature (Polly 2010). Paleontologists can use these community ecomorphologic indices in fossil assemblages as a tool for reconstructing paleoenvironment (Polly et al. 2011).

Herpetofauna have the potential to offer precise estimates of paleoclimate and paleoenvironment. As ectotherms whose internal body temperatures are regulated primarily by environmental temperatures, amphibian and reptile diversity, distributions, and ecology are ultimately limited by climatic parameters. For example, species richness in amphibians is explained primarily by the amount of energy and water available in the environment and in reptiles is explained mostly by the amount of atmospheric energy (Rodríguez et al. 2005).

The dependency of extant herpetofaunas on climate has been previously used to infer paleoenvironments from fossils. Blain et al. (2010) use an amphibian and reptile assemblage to infer the climate and environment of the earliest West

European hominins by using mutual climate ranges of the extant local herpetofauna and habitat weighting. Böhme et al. (2006) developed a method categorizing ecophysiological groups within herpetological communities that is highly associated with annual precipitation. Both of these methods require fossil taxonomic identification and assume conserved ecological restraints and roles of species through time.

An ecometric tool for reconstructing paleoclimate with snakes has been developed for body size. The maximum size an ectotherm can reach is limited by the ambient temperature in the environment and mass-specific metabolic rate (Makarieva et al. 2005). Head et al. (2009) used this relationship to determine mean annual paleotemperature of the Paleocene Neotropics based on comparisons between body size and climate in living anacondas and giant fossil boid snakes. This method of paleothermometry has been extended to other fossil reptiles (Head 2010).

Additional metrics of snake anatomy have been correlated to habit, and may represent useful ecometric tools. Lindell (1994) examined vertebral counts and body size in modern colubroid snakes and found that the number of vertebrae relative to body size predicted locomotory habits and constriction behavior. Guyer and Donnelly (1990) categorized an assemblage of tropical snakes into four morphological groups that are associated with habitat preference. Johnson (1955) recognized differences in length/width ratios between locomotory habits, but could not separate them from phylogenetic effects. Martins et al. (2001) showed body size, tail length, and stoutness is associated with macrohabitat in Neotropical pitvipers. Wiens et al. (2006) examined body/tail length ratios in snakes and other limbless squamates and found a general correspondence between relative tail length and fossorial vs. surface dwelling habits.

Here we explore three morphological traits in snakes as a potential proxy for paleoenvironmental reconstruction with a two pronged approach, ultimately developing a taxon-free ecometric. First, we investigate the relationship between three traits and substrate use. The traits are vertebral length-to-width ratio, vertebral shape and relative tail length. Substrate use is related to locomotion and is defined here categorically as arboreal, semiarboreal, terrestrial, fossorial, semifossorial, aquatic, and semiaquatic. Second, we develop relative tail length into an ecometric using North American snake communities. We show the strong relationship between the average relative tail lengths in a snake community and ecological province, vegetation cover, and mean annual temperature.

7.2 Methods

Three datasets were used in this study to examine the ecometric potential of vertebral length-to-width ratio, vertebral shape and relative tail length in snakes (Fig. 7.1). The dataset with the strongest environmental correlation was then further explored as an ecometric index using communities of North American snakes.

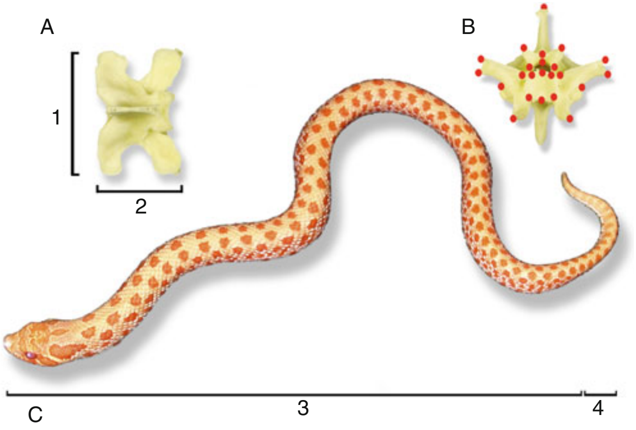

Fig. 7.1 Three traits explored for snake ecometrics. (**a**) Mean vertebral length-to-width ratio (2/1), averaged for all vertebrae within an individual; (**b**) Vertebral shape represented by principal components of Procrustes superimposed landmarks ($n = 23$); (**c**) Relative tail length (4/3)

Each dataset was derived from available trait information collected by the authors. In all analyses, we compare potential ecometric variables with environmental substrate use. Substrate use was categorized for each species as arboreal, semiarboreal, aquatic, semiaquatic, fossorial, semifossorial, or terrestrial. Due to the low sample size in some groups, we combined arboreal and semiarboreal, aquatic and semiaquatic, and fossorial and semifossorial. We note that lumping these locomotor types combines snakes with very different anatomical specializations and we discuss potential effects of this grouping on the results. The dataset associated with each trait is described below. To determine whether the traits are reliable predictors of substrate use we used Analysis of Variance (ANOVA) to test the mean ratio (corrected for evolutionary relatedness) against substrate category as the factor. To correct for relatedness, we calculated the ANOVA test statistic and then obtained a null distribution of test statistics by simulating data along a phylogenetic tree using the R package GEIGER (Garland et al. 1993). The phylogenetic hypotheses that we considered are discussed below in Sect. 7.2.5. Analyses were performed in the R Statistical Programming Language.

7.2.1 Mean Vertebral Length-to-Width Ratio

Twenty-nine snake species were selected from across the globe to represent a taxonomically and ecologically diverse sample (see Supplementary Appendix Table 1, available from IU Scholarworks at http://hdl.handle.net/2022/14288). Length and width measurements were collected for all the vertebrae of one specimen from each of the species. These measurements were then averaged across each specimen and the mean length to mean width ratio (heretofore, mean length-to-width ratio) was tested as an ecometric trait.

7.2.2 Vertebral Shape

A mid-trunk vertebra was selected from 60 snake species and photographed in anterior view. Snake species were selected to represent a diverse taxonomic and ecological sample as well as for the availability of disarticulated skeletal material (see Supplementary Appendix Table 2, available from IU Scholarworks at http://hdl.handle.net/2022/14288). Figure 7.1b shows the landmark scheme we used to represent vertebral shape. After digitizing the landmarks, we removed the effects of location, position and size by translation, rotation and scaling of the landmarks using Procrustes superimposition (Sneath 1967; Gower 1975; Rohlf and Slice 1990). Due to the low sample size in some groups, we combined arboreal and semiarboreal, aquatic and semiaquatic, and fossorial and semifossorial.

To determine if variation in substrate use is explained by vertebral shape, we performed a MANOVA on the principal components (PCs) of Procrustes superimposed landmarks with substrate use as the factor and in a phylogenetic context (the use of PCs follow Dryden and Mardia 1998). We also performed ANOVA with each PC to further investigate each uncorrelated shape variable and its relationship with substrate use. To perform MANOVA and ANOVA, we calculated the test statistic (Wilks' lambda and F, respectively) and then corrected for relatedness, using the method described above.

7.2.3 Relative Tail Length

The length of each species' tail relative to its total body length was obtained from literature for 588 North American snake species. Snake species were selected to represent the full North American snake fauna (see Supplementary Appendix Table 3, available from IU Scholarworks at http://hdl.handle.net/2022/14288). Species missing relative tail lengths were a result of (1) broken or damaged tails in their species description; (2) tail length not reported in the species description; or (3) taxonomic changes make it unclear as to which species the reported tail lengths are associated with. Relative tail lengths were obtained by taking the percentage of the length of the tail to the total body length.

In many cases, tail lengths were not reported, but the scale counts for the ventrals and subcaudals were reported. To maximize the number of species used to represent the North American snake fauna, we also calculated relative tail length by taking the percentage of the max scale count for subcaudals to the max scale count for ventrals plus subcaudals. Both tail lengths and scale counts were reported for 160 snakes and the relative tail length calculated from both measurements are highly correlated ($R^2 = 0.89$) with the slope and intercept of a fitted linear regression suggesting the usage is fairly interchangeable (slope = 1.07, intercept = 0.026). Scale counts were reported in the literature more often than tail lengths, so when both were reported we used scale counts to calculate relative tail lengths.

Snake tails are sexually dimorphic (King 2008), and tail lengths were reported for both males and females of some species. Sex-specific characteristics are not well studied in snake skeletons, so for application of this ecomorphological trait in the fossil record we grouped males and females into the same analysis. We averaged the male and female tail lengths in order to obtain an overall estimate. However, repeating the analysis with only males or females produces slightly different quantitative results, but did not change the significance or produce qualitatively different results.

7.2.4 Ecometric Analysis

Because it was the trait most closely correlated with substrate use, we further explored relative tail length as an ecometric index. Relative tail length has an added advantage for use in ecometrics because it is reported often in species accounts, making data compilation tractable for large numbers of species. Geographic distributions of species with relative tail lengths were obtained from species entries in the Catalogue of American Reptiles and Amphibians. Ranges were digitized in ArcMap 9.2. Only 494 of the 588 species had geographic distributions that were known well enough to be included in our analysis. Our data are geographically biased in that species distributions in the United States and Canada are almost completely documented, but those in Mexico, Central America, and the Caribbean less so. Nevertheless, reasonable data are available for most species with widespread distributions in these regions and we do not believe that this bias has a substantial effect on our results, except that species-level diversity may be undercounted in some of these areas. We sampled our data using a grid of equidistant points spaced 50 kmapart across the whole of North America (following Polly (2010). Grid point coordinates are available for download at http://mypage.iu.edu/~pdpolly/Data.html). This scale is similar to the geographic mixing that is likely to be present in fossil assemblages, therefore this level of sampling is appropriate for establishing patterns that can be measured both in the fossil record and the modern world (Fortelius et al. 2002). The species present at each grid point were recorded and the mean and standard deviation of their relative tail length was calculated.

We tested the association between the geographic distribution of the mean relative tail length and species number, elevation (Row and Hastings 1994), mean annual temperature (Willmott and Legates 1998), annual precipitation (Willmott and Legates 1998), local vegetation cover (Matthews 1983; Matthews 1984), and ecoregion province (Bailey 1998, 2005). See Fig. 7.2 modified from Polly (2010) for maps of these environmental variables sampled using the same 50 km grid that we used for the species assemblages. We calculated Pearson's product moment correlation (R) for

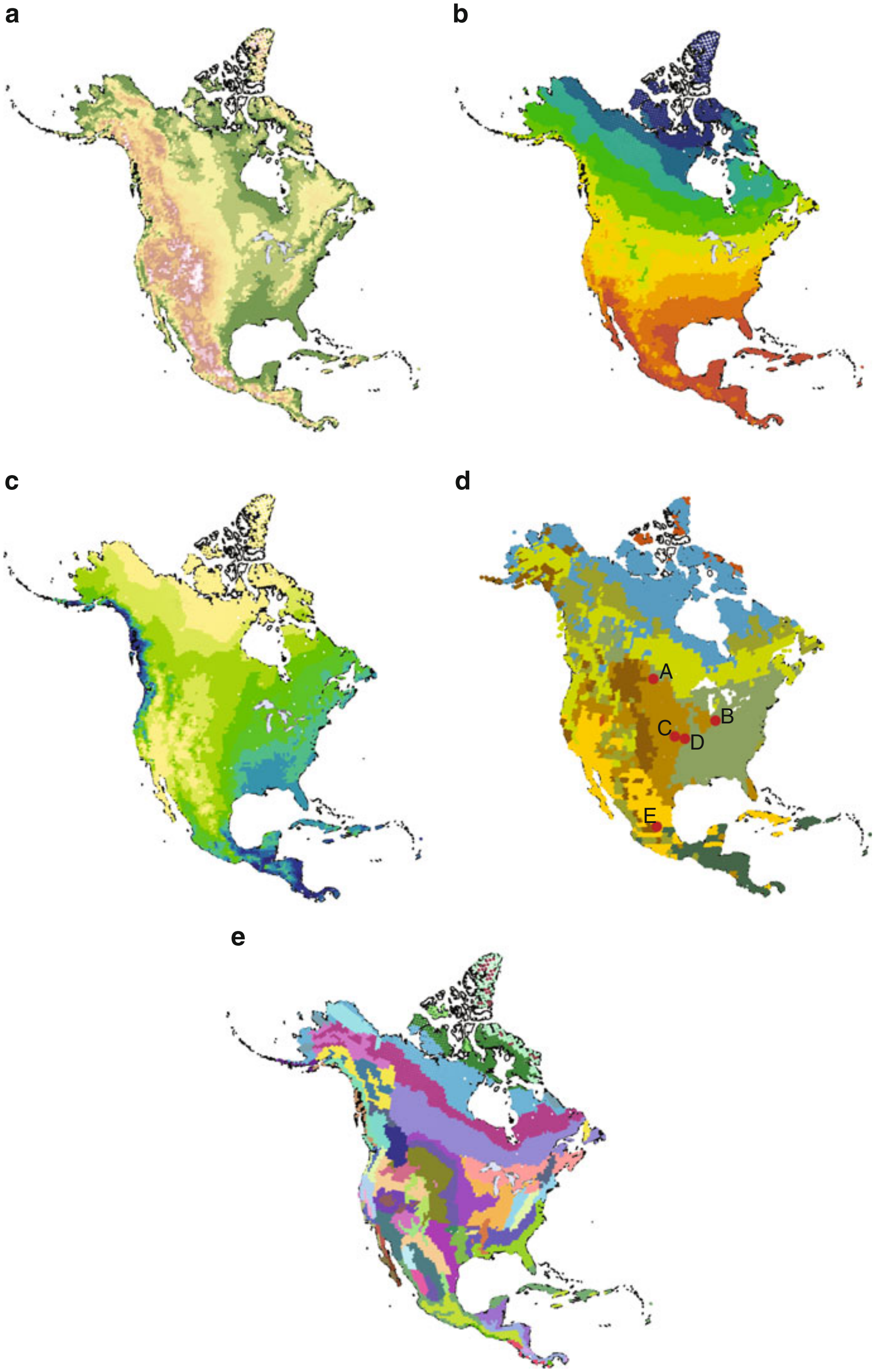

Fig. 7.2 Environmental variables in 50 km grid point spacing modified from Fig. 7.2 of Polly (2010). (**a**) Elevation is divided into 10 categories using Jenk's natural breaks algorithm. Each category is colored to represent terrain height from the lowest elevation colored as *dark green* (1–173 m) to the

continuous variables and ANOVA-derived R^2 for categorical variables. We squared species number, took the square root of elevation, and the natural log of precipitation to transform variables for normality. A randomization and bootstrap procedure was performed to calculate significance and confidence intervals for the Pearson's product moment correlation and ANOVA (following Polly (2010)).

Finally, we summarized the relationship between the relative tail length and macrovegetation by creating an "ecometric space" for macrovegetation types. To do this we calculated the mean and standard deviation of relative tail length for each of the 50 km snake community assemblages and recorded the macrovegetation type at each point. We then binned the means and standard deviations into a 25 × 25 cell bivariate histogram, tallying the frequency of different macrovegetation types in each cell. The most frequent vegetation type associated with the points in the bin was taken to be the "expected" vegetation given a particular community mean and standard deviation. Macrovegetation types were modified from the Matthews vegetation cover dataset described above, but modified by amalgamating similar vegetation types when they could not be distinguished by ecometric analysis: cold-deciduous forest and cold-deciduous woodland were amalgamated into "cold-deciduous forest"; tall, medium and short grasslands were amalgamated into a single "grassland" category; meadow and forb formations were amalgamated into "meadow"; evergreen needleleaved or microphyllous shrubland/thicked and evergreen needleleaved woodland were amalgamated into "needleleaved evergreen forest"; eight categories of drought-deciduous, sclerophyllous, and xeromorphic woodlands, thickets and shrublands were amalgamated into a single category "scrub"; and tropical evergreen rainforest, tropical/subtropical evergreen needle-leaved forest, and tropical/subtropical evergreen broad-leaved forest were amalgamated into "tropical forest". Note that the correlations between relative tail length and vegetation above were performed using Matthews' original categories.

7.2.5 Phylogenies

We explored several phylogenetic hypotheses for the comparative analysis. For each trait, different species were included in the analysis and a relevant phylogenetic hypothesis was assembled. The assembled phylogenies were first built to be as

Fig. 7.2 (continued) highest elevation colored as *white* (2596–3660 m); (**b**) Mean annual temperature is divided into 10 categories using Jenk's natural breaks algorithm. Each category is colored to represent temperature from the lowest temperature colored *dark blue* (−19.9°C to −12.5°C) to the highest temperature colored *dark red* (21.4–28.6°C); (**c**) Annual precipitation is divided into 10 categories using Jenk's natural breaks algorithm. Each category is colored to represent precipitation from the lowest precipitation colored *light yellow* (49.1–257.4 mm) to the highest precipitation colored *dark blue* (2988.8–5239 mm); (**d**) Matthews' vegetation cover is represented with a categorical color scheme, with some categories amalgamated as described in the text. The vegetation approximately ordered from densest vegetation colored *dark green* (tropical evergreen forest and subtropical evergreen seasonal broad-leaved forest) to sparsest colored *bright red* (ice). Letters on the map indicate the conservation sites shown in Fig. 7.8; (**e**) Bailey's ecoregion provinces are represented with an arbitrary categorical color scheme fully resolved as possible (i.e. to the species level). However, not all species were represented in these phylogenies so we also ran an analysis where the phylogenies were only resolved to the genus level and the relationships of the species within them were treated as unresolved polytomies. The second analysis produced qualitatively similar results as the first, so we present results only from the fully resolved phylogenetic hypotheses.

We compiled phylogenetic relationships from several sources as follows. Higher interrelationships follow a morphological phylogeny compiled by Wilson et al. (2010). Changing the relationship of the dwarf boas, Tropidophiinae, and the Mexican sunbeam snake *Loxocemus*, to follow the molecular phylogeny slightly changes the quantitative results of this study. It does not change the significance of the relationships determined here nor does is change the qualitative results or implications of this study. Other relationships within the phylogenies follow Pyron et al. (2011), Sanders et al. (2010), Adalsteinsson et al. (2009), Burbrink (2005), Lawson et al. (2005), Slowinski and Lawson (2002), and Wilcox et al. (2002). Most within-Colubroidea relationships follow Pyron et al. (2011) with the exception of the following listed families and genera. Within Crotalinae relationships follow Castoe and Parkinson (2006) and Jadin et al. (2010). The placement of *Enulius*, *Cristantophis*, and *Urotheca* follow Crother (1999). The placement of species within *Tantilla*, *Ficimia*, and *Gyalopion* follow Holm (2008). *Rhinobothryum's* placement is according to Vidal et al. (2000). Newick formatted phylogenies can be found in our Supplementary Appendix (available at http://mypage.iu.edu/~pdpolly/Data.html and from IU Scholarworks).

7.3 Results

7.3.1 Three Ecomorphological Traits

Mean vertebral length-to-width ratio and relative tail length were both significantly correlated with substrate use, both with and without respect to phylogenetic relationships (Table 7.1; Fig. 7.3). Substrate use explained 66% of the variance in mean vertebral length-to-width ratio and 71% of the variance in relative tail length. Vertebral shape represented by all of its PCs does not have a significant portion of its variation explained by substrate use; the first PC alone does, however, have a significant portion of its variation (46%) explained by substrate use (Table 7.1; Fig. 7.3). The shape described in PC1 captures 41.5% of the total variation in shape between species. No other principal component alone has a significant portion of its variation explained by substrate use. Most of the geometric shape variation was, therefore, not explained by substrate use (see below).

For the mean length-to-width ratio, the variances in the arboreal and fossorial substrate use categories do not overlap with each other or with the terrestrial and aquatic categories (Fig. 7.3a). The arboreal category has a range of ratios close to 1

Table 7.1 ANOVA and MANOVA results for vertebral mean length-to-width, vertebral shape, and relative tail length. The null distribution for the phylogenetic correction was built from simulating new dataset of the dependent variable on a phylogenetic tree with a Brownian motion model of evolution. The test statistics (degrees of freedom- *d.f.*; *F*; and the associated probability that the correlation departs from zero – *P*) were compared from the original data and the simulated null distribution. *Asterisk* denotes significance at alpha equals 0.05. Adjusted R^2 is the amount of explained variance by substrate use in the model (ranges from 0 to 1)

	Error d.f.	F-value	P	R^2
Vertebral length-to-width				
Substrate use	25	4.3736	0.0132*	0.66
Phylogenetic correction			0.0210*	
Vertebral shape				
All Principal components				
Substrate use	56	1.1534	0.3008	0.00
Phylogenetic correction			0.3237	
First Principal component				
Substrate use	56	21.684	1.90e–9*	0.46
Phylogenetic correction			9.99e–4*	
Relative tail length				
Substrate use	327	22.615	2.2e–16*	0.71
Phylogenetic correction			9.99e–4*	

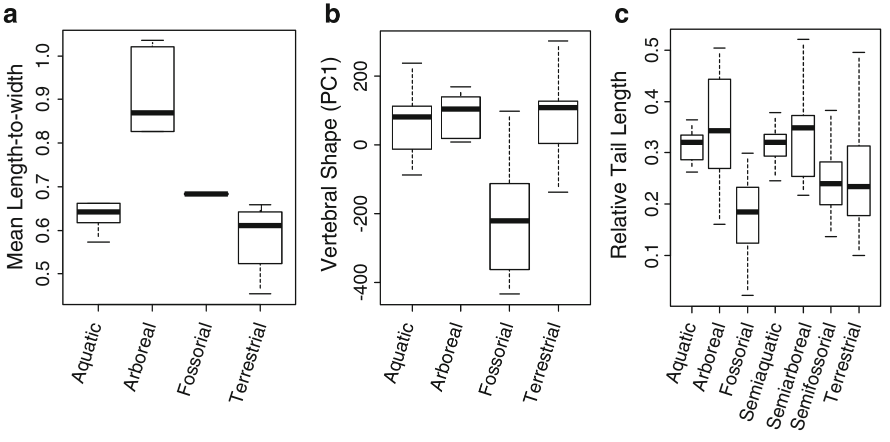

Fig. 7.3 Box plots of three potential ecometrics grouped by substrate use. The thick line in the center of each box represents the median, the box represents two quartiles (50% of the data), and the ticks off the box represent the range of the data. (**a**) Mean length-to-width ratio ($n = 29$); (**b**) PC1 of vertebral shape ($n = 60$); (**c**) Relative tail lengths ($n = 588$)

(equal length and width of vertebrae) and the others have vertebrae with greater widths than lengths on average. Terrestrial and aquatic substrate categories overlap with each other, possibly due to the grouping of semi-aquatic and aquatic snakes substrate use categories. We repeated the box plots and ANOVA with the original substrate use categories and found aquatic and terrestrial overlap only in their

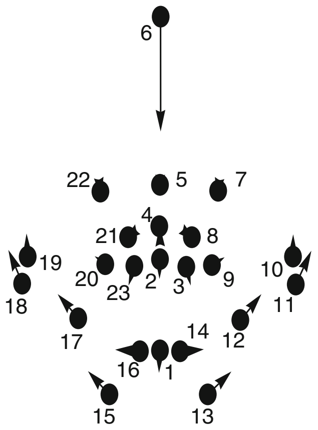

Fig. 7.4 Variation in the first PC of vertebral shape represented by the landmark scheme of a hypothetical vertebra at two positive standard deviations away from the mean (*dark circles*) pointing to two negative standard deviations away from the mean (*arrow tips*). Each landmark is arbitrarily numbered

lowest (aquatic) and highest (terrestrial) quartiles (data not shown). Including substrate use categories with very low sample sizes decreases the power of the ANOVA to detect differences in the factor and may decrease the explanatory variance; however, with this conservative approach the substrate use category still explains a significant amount of the variation ($R^2 = 0.41$; $p < 0.001$).

The relationship between substrate use and PC1 of vertebral shape is mainly driven by the fossorial category, although its variation does have some overlap with the other three substrate use categories (Fig. 7.3b). Figure 7.4 shows variation in the first PC represented by the landmark constellation of a hypothetical vertebra at two positive standard deviations away from the mean and arrow tips at two negative standard deviations away from the mean. PC1 of vertebral shape is mainly characterized by the dorso-ventral flattening of the vertebra, achieved primarily through the shortening of the neural spine (landmark 6). The aquatic, arboreal, and terrestrial categories overlap extensively, but not because of the grouping of substrate categories. Box plots with the original substrate use categories show extensive overlap in all categories, except fossorial and semifossorial (data not shown). An ANOVA with the original substrate use categories is in close agreement with the grouped substrate use categories ($R^2 = 0.46$ and $R^2 = 0.45$, respectively).

Like mean length-to-width ratio, the relationship between substrate use and relative tail length is strongly driven by the fossorial category (Fig. 7.3c). The terrestrial snakes overlap with most of the variation in all substrate use categories. The arboreal and semiarboreal categories have the longest tails (represented by the medians) followed closely by aquatic and semiaquatic. As expected, the fossorial snakes have the shortest tails.

We further explored relative tail length as an ecometric index because it explains the substrate use category better than the other two potential ecometrics (71%) and it will be used for the remaining analyses. In addition, relative tail length is widely available in the literature for most North American snake taxa.

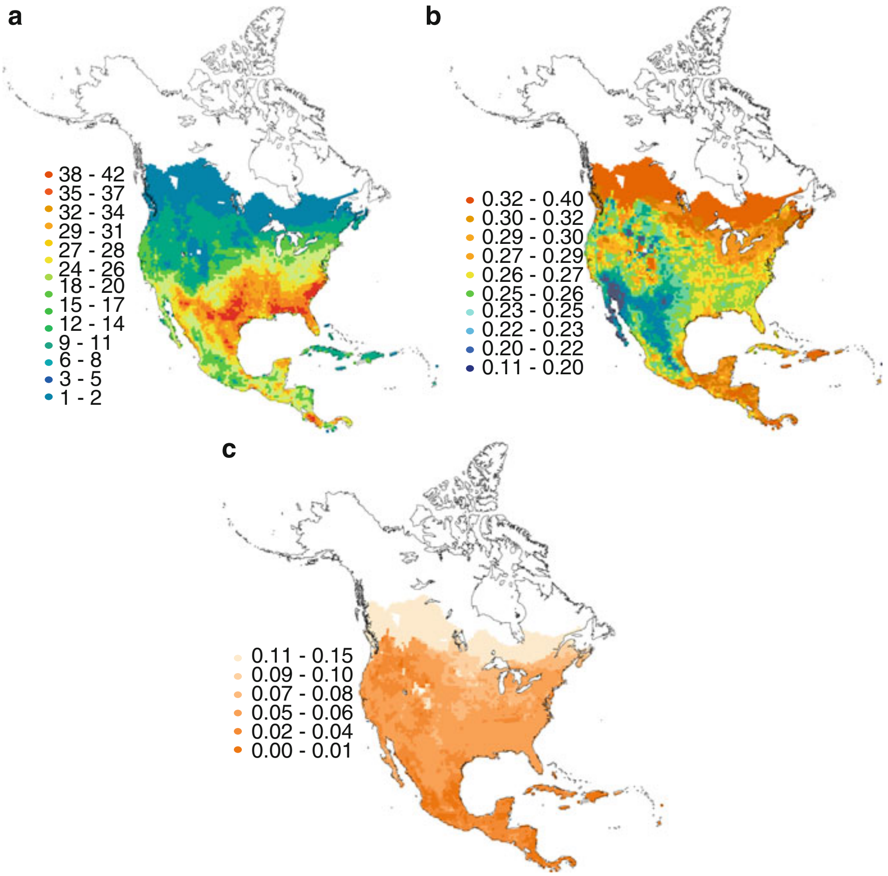

Fig. 7.5 Species diversity and relative tail length ecometrics. (**a**) Number of snake species within a 50 km grid community as used to calculate the relative tail length ecometric. Color scheme ranges from *light blue* (1–4 species) to *dark red* (38–42 species); (**b**) Relative tail lengths averaged within each 50 km grid community. Color scheme ranges from *orange* (longest tail averages) to *dark blue* (shortest tail averages); (**c**) Standard deviations of relative tail lengths. *Darker orange* represents the highest standard deviations where the lightest orange represents little or no standard deviation (sample size here is usually one). The *red* points are four representative locations shown in Fig. 7.7

7.3.2 The Geography of Morphology and Its Ecometric Implications

The geographic distribution of North American snakes covers approximately 57% of the North American continent (5,496 of 9,699 grid points are occupied by at least one species). Each North American grid point represents a potentially different community composition where communities range from 1 to 42 species, have a median of 11 species, a mean of 13.24 species, and a standard deviation of 10.29 species (Fig. 7.5a). Figure. 7.6 shows the ordering of relative tail lengths in the 494

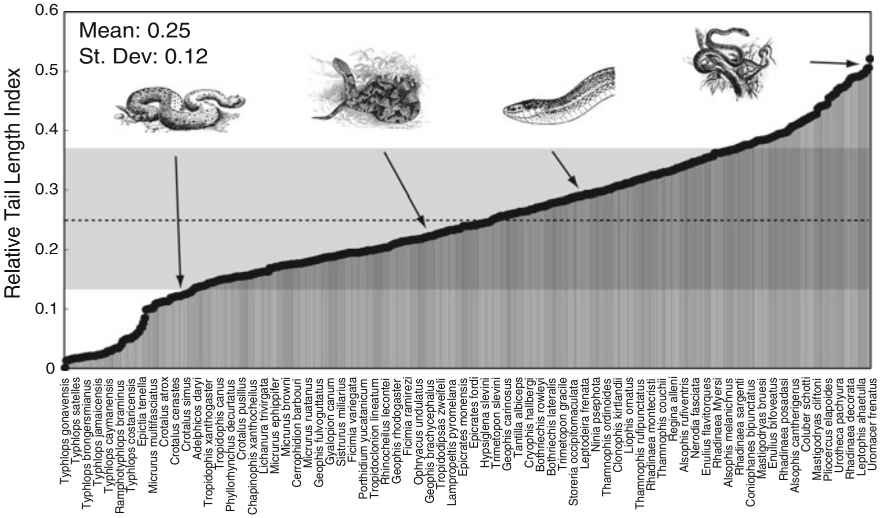

Fig. 7.6 Rank order plot of relative tail lengths in North American snakes. Short tail lengths generally correspond to fossorial lifestyles and the longest tail lengths generally correspond to arboreal lifestyles. The taxon axis is labeled every tenth species to accommodate many species labels and to indicate the type of species in that relative tail length vicinity. Illustrated taxa from *left* to *right* are sidewinder, copperhead, garter, and common *green*

species with associated geographic distributions. Generally, the shortest tailed snakes are fossorial and the longest tailed snakes are arboreal.

The geographic distribution of mean relative tail lengths is mapped in Fig. 7.5b. The mean relative tail lengths are grouped into 10 bins using Jenks natural breaks algorithm (Jenks 1977). The color scheme ranges from dark blue, representing the mean shortest tailed snakes, to dark red, representing mean longest tailed snakes. The mean relative tail lengths range from 0.11 to 0.40 and their mean is 0.28. Standard deviations for mean relative tail lengths for each 50 km community are mapped in Fig. 7.5c. Darker colors represent higher standard deviations within snake 50 km communities. Latitude generally corresponds to the distribution of the standard deviations.

Mean relative tail length is significantly correlated with species number (Fig. 7.5a), elevation (Fig. 7.2a), mean annual temperature (Fig. 7.2b), and annual precipitation (Fig. 7.2c). However, elevation and annual precipitation explain little of the variance in mean relative tail length (7 and 12%, respectively; Table 7.2). The categorical variables vegetation cover (Fig. 7.2d) and ecological province (Fig. 7.2e) explain a high amount of the variation in relative tail length (47 and 65%, respectively; Table 7.2).

Table 7.2 The relationship between mean relative tail length and climate and environment. Pearson's product moment correlation coefficient (*R*) is reported for the continuous variables along with their 95% confidence intervals and significance cut-off. The significant cut-off is the maximum value *R* can have when there is no correlation. The amount of explained variance (R^2) and its 95% confidence interval is reported for categorical variables

	R	(95% CI)	Significance cut-off	R^2	(95% CI)
Number of species	−0.58	(−0.56– − 0.60)	0.043	0.34	(0.32–0.36)
Elevation	−0.26	(−0.24– − 0.28)	0.044	0.07	(0.06–0.08)
Mean annual temperature	−0.47	(−0.45– − 0.49)	0.042	0.22	(0.20–0.24)
Annual precipitation	0.34	(0.32–0.36)	0.044	0.12	(0.10–0.13)
Vegetation cover				0.47	(0.45–0.49)
Ecological province				0.65	(0.64–0.67)

7.4 Discussion

7.4.1 Three Ecomorphological Traits

Of the three potential ecometric traits explored here, relative tail length has the closest association with substrate use. Many species descriptions report total body length and either tail lengths or scales counts from which we can derive tail lengths, making this variable attractive to develop into an ecometric. In the fossil record, total body skeletons of snakes are rarely preserved, making it difficult to estimate relative tail length for fossil taxa. A more strategic ecometric for the fossil record might therefore include the first PC of vertebral shape from the anterior view of one midtrunk vertebra, as explored in this study. The necessity of photographs of disarticulated skeletonized specimens *en masse* for a majority of the North American snake fauna prevented us from further developing this ecometric along with relative tail lengths. Future efforts in developing snake ecometrics should consider vertebral shape.

Phylogenetic relatedness has been shown to contribute to snake community structure (Franca et al. 2008), so we wanted to assess the phylogenetic correlation of the morphological traits to better understand the history of their association with substrate use. In all cases, controlling for phylogeny did not change the significance of the test (Table 7.1). However, this is not to say that the traits have not arisen phylogenetically, nor is it to say that substrate use in snakes is not phylogenetically structured; rather our results simply highlight that these morphological traits have a strong convergence across clades with respect to substrate use and that phylogeny does not complicate the interpretation of the environmental signal derived from the community-level averages in the traits.

7.4.2 The Geography of Morphology and Its Ecometric Implications

Mean relative tail length has a strong geographic structure and varies with climate and the environment. The shortest-tailed communities are distributed in the desert southwest and in central Mexico, where the longest-tailed communities are distributed in Mexican coastal regions, Central American, the Caribbean and at the northern extent of North American snake distributions in Canada. High mean relative tail length in the northern parts of North America is partially an artifact of extremely low species number. Throughout most of the northernmost region the snake communities consist only of *Thamnophis sirtalis*, which has a relative tail length of 0.33. Determining whether the lack of fossorial snakes at high latitudes is due to ecometric sorting or to coincidental physiological specialization for cold-resistance in a relatively long-tailed species (cf. Fig. 7.6) is beyond the scope of our data. Generally, within-community variation in relative tail length is correlated with latitude (the further south, the higher the standard deviation within a grid point), with exception of the northwestern and western steppe and mountain provinces.

Fischer (1960) suggested that species diversity increases with decreasing latitude, citing that species numbers in Canada, the United States and Mexico are 22, 126, and 293, respectively. Although species number increases by country, diversity on a smaller scale may show a different signal due to size of geographic distributions. We mapped the number of species within North American snake communities with a spacing of 50 km points across North America (Fig. 7.5a). Within the United States and Canada, species number increases with latitude, but farther south, species number is higher in coastal regions and lower inland suggesting that proximity to the moist Gulf of Mexico is as important a driver as latitudinal temperature gradients. The species diversity we present reflects our 50 km sampling and does not necessarily reflect the exact species diversity at any given field locality; however our data are likely to be a good proxy for local community diversity observed in the field over areas of several square kilometers.

As examples, the community distribution of ecometric variation among local snake taxa are compared directly with the local climate at four points from different regions of North America to illustrate the association between climate, environment and ecometric (Fig. 7.5a). The within-community mean relative tail lengths are shown in Fig. 7.7. Point (a) is in the Canadian province Ontario, close to the northern extent of all snake distributions in North America. This location, which is part of Bailey's Warm Continental Division, has mixed deciduous and coniferous forest vegetation cover, warm humid summers and cold winters. Two snakes occur at this sampling point with a mean relative tail length higher than average and a low standard deviation. Point (b) is in the state of Missouri in the United States. It is classified in the Prairie Division of Bailey's ecoregion classification, has forests with steppes and prairies, has cold winters and has hot and humid summers. Twenty-five species occurred at this sampling point that have a mid-range mean and standard deviation for relative tail length. Point (c) is in the state of Arizona in the United States. This point is part of the Tropical/Subtropical Desert Division of Bailey's ecoregion classification; it has mainly deserts

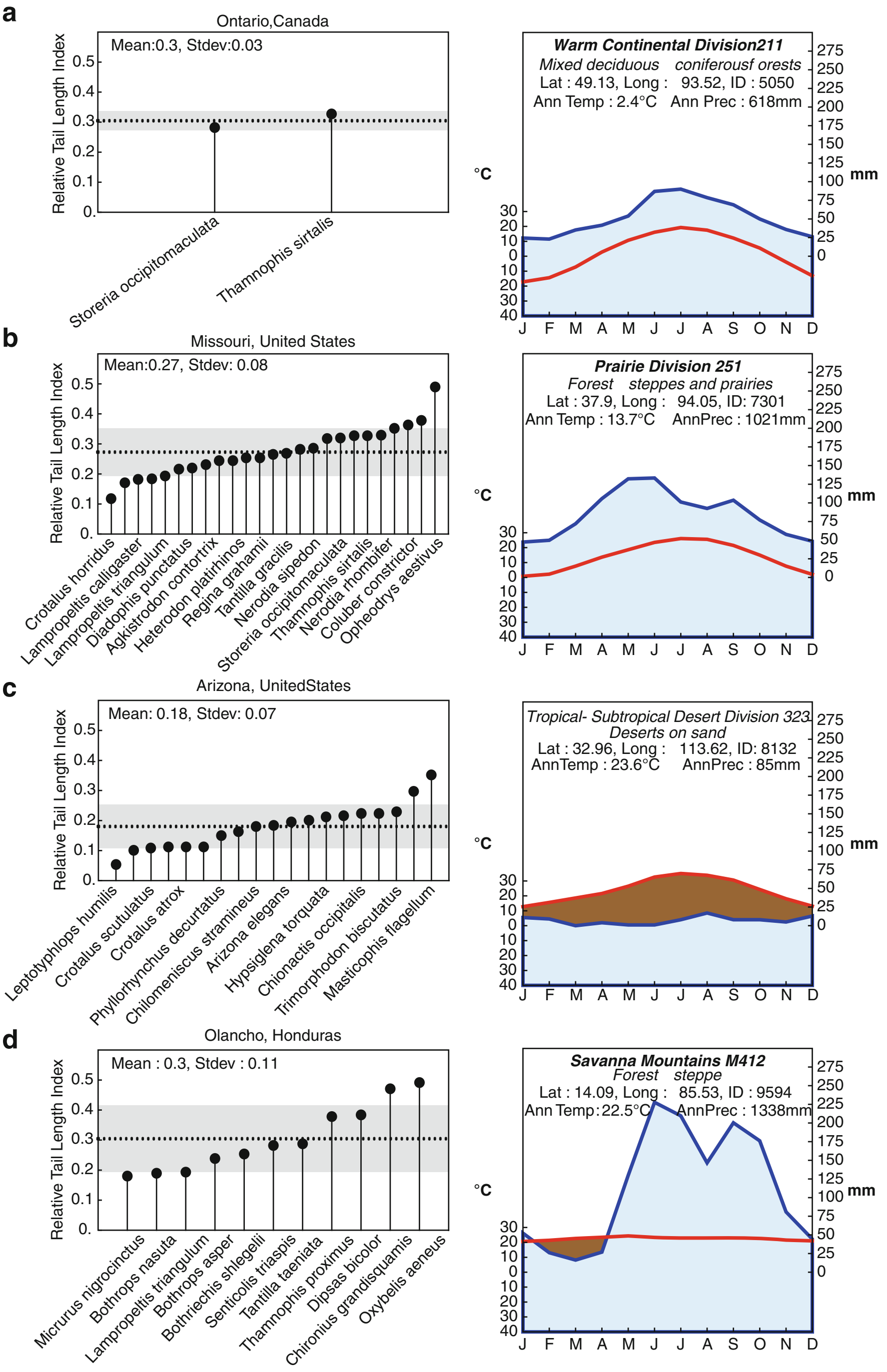

Fig. 7.7 Four representative locations showing the association between species community composition, relative tail lengths within that community, climate and ecoregion. (**a**) A representative

on sand, mild winters, hot summers and is arid year around. We sampled 19 species in this snake community, which has a very low mean relative tail length with a mid ranging standard deviation. Point (d) is in the department of Olancho in Honduras. This point in Olancho is categorized as Bailey's Savanna Mountains and it is covered with forest steppe; it has a consistently hot temperature year around and has highly seasonal wet and dry periods. We sampled 11 species in this snake community, which has a higher than average mean relative tail length and a high standard deviation.

Mean relative tail length is significantly correlated with species number, elevation, mean annual temperature, and annual precipitation. In addition, a high amount of the variation in mean relative tail length is explained by vegetation cover (47%) and ecological province (65%). Interestingly, these results are similar in magnitude to the ecometric related to average posture in mammalian carnivores. Polly (2010) found vegetation cover explained 49% and ecological province explained 70% of the variation in average posture. Low postures correspond to plantigrade stance and high posture corresponds to digitigrade stance. Comparing the geographic distribution of average posture (Fig. 7 in Polly 2010) with the geographic distribution of relative tail length (Fig. 7.5), the shortest tailed snake communities are distributed with the highest postured mammalian carnivore communities.

Olalla-Tarraga et al. (2006) mapped the geographic distribution of average snake body size in North America and Canada and showed that mean annual temperature, potential evapotranspiration, and elevation are the best descriptors of the distribution of average snake body size. Their map of average body sizes showed that the largest average body sizes are distributed in northwestern North America, specifically in the Rocky Mountain, Columbia Plateau, Basin and Range, and Colorado Plateau Geological Provinces. Those authors note that the geographic area with the largest average body sizes also has the highest variation. Those regions correspond roughly to the areas of highest variation in relative tail length on our maps (Fig. 7.5c). We found higher standard deviations in Mexico and Central America, but could not compare these areas with Olalla-Tarraga et al.'s results because their analysis was limited to the United States and Canada. These southern regions of North America have a very complex topography compared to the United States and Canada and foster complex and variable microhabitats. This complexity probably contributes to the high variability of average body sizes and relative tail lengths.

Fig. 7.7 (continued) cold-climate fauna. Ontario, Canada has two species for the representative grid point with 0.3 mean relative tail length; (**b**) A representative temperate climate fauna. Missouri, USA has 25 species for the representative grid point with 0.27 mean relative tail length; (**c**) A representative hot-weather climate fauna. Arizona, USA has 19 species for the representative grid point with 0.18 mean relative tail length; (**d**) A representative seasonally wet tropical climate fauna. Olancho, Honduras has 11 species for the representative grid point with 0.3 mean relative tail length. The right side panels depict mean monthly temperatures (*red line* with *brown fill*) and precipitations (*blue line* and *fill*). Also reported in each graph are Bailey's ecoregion division and province, latitude, longitude, mean annual temperature and precipitation (see Fig. 7.5a for geographic locations). In (**b**) and (**c**), taxa are labeled every other species to accommodate many labels and to indicate the type of species in the vicinity of relative tail lengths

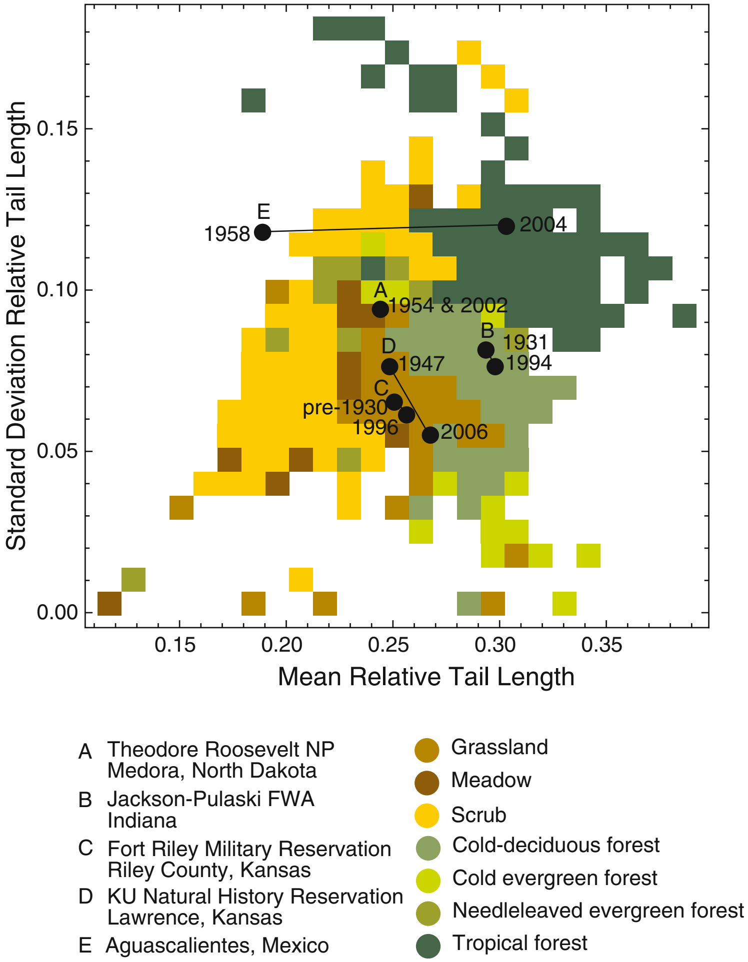

Fig. 7.8 Most common macrovegetation types for combinations of mean and standard deviation of relative tail length in North American snake assemblages. Historical and contemporary ecometric values are plotted for the snake communities at five conservation areas. Locations of the conservation areas are shown in Fig. 7.2d

7.4.3 Macrovegetation and Community Ecometrics

Because of the close correlation between the distribution of relative tail length in local snake assemblages and macrovegetation cover, an expectation exists for the kinds of vegetation expected given a particular mean and standard deviation and vice versa. The most frequent vegetation associated with means and standard deviations of relative tail lengths in our data is shown in Fig. 7.8 as an "ecometric space". Tropical vegetation is associated with snake assemblages in which the tail is relatively long (as it is in arboreal snakes) and the variation among species is relatively high. Cold deciduous forests (forests where leaves are lost due to cold winter temperatures rather than drought) are associated with assemblages that have relatively long tails but little variation among guild members. Grasslands are associated with assemblages whose average tail length is medium with little variation among species. Scrublands have assemblages with comparatively short tails, but some local assemblages have low variance and some high variance. Needle leaved forests are not readily distinguished from cold-deciduous forests or scrublands based on tail ecometrics, nor are meadowlands.

7.5 Case Studies in Conservation Ecometrics

In the ecometric approach, functional traits provide a common denominator for comparing biotic-environmental dynamics across spatial and temporal scales, potentially integrating patterns observed in the paleontological record with those observed through ecological and conservation studies (Eronen et al. 2010a; Polly et al. 2011). The strategy of ecometrics is to simplify the modern world to make it as coarse as the fossil record, sampling only at spatial scales similar to those from which the faunas of paleontological sites are drawn (50 km grids and simple presence-absence occurrence data in the case of this study), and using environmental data that are no more specific than can be estimated for fossil sites. While this scale of analysis has been shown to be effective for paleontological data (Fortelius et al. 2002; Eronen et al. 2010b) and for continental scale analysis of vertebrate faunas (Polly 2010; Eronen et al. 2010c), it remains to be shown whether ecometrics have the precision necessary to be meaningful on the spatial and temporal scales of ecological and conservation studies. If they do, then ecometrics has the potential to provide much deeper historical baselines for the modern world (Willis et al. 2005) and new avenues for modeling biotic responses to changing climates and environments (Maurer 1999). We evaluated the potential of ecometrics to be applied to conservation-scale problems using five recently surveyed snake communities that have historical baseline data from the first half of the twentieth century.

7.5.1 Theodore Roosevelt National Park, North Dakota

Theodore Roosevelt National Park (TRNP) is a 28,509 ha reserve in the Little Missouri Badlands of North Dakota that has been a US National Wildlife Refuge since 1946 (Fig. 7.2d). The park is located in the drainage of the Little Missouri, with a mixture of riparian vegetation and wetlands set within a region that is naturally mixed-grass prairie. A study of the changes in the reptile and amphibian faunas of TRNP between 1920 and 2002 was recently published by Hossack et al.

Table 7.3 Ecometric changes in snake assemblages from Theodore Roosevelt National Park, North Dakota 1954–2002. The dates of the historical baseline and the most recent survey are given, along with species lists, relative tail length for each species, and the status of each species today. The historical and current mean and standard deviation of relative tail length are reported

Species	Relative tail length	Status
Coluber constrictor	0.365	Persists
Crotalus viridus	0.113	Persists
Heterodon nasicus	0.223	Persists
Pituophis catenifer	0.22	Persists
Thamnophis radix	0.296	Persists
	Mean	STD
1954	0.243	0.094
2002	0.243	0.094

(2005), who found that the herpetofauna in general had changed very little during that time, and the snake fauna had not changed at all (Table 7.3). Hossack et al. (2005) concluded that the prairie habitats at TRNP have been minimally disturbed compared to other areas of the Great Plains, thus explaining the apparent stability of the herpetofauna. We calculated the ecometrics of the TRNP species, which have a mean relative tail length of 0.243 and standard deviation of 0.094, a combination most frequently associated with grassland or meadow in our study (Fig. 7.8). Even though the ecometric signal does not correspond to some local habitats at TRNP, such as wetlands and prairie, it does place the fauna in the correct regional habitat: grassland. The habitat TRNP was relatively unchanged over the period of study, as was the snake fauna, which means that our estimate of the ecometric change is technically consistent with field observations, though this particular example obviously does not test the ecometric approach very rigorously.

7.5.2 Jackson-Pulaski Fish and Wildlife Refuge, Indiana

Brodman et al. (2002) described changes to the herpetofauna at natural reserves in the Kankakee River drainage of northwestern Indiana between 1931 and 1994. They resurveyed the Jackson-Pulaski, Willow Slough, and LaSalle Fish and Wildlife Areas (Fig. 7.2d). Before 1800, the area was covered by marsh, wetlands, and dry prairie (Lindsey et al. 1965), but by the time of the first herpetological surveys the area had been largely drained for agricultural use. Since then the area has seen the return of closed-canopy oak woodlands and a general homogenization of the mosaic of habitats that were part of the highly altered early twentieth century landscape. The snake fauna declined from 13 species in the 1930s to 10 in the 1990s, producing an ecometric shift in mean relative tail length from 0.295 to 0.300 and a drop in standard deviation from 0.080 to 0.076 (Table 7.4). While the ecometric difference seems small, it is substantial enough to be detected in our continent-scale ecometric analysis, but our vegetation categories are too coarse to

Table 7.4 Ecometric changes in snake assemblages from Jackson-Pulaski Fish and Wildlife Refuge, Indiana 1930s–2002. The dates of the historical baseline and the most recent survey are given, along with species lists, relative tail length for each species, and the status of each species today. The historical and current mean and standard deviation of relative tail length are reported

Species	Relative tail length	Status
Coluber constrictor	0.365	Persists
Heterodon platirhinos	0.26	Persists
Lampropeltis triangulum	0.195	Decline
Nerodia sipedon	0.323	Persists
Opheodrys vernalis	0.38	Absent
Pantherophis vulpina	0.221	Persists
Pituophis catenifer	0.22	Persists
Sistrurus catenatus	0.159	Absent
Storeria dekayi	0.291	Persists
Thamnophis proximus	0.379	Persists
Thamnophis radix	0.296	Absent
Thamnophis sauritus	0.42	Persists
Thamnophis sirtalis	0.33	Decline
	Mean	STD
1930s	0.295	0.08
2002	0.3	0.076

distinguish the habitat changes that occurred (Fig. 7.2d). Finer scale vegetation data would improve the power of an ecometric analysis in this particular example, but such resolution is probably too fine for making comparisons with data derived from the paleontological and geological records.

7.5.3 Fort Riley Military Reservation, Kansas

Fort Riley is located in the Flint Hills of east central Kansas (Fig. 7.2d). This area, like Theodore Roosevelt National Park, is naturally grassland, but is more highly impacted than TRNP. Busby and Parmelee (1996) reported a decline in snake species at Fort Riley from 22 in 1930 to 17 in 1996, corresponding to an ecometric shift from a mean relative tail length of 0.250 to 0.257 and standard deviation from 0.064 to 0.062 (Table 7.5). The change at Fort Riley is also small but detectable in our continental-scale ecometric analysis (Fig. 7.8). The ecometrics of both the 1930s and 1990s snake faunas indicate grassland as the most likely macrovegetation of the area, which is consistent with observed conditions in both the 1930s and 1990s: the area retains native vegetation as the dominant land cover, even though the river valleys have been altered by agriculture and settlement and there are more trees and herbaceous vegetation than in the 1930s.

Table 7.5 Ecometric changes in snake assemblages from Fort Riley Military Reservation, Kansas 1930–1996. The dates of the historical baseline and the most recent survey are given, along with species lists, relative tail length for each species, and the status of each species today. The historical and current mean and standard deviation of relative tail length are reported

Species	Relative tail length	Status
Agkistrodon contortrix	0.247	Persists
Carphophis vermis	0.187	Absent
Coluber constrictor	0.365	Persists
Crotalus horridus	0.12	Absent
Diadophis punctatus	0.23	Persists
Heterodon nasicus	0.223	Persists
Heterodon platirhinos	0.26	Absent
Lampropeltis calligaster	0.185	Persists
Lampropeltis getula	0.174	Persists
Lampropeltis triangulum	0.195	Persists
Nerodia sipedon	0.323	Persists
Pantherophis emoryi	0.235	Persists
Pantherophis obsoleta	0.246	Persists
Pituophis catenifer	0.22	Persists
Regina grahamii	0.265	Absent
Storeria dekayi	0.291	Persists
Tantilla gracilis	0.272	Persists
Tantilla nigriceps	0.257	Persists
Thamnophis proximus	0.379	Persists
Thamnophis radix	0.296	Absent
Thamnophis sirtalis	0.33	Persists
Tropidoclonion lineatum	0.199	Persists
	Mean	STD
1930	0.25	0.064
1996	0.257	0.062

7.5.4 University of Kansas Natural History Reservation

A more interesting example is found at the University of Kansas Natural History Reservation at Lawrence, Kansas (Fig. 7.2d). Lawrence is situated in the ecotone between the eastern deciduous forest biome and the grasslands of the North American plains (Fig. 7.2d). In 1947 when the reserve was established the area had been largely cleared for agriculture and was otherwise covered with tall-grass prairie (Fitch 2006); since then the agricultural areas reverted first to a grass-weed mixture, with the subsequent invasion of forest habitats because the area was protected from burning. Fitch (2006) reported a major change in the herpetofauna of the reserve between 1947 and 2006, over which time four of the original 10 species had disappeared and another four had declined notably in abundance (Table 7.6). The ecometric mean of the 1947 snake fauna was 0.251 and its standard deviation was 0.076, values firmly associated with grassland macrovegetation in our "ecometric space" (Fig. 7.8). The 2006 fauna had a higher

Table 7.6 Ecometric changes in snake assemblages from University of Kansas Natural History Reservation 1947–2006. The dates of the historical baseline and the most recent survey are given, along with species lists, relative tail length for each species, and the status of each species today. The historical and current mean and standard deviation of relative tail length are reported

Species	Relative tail length	Status
Coluber constrictor	0.365	Absent
Croatalus horridus	0.12	Absent
Diadophis punctatus	0.23	Decline
Lampropeltis calligaster	0.185	Absent
Lampropeltis triangulum	0.195	Decline
Nerodia sipedon	0.323	Persists
Pantherophis obsoletus	0.246	Decline
Pituophis catenifer	0.22	Absent
Storeria dekayi	0.291	Decline
Thamnophis sirtalis	0.33	Persists
	Mean	STD
1947	0.25	0.076
2006	0.27	0.054

mean (0.269) and a lower standard deviation (0.054), a shift that moved the reserve from area of ecometric space associated with grasslands to one associated with deciduous forest, mirroring the actual vegetative changes at the reserve (Fig. 7.8). In this case where the area experienced a real biome shift, changes in the fauna and changes in the vegetation were correctly, albeit coarsely, modeled by our ecometric analysis.

7.5.5 Aguascalientes, Mexico

A different kind of example of a major ecometric shift is provided by the herpetofauna of Aguascalientes in central Mexico, where a resurvey in 2004 found a total of 12 snake species, whereas a 1958 survey of the same area found only 3 (Table 7.7; Sigala Rodríguez and Greene 2009). Sigala and Green attributed the increased number of species to better surveying rather than real changes in the community composition (some real changes may have occurred but they were impossible to document because of lack of a good historical baseline). Aguascalientes, an area of 5,600 km^2, is substantially larger than our other examples and covers a wider range of habitats, including tropical deciduous forests, grasslands, shrub forests, and agricultural lands. The ecometric mean and standard deviation of the under-sampled snake fauna of 1958 were 0.189 and 0.118 respectively, outside the range of our data (Fig. 7.8). The resurveyed fauna falls ecometrically within the tropical forest macrovegetation, which is largely consistent with the actual vegetation cover of Aguascalientes, more so since a substantial proportion of the species occur in the forested areas (Sigala Rodríguez and Greene 2009). The ecometrics of the 1958 fauna, which are inconsistent with any extant North American snake assemblage, serve as an indicator that the fauna was poorly sampled.

Table 7.7 Ecometric changes in snake assemblages from Aguascalientes, Mexico 1958–2004. The dates of the historical baseline and the most recent survey are given, along with species lists, relative tail length for each species, and the status of each species today. The historical and current mean and standard deviation of relative tail length are reported

Species	Relative tail length	Status
Coluber bilineatus	0.42	New
Coluber mentovarius	0.368	New
Coluber taeniatus	0.407	New
Conopsis nasus	0.197	New
Crotalus lepidus	0.128	Persists
Crotalus molossus	0.113	Persists
Hypsiglena torquata	0.214	New
Oxybelis aeneus	0.491	New
Pituophis deppei	0.228	New
Salvadora bairdi	0.508	New
Senticolis triaspis	0.284	New
Tantilla bocourti	0.24	New
Tantilla wilcoxi	0.296	New
Thamnophis melanogaster	0.314	New
Thamophis eques	0.325	Persist
	Mean	STD
1958	0.189	0.118
2004	0.302	0.12

7.6 Conclusions

Like body mass (Olalla-Tarraga et al. 2006; Head et al. 2009; Head 2010), tooth hypsodonty (Janis and Fortelius 1988; Fortelius et al. 2002), and mammalian digitigrady (Polly 2010), we found that mean relative tail length, a trait-based proxy for locomotor specialization, is geographically sorted among snake communities at a continental scale. The sorting of this ecometric trait is most strongly associated with ecological provinces and vegetation cover. We showed that some North American environments, such as those found in the Warm Continental Division (Fig. 7.7a), appear to favor little variation among the species in local communities, probably because the substrates available in this region are comparatively homogenous; other environments, such as Savanna Mountains (Fig. 7.7d), favor more variation among community members, probably because of locally heterogeneous substrate types. The shortest mean relative tail lengths are distributed in the desert southwest, suggesting sparse vegetation and aridity associated with unconsolidated soils and sediments facilitate burrowing habits.

The strong association between relative tail length and environment in North American snake communities open the possibility of using the ecometric approach as a bridge between broad-scale studies, such as continental or global analyses of the dynamics between changing climates, vegetation, and faunas (e.g., Prentice et al. 1992; Scheiter and Higgins 2009) or paleontological analyses of those dynamics through time (e.g., Mosbrugger et al. 2005; Fortelius et al. 2002; Williams et al. 2011). With the knowledge of the mean relative tail length of a North American fossil snake community, one can estimate with reasonable confidence the macrovegetation cover and ecological province associated with that community at a resolution that is commensurate with the best proxy data from the paleontological and geological record, making ecometrics an additional tool along with related tools like species distribution modeling (e.g., Maguire and Stigall 2009; Myers and Lieberman 2010; Varela et al. 2011; Svenning et al. 2011) and faunal-based distribution modeling of paleoclimate (e.g., Polly and Eronen 2011).

The resolution of our ecometric data were just fine enough to detect major changes on the scales relevant to conservation and ecology. In the five examples we reviewed, ecometric changes to all the snake faunas over intervals of 50–100 years were detectable, though the associated changes in vegetation were only detectable in cases where the local area shifted from one biome to another. The ecometric method as developed by us is not fine-scaled enough model changes in local abundance or the threat to individual species, but it is capable of measuring faunal-wide changes related to the extirpations, range expansions, and extinctions that accompany regional or continental changes in climate or land use. Ecometrics also appears to be useful as a crosscheck on whether local faunas have been fully sampled by comparing observed values to trait baselines derived from continental scale analyses.

The trait-based ecometric approach is a promising mid-level analysis that bridges the scale of paleontology, with its rich historical record of climate and faunal change, and the scale of ecology and conservation. By applying ecometrics to paleontological data, the potential exists for measuring the rates of climatic and biotic change that result in major extinctions or massive ecological reorganizations, which can then be compared to historical changes in ecological data to gauge the threat to local and regional ecosystems, communities, and species.

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Chapter 8
Biodiversity, Paleozoology, and Conservation Biology

R. Lee Lyman

Abstract A major concern in modern conservation biology is the loss of biodiversity. Such loss has, however, been common throughout the history of life. The source of the modern concern is that biodiversity loss is thought to be exacerbated by anthropogenic (human) causes in general, a top-down ecological process. But contrary to the ecologically noble savage notion, today is not different in kind from the past. Humans have depleted and extirpated populations and species for thousands of years. Climate change has also reduced biodiversity throughout history, such as when primary productivity is reduced by increased aridity in a bottom-up ecological process. The paleozoological record provides examples of normal background fluctuation in biodiversity and indicates bottom-up processes have been commonplace and top-down (particularly anthropogenic) causes can be distinguished from them in zooarchaeological collections. Both the loss and gain of species and of morphological variants can be tracked in the paleozoological record. Given that instances of biodiversity decrease on many continents at the end of the Pleistocene were coincident with climatic warming, the threat to modern biodiversity of modern global warming driven by anthropogenic processes is quite real.

Keywords Anthropogenic processes • Biodiversity • Bottom-up processes • Ecologically noble savage • Morphological diversity • Normal fluctuation • Taxonomic richness • Top-down processes

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8.1 Introduction

The utility of paleozoological (and other paleoecological) data for purposes of conservation biology, restoration ecology, and wildlife management (conservation biology, hereafter) has become clear over the past two decades (Lyman and Cannon 2004; Lyman 2006; Dietl and Flessa 2009, 2011). There are still a few skeptics and even a few naysayers, though both populations seem to be decreasing in number and in vocality. I take the position, therefore, that there is little necessity to justify the doing of what I think of as *applied paleozoology*. To me this term signifies the use of zooarchaeological (ancient animal remains with associated artifacts) and paleontological (ancient animal remains without associated artifacts) remains in an applied context, particularly in the service of conservation biology.

In this chapter I do four things. First, I begin with a brief discussion of the concept of biodiversity, arguably one of the central concerns of modern conservation biologists. It is easily measured as the number of kinds of organisms represented in an extant biological community or in a paleozoological collection. Second, I outline the difference between notions of biodiversity being influenced by bottom-up processes and being influenced by top-down processes. This framework provides an explanatory context for changes in biodiversity as manifest over the long spans of time represented by the paleozoological record. Third, I reiterate a point made earlier by Hadly and Barnosky (2009) that is highly significant. Simply put, if we can determine the "normal" or background magnitude and rate of flux in ecological and biological variables such as biodiversity, then we will be at an advantage when it comes to determining if modern flux in those variables is being driven by bottom-up processes or top-down processes, and whether those processes are largely natural or largely anthropogenic. Finally, I review several examples to demonstrate how paleozoological data may help us decipher and predict particular changes in modern biodiversity and how we can determine which of those changes are causes for concern and should be mediated.

8.2 Biodiversity

The concept of biodiversity (biological diversity) should be a familiar one (Wilson 1988; Reaka-Kudla et al. 1997). It emerged in conservation biology in the 1970s and 1980s when it was realized that ecological benchmarks or restoration reference conditions such as "natural ecosystems" and "pristine wildernesses" no longer exist anywhere on earth (Maclaurin and Sterelny 2008, p. 3). As Thomas (2011, pp. 216–217) recently pointed out, "A philosophy of conserving the composition of biological communities as they are, or restoring them to some specified (or imagined) historical state, sits uneasily with the reality of environmental and biological change." The concept of biodiversity is straightforward – the diversity of life – in such a historical context. Biodiversity can, however, be measured at any number of scales or levels of inclusiveness (DeLong 1996; Purvis and Hector 2000; Hamilton 2005; Maclaurin and Sterelny 2008; Scholes et al. 2008). These scales and levels include, but are not limited to: gene, phenotype (morphological disparity or diversity), species or higher taxon (typically richness or number of taxa represented), and community (taxonomic composition, richness, abundances or heterogeneity, evenness). All of these have gained increasing importance in studies of and efforts to conserve biodiversity (e.g., Landres 1992; Callicott 2002; Frankham and Brook 2004; Dawson et al. 2011). Numerous metrics have been developed to measure biodiversity conceived at one or more scales and in one or more ways (e.g., Magurran 2004). Here I examine two kinds of biodiversity observable in the paleozoological record – species richness or the number of species or taxa represented, abbreviated as NTAXA, and morphological disparity or variation measured as the number of morphometric variants within a taxon, abbreviated as NMORPHS.

Paleontologist J. John Sepkoski, Jr. (1997) explored the implications of the paleozoological record for the practice of conservation biology and defined biodiversity as "the number and variability of genes, species, and communities in space and time" (1997, p. 533). Importantly, he considered not just the loss of biodiversity through extinction but also the creation of biodiversity via speciation and other processes of diversification. In the long temporal duration of the paleozoological record both generic processes – extinction or loss, and diversification or addition – are always and everywhere at work. Biodiversity is not static over time or across space. The typical focus of conservation biologists is on extinction (e.g., Wilson et al. 2011), and while that cannot and should not be de-emphasized, those with a longer-term view such as paleozoologists are trained to think about *both* the subtraction (through any of a variety of processes) and the addition (again, through any of a variety of processes) of biodiversity, and both are important in the context of conservation biology.

With respect to worries about long-term biodiversity, ecological "neutral theory" – the fact that two or more species may be "ecological" or "functional equivalents" (Hubbell 2005) – is a consideration. The loss of one species may not completely disrupt ecological processes and the sustainability of a community despite a decrease in biodiversity at the species (and genetic) level(s) because an ecologically equivalent taxon survives. However, shifting from the loss of taxonomic (and genetic) diversity to the non-loss of ecological processes constitutes a shift from one kind of phenomena – stuff – to another kind – dynamic processes. Further, the only reason that Darwinian natural selection works is because it can select from available variation. Minimal variation means minimal selection and thus minimal evolution (change, adaptation, diversification) and perhaps minimal persistence of ecosystems. Bottlenecks (taxonomic, morphological, genetic) have long-term effects that are revealed by studies of ancient DNA (e.g., Leonard 2008; de Bruyn et al. 2011) and of ancient morphology (e.g., Lyman and O'Brien 2005; Leonard et al. 2007). These studies suggest that loss, even of functionally or ecologically equivalent taxa, may jeopardize the long-term resilience and sustainability of the affected communities simply because there is less variation from which the shifting forces of natural selection may choose. In short, then, a key question to consider in the context of this discussion is: What drives species loss?

8.3 Bottom-Up or Top-Down

Extinction is typically defined as the loss of the last member of a species lineage (Raup 1991). The processes that drive extinction are many and diverse but can be characterized as the plethora of factors that reduces a population beyond the point of persistence. Conservation biologists often speak of the "minimum viable population" size of a species – the minimum number of organisms of a species that is necessary to insure the lineage does not go extinct (Flather et al. 2011). The critical question in ecology and conservation biology thus is: What kinds of variables and processes influence the size of a population? This question once was answered with such things as food limits, or perhaps climatic parameters that influence primary productivity (see discussion in Hairston et al. 1960). These sorts of processes are referred to as bottom-up processes that are founded on the model of the standard ecological trophic pyramid (simplified as primary producers (photosynthesis) at the bottom, herbivores in the middle level, and carnivores on top).

Recently it has become clear that top-down processes can also strongly influence the structure of ecosystems; that is, the absence of carnivores, or their reintroduction to an ecosystem, can have cascading ecological effects on that ecosystem such that lower levels in the trophic pyramid are influenced by change in higher levels (Hunter and Price 1992; Estes 1996). Long-term studies indicate, perhaps not surprisingly, that it is hardly ever just one or the other – bottom-up or top-down – kind of process, but rather both are in play, with, say, bottom-up processes exerting greater influence than top-down processes at one time but shifting to the latter kind of process at other times (Meserve et al. 2003). Given these insights, the issue with respect to conservation biology and the preservation of biodiversity becomes one of identifying the particular processes that influence the sizes of populations in an ecosystem (and potentially driving a population below its minimum viable size and thus ultimately to extirpation), and deciphering which processes are natural and which are anthropogenic under the presumption that we can control (reduce) the latter.

We are presently experiencing what has been referred to as the "sixth [mass] extinction" (e.g., Leakey and Lewin 1996). Among the general public the best-known previous mass extinction event was the loss of the dinosaurs 65 million years ago. "Mass extinction" means the extinction of a number of species that exceeds the normal or "background" number, and it occurs over a relatively short time. A key issue with respect to the sixth extinction is that it is believed by some to be largely anthropogenically driven, either directly (e.g., over-exploitation) or indirectly (e.g., habitat destruction, industrially driven climate change). Some paleozoological data suggest that thus far, our (industrially based) activities have not resulted in an extinction rate that exceeds the normal background rate, but we are rapidly coming close to exceeding it (Carrasco et al. 2009; Barnosky et al. 2011). Although some researchers have long suggested that humans have driven previous extinction events, particularly the loss of mammoths, mastodons, and other megafauna near the end of the Ice Age 10,000 years ago (Grayson 1980), it is perhaps because of the (modern) social context of the discussion of the sixth extinction that a number of researchers who work with modern faunas are now suggesting that humans have depleted many subpopulations over many thousands of years (e.g., Kay 1994; Kay and Simmons 2002). They may be correct (but they may not be; Turvey 2009), and if they are, then the sixth mass extinction (assuming we will eventually exceed the background rate) began long before the industrialization era.

Pre-industrial humans indeed seem to have depleted some populations, but the key word is *some*; a growing body of evidence indicates they did not impact every population they exploited (Butler and Campbell 2004; Wolverton 2005; Lyman 2010a). Determining if anthropogenic processes were the cause in any given instance involves deciphering the paleozoological record and determining whether fluctuation in the apparent abundance of a taxon represents mere background flux or the sign of a longer-term trend in population size that jeopardizes the persistence of that taxon. What, then, is background flux?

8.4 Background Flux

Critics suggest using the paleozoological record for purposes of conservation biology is inappropriate for several reasons. One of these involves the fact that one cannot estimate the population size of a taxon or its presence/absence based on the paleozoological record. Authors of chapters in this volume and many readers will know that it is not a straightforward matter to estimate the prehistoric abundance of an animal taxon on the landscape based on its mortal remains. There are numerous reasons for this, and because the same processes may obscure the detection of long-term trends in estimates of taxonomic abundance or create the appearance of fluctuation in those abundances, I briefly review them here.

Although every animal (eventually) dies, the remains of only some of those dead animals will be deposited or accumulated in a place on the landscape eventually inspected by a paleozoologist (a taphonomic issue). Second, the remains in an inspected deposit may not be sampled by the paleozoologist (a sampling issue). Third, the remains may not be preserved (a taphonomic issue). Fourth, if the remains are preserved and their encompassing deposit inspected, they may not be collected (a recovery issue). Fifth, even if recovered, the remains may not be identifiable to a taxonomic level of interest. These considerations apply differentially to taxa and also to the particular skeletal elements of each taxon, and from deposit to deposit (Grayson 1984; Lyman 1994, 2008b). Ultimately we can never (in some sort of empirically testable way) analytically estimate with a known level of accuracy the living population on the landscape that the animal remains before us represent. Recent fidelity studies – studies of how accurately animal remains recently accumulated in caves by raptors and carnivores, or remains accumulated on landscapes, reflect the recently living fauna – indicate, however, that we can often come up with accurate estimates of *relative* taxonomic abundances. That is, analyses of the mortal remains of recently dead animals drawn from faunas of known composition quite often show that the relative abundances of taxa – is taxon A more abundant than taxon B – can be estimated with some accuracy (e.g., Western and Behrensmeyer 2009; Terry 2010a, b; Miller 2011). Assuming on the basis of fidelity studies that abundances of osteological remains of prehistoric animals reflect the relative abundances of the represented taxa allows us to analytically monitor general trends in relative taxonomic abundances in an area over time, though we must do so cautiously and not attempt to estimate actual abundances of individual taxa.

Minor levels of fluctuation in abundances of a taxon's remains likely reflect variations in sampling, recovery, preservation, or some other factor, including perhaps actual random flux in the size of the population on the landscape. We of course seek to determine those shifts in taxonomic abundances that are larger than random or normal background flux; the distinction can be determined statistically if so desired (e.g., Lyman 2008b; Magurran et al. 2010). And as should be clear we are most interested in those trends indicating a decrease in the abundance of a taxon, although it will be helpful to recognize increases in abundance because if we can identify the cause of an increase, we will have insight to how we might halt or even reverse a decrease.

If we want to track values in biodiversity across prehistoric time using the remains of animals, then we need to be cognizant of the fact that there are well-founded theoretical and empirical reasons to ensure that any change in NTAXA (or NMORPHS) is not merely a reflection of change in sample size (e.g., Barnosky et al. 2005). This involves the well-known species-area relationship (Arrhenius 1921; Gleason 1922; Lomolino 2000). This ecological relationship acknowledges that the greater the geographic area examined, the more species will be found. In paleozoological terms, the species-area relationship finds expression as the greater the sampling effort (usually measured as sample size, or the number of identified specimens (NISP) where a specimen is a bone or tooth or fragment thereof), the greater the value of NTAXA or NMORPHS (Lyman and Ames 2007 and references therein). One way paleozoologists have dealt with this is through rarefaction (Sanders 1968; Simberloff 1972, 1978), or drawing a random sample of some predetermined size from a large collection of remains in order that it can be compared to a small sample of remains without fear that sample-size effects are influencing the comparison (e.g., Barnosky 2004). It has been argued that rarefaction violates some statistical assumptions (Tipper 1979; Grayson 1984; Lyman 2008b), but it can be used with caution.

Along similar lines, tracking whether a taxon was present in or absent from an area during a particular span of time is not a straightforward enterprise. This is because, as the discussions of taxonomic abundances and of rarefaction imply, remains of a taxon may be absent for several reasons other than that the organism was not in the area when the sampled deposits were laid down (Grayson 1981). A taxon's remains may be absent for reasons of inappropriate sampling, for reasons of inadequate recovery (too-coarse screen mesh), or for reasons of lack of preservation (Lyman 2008a). Thus, monitoring the presence/absence of a taxon in the paleozoological record must in reality be one of monitoring the presence of a taxon, because its absence could be more apparent (no remains of it recorded) than real (it wasn't there).

Assuming we can analytically circumvent sample size effects, we must make an analytical assumption with respect to identifying the cause of change in taxonomic abundances. If abundances of taxa or the presence/absence status of taxa shift coincident with episodes of climatic change documented with independent (say, pollen) data, then it is reasonable to conclude that those shifts were driven by climatic change (were bottom-up, such as when climate change alters local primary productivity). The collection of paleozoological remains can be, but need not be paleontological; it can instead be zooarcheological (e.g., Lyman and Wolverton 2002). If the collection is archeological, then shifts in taxonomic abundances or the presence/absence status of taxa may occur coincident with change in the artifact assemblage but temporally independent of climate change, suggesting the driving processes were top-down. The slippery issue here is that people may alter their hunting or fishing strategies yet leave no trace of such among their artifacts. Changes in taxonomic abundance or presence without coincident change in climate and without coincident change in artifacts could represent an instance of this slippery issue. But efforts to identify the cause of change in taxonomic abundances and presence/absence status must be expended. If we are successful, then we will have gained insight to whether the critical processes were of the bottom-up or top-down sort. When learned in conjunction with long-term data, then we will have also gained insight to the magnitude and frequency of normal flux and also perhaps how and why normal flux might be exceeded.

8.5 Examples of Prehistoric Change in NTAXA

8.5.1 Background

The ecologically noble savage notion holds that primitive peoples were largely ecologically benign (see Hames (2007) for a recent overview and pertinent references). Over the past 25 years or so, the notion has fallen from favor (Krech 1999), though a few still seem to argue for the position when they advocate use of American Indian land use practices to "restore" pre-Euroamerican conditions because the latter are less artificial than industrially influenced conditions (e.g., Anderson 1996; Anderson and Barbour 2003). There is also still a bit of dispute over the magnitude of the effects that prehistoric peoples had on local ecologies, floras, and faunas (Krech 2005 and references therein). Within the context of these discussions, the pendulum has swung from the ecologically noble savage notion to the other side in some circles, by which I mean that a non-ecologically noble savage is now perceived by some as the key variable in structuring ancient ecosystems (e.g., Kay 1994, 1995; Martin and Szuter 1999a, b, 2004; Kay and Simmons 2002; Laliberte and Ripple 2003; Rick and Erlandson 2008; Braje and Rick 2011). Prehistoric humans were, in this view, a *keystone species*; they were of high trophic status and thus their activities exerted a disproportionate influence on the species diversity (richness and/or evenness) of a community (Paine 1969a, b; see also Davic 2003). Much of the anthropogenic-impact (non-ecologically noble savage) literature is intriguing, but much of it neither utilizes the insights gained for conservation purposes nor does it reflect the fact that there is a growing body of literature that shows that humans did not always have significant influences on prehistoric faunas.

The complexity of determining whether or not people as a keystone predator (top-down) or climate change and attendant change in primary productivity (bottom-up) influenced the abundances or presence of ungulates that were primary prey of ancient human hunters (e.g., reviewed in Broughton et al. (2008)) has likely contributed to the view that zooarcheological data are less secure indicators of non-anthropogenic causes of changes in animal abundances. Paleontologists regularly imply that their data can be used to better effect than zooarcheological data because the former date to pre-human times and thus are uninfluenced by human behaviors (e.g., Barnosky et al. 2004). Although there certainly is a degree of truth to such a contention, I believe that the presumption that zooarcheological faunas are somehow biased or provide a murky signal of the ecological processes underlying them because people had something to do with their creation is not always correct. Rather, the murkiness depends in part on the questions asked and in part on the data available.

The questions I ask here are straightforward. Are there changes in NTAXA or NMORPHS that are not correlated with changes in sample size? If the answer to the first question is affirmative, then we must determine if the changes are coincident with environmental or with technological change. If the shifts in taxonomic abundances or losses of taxa correlate temporally with shifts in climate, then it will be difficult to argue that people were the driving force behind shifts in NTAXA or NMORPHS. If the changes correlate temporally with shifts in artifact types or frequencies and independent of (do not correlate temporally with) climatic change, then it will be difficult to suggest climate was the driving force. For present purposes I ignore the very possible (and perhaps quite probable) scenario that climate change and human exploitation simultaneously influenced prey populations.

8.5.2 Methods and Materials

To exemplify how paleozoological remains in general, and zooarcheological remains in particular, can be used to monitor trends in taxonomic abundances and local extirpations that may presage extinctions, I summarize data and analyses from two geographically distinct sites the data for which have been previously published by other analysts. Both sites are located in the western United States, and both collections span the terminal Pleistocene, the Pleistocene-Holocene transition, and the Holocene. I review NTAXA at both sites and NMORPHS for one taxon at one of the sites. I also present an updated analysis of a single taxon's relative abundance in a region to show how top-down and bottom-up influences might be distinguished.

8.5.2.1 Decrease in NTAXA During the Pleistocene: Holocene Transition

It has become almost commonplace for paleozoologists to suggest that the end of glacial periods such as the transition from the Pleistocene to the Holocene 10,000–11,000 RCYBP (ages are radiocarbon years before present unless otherwise noted) are reasonable (if not completely accurate) approximations of what we may see as a result of global warming (Barnosky 2009). Numerous paleo-faunas show the effect of natural global warming on the richness of mammal taxa. I review two of them here because of the clarity of their respective signals and because they illustrate two ways that NTAXA can be monitored across a well-documented episode of climatic change. That episode involves not only warming, but in the two areas from which the examples are drawn, climate also became drier, that is, there was less precipitation which in turn reduced primary productivity, or the rate of creation by photosynthesis of organic (plant) biomass (e.g., Whittaker 1975).

The first fauna derives from Homestead Cave in northwestern Utah. The mammalian fauna was studied by Grayson (1998, 2000) who examined the ecological hypothesis that decreased primary productivity driven by decreased effective precipitation would result in decreased biodiversity. That is in fact what he found; NTAXA (rodents and lagomorphs only) decreased during the Pleistocene-Holocene transition. Grayson's (2000) data are summarized in Table 8.1. Being aware that NTAXA may be a function of sample size, Grayson (1998, 2000) choose to analyze the data from Homestead Cave in a particular way. As indicated in Fig. 8.1, he showed that the relationship between NISP and NTAXA for the three earliest strata, representing the terminal Pleistocene and earliest Holocene when conditions were relatively moist, was different than the relationship between the two variables during the middle and late Holocene when climate was warmer and drier. In short, in relative terms, more taxa were represented by fewer NISP during the terminal Pleistocene and earliest Holocene than during the middle and late Holocene, when fewer taxa were represented by more NISP. Given that the faunal remains were accumulated and deposited largely by raptors and that the change in NTAXA is temporally coincident with climate change, it is safe to conclude that the bottom-up process of climatic influence on primary productivity drove biodiversity.

In another study, Blois et al. (2010) showed a similar loss of small mammal taxa across the Pleistocene-Holocene transition. Their data originate from a woodrat midden deposited in Samwell Cave in northern California and are summarized in Table 8.2. Being aware that NTAXA may be a function of sample size, Blois et al. rarified the sample of each Samwell Cave stratum 1,000 times to the size of the smallest collection (stratum e5b, NISP = 132) and determined the mean rarified

Table 8.1 Homestead Cave NISP and richness of lagomorphs and rodents per stratum, and calibrated radiocarbon age. Note faunal remains from strata X, XIII, XIV, and XV were not studied; no radiocarbon dates available for strata III, VIII, IX, XI, and XVIII

Stratum	NISP	Richness	Calibrated age BP
XVIII	1,045	8	
XVII	15,537	16	933
XVI	6,289	16	1,078
XII	22,827	13	3,632
XI	10,077	14	
IX	22,049	16	
VIII	8,281	13	
VII	13,887	15	7,075
VI	24,299	20	7,912
V	5,101	14	9,210
IV	26,582	20	9,115
III	2,883	16	
II	7,848	22	9,600
I	10,247	21	12,400

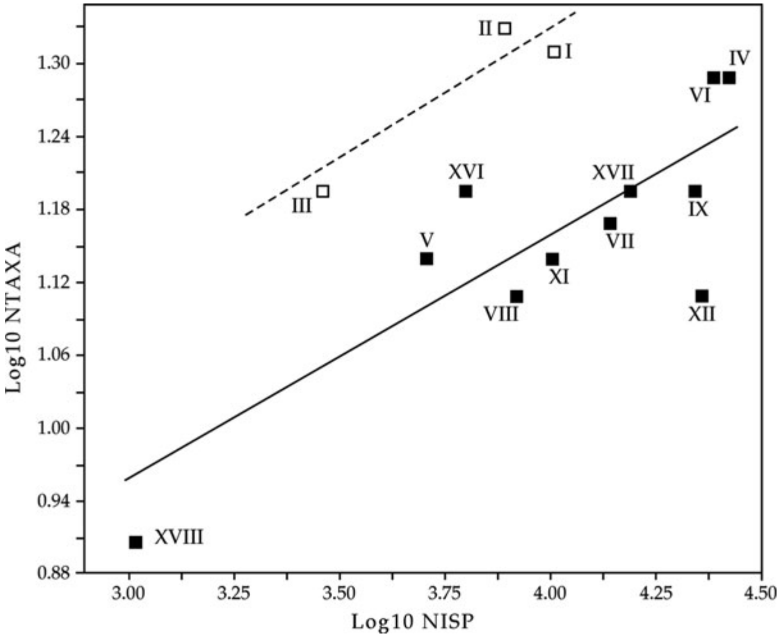

Fig. 8.1 Relationship between NISP and NTAXA in strata at Homestead Cave, Utah (Data from Table 8.1). *Open squares* and *dashed* (best fit regression) *line* are late Pleistocene and early Holocene; *filled squares* and *solid* (best fit regression) *line* are middle and late Holocene

NTAXA per stratum. They then plotted each mean rarified NTAXA value against its stratum to show that biodiversity was lost as climate warmed from the terminal Pleistocene into the Holocene (Fig. 8.2). This represents a second way, different

Table 8.2 Samwell Cave NISP, richness of small mammals, and mean rarified richness per stratum, and estimated calibrated radiocarbon age

Stratum	NISP	Richness	Mean rarified richness	Calibrated age BP
e1	251	10	7.32	900
e2	285	13	8.02	2,900
e3a	214	10	7.53	4,800
e3b	274	13	8.52	6,200
e4a	321	13	9	7,300
e4b	189	9	6.74	8,400
e5a	301	15	9.92	9,400
e5b	132	8	7.07	10,700
e6a	229	15	11.76	12,000
e6b	204	11	9	13,300
e7a	261	15	11.78	14,500
e7b	175	14	12.33	16,100
e8a	302	14	11.17	17,500
e8b	287	15	12.03	18,500

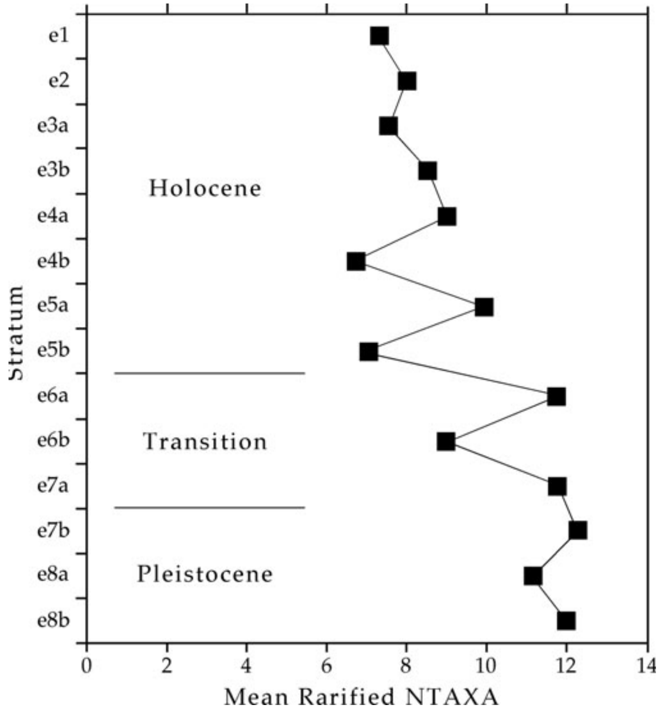

Fig. 8.2 Mean rarified NTAXA per stratum at Samwell Cave, California (Data from Table 8.2). See text for explanation of mean rarified NTAXA

from Grayson's (Fig. 8.1), to monitor NTAXA over time without fear of sample-size effects influencing results. Interestingly, two relationships between NISP and NTAXA similar to those found by Grayson (2000) for Homestead Cave – one for the

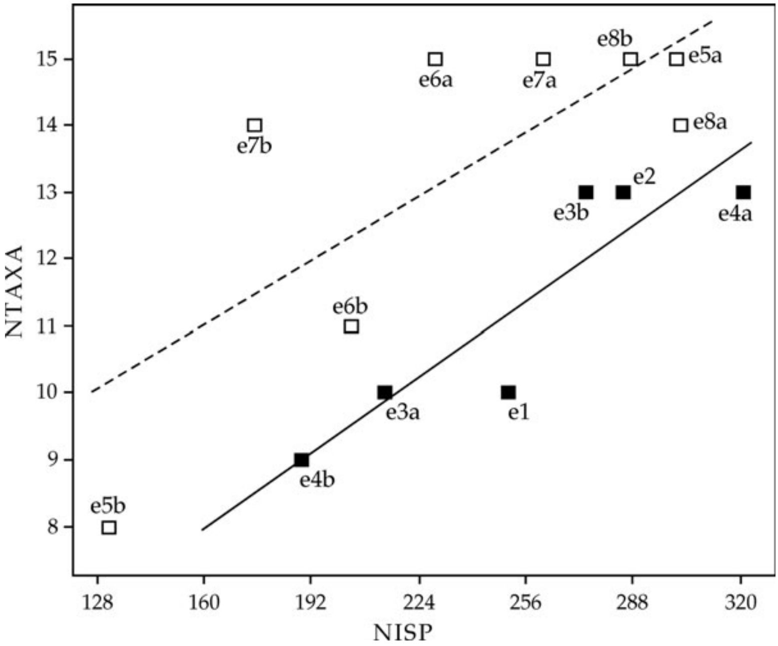

Fig. 8.3 Relationship between NISP and NTAXA in strata at Samwell Cave, California (Data from Table 8.2). *Open squares* and *dashed* (best fit regression) *line* are late Pleistocene and early Holocene; *filled squares* and *solid* (best fit regression) *line* are middle and late Holocene

late Pleistocene and earliest Holocene, another for the middle and late Holocene – are apparent in the Samwell Cave data (Fig. 8.3). Like at Homestead Cave, the late Pleistocene-early Holocene relationship suggests that more taxa are represented by fewer NISP than during the middle and late Holocene. Given that the faunal remains were accumulated by woodrats and not of anthropogenic origin, and the coincidence of climate change and decrease in NTAXA, it is straightforward to conclude that the change in the fauna at Samwell Cave was the result of bottom-up climatically driven processes.

8.5.2.2 Decrease in NMORPHS During the Middle Holocene

There are many paleozoological examples of changes in the mean size of animals that are coincident with episodes of environmental change (e.g., Klein 1986; Purdue 1989; Smith et al. 1995; Hadly 1997; Smith and Betancourt 2003). Seldom, however, has change in the extent of variation in size shown by fossils during multiple successive time periods been the subject of analytical attention. As implied above, reduced morphometric diversity within a taxon reduces the material upon which natural selection can operate, and it is thought that this reduces the probability that a population will survive over the long term. Learning something about how

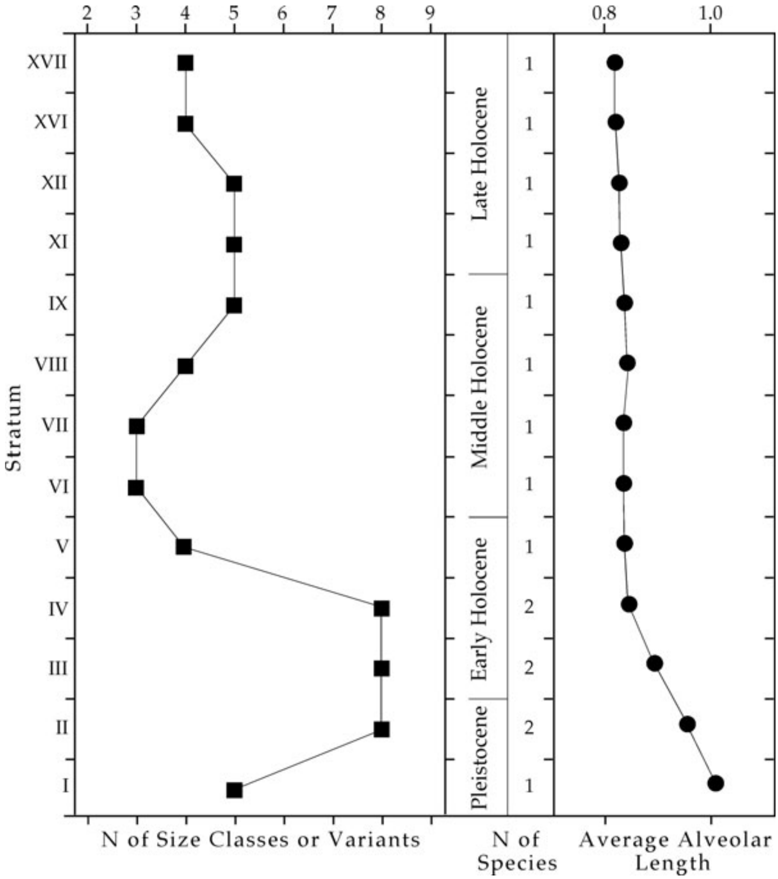

Fig. 8.4 Number of size classes (NMORPHS) and average mandibular alveolar length of *Neotoma* spp. at Homestead Cave, Utah

much variation – in this case, how many kinds of variants – can be lost and yet the population survives, would seem to be important for predicting how jeopardized a population is when it looses some variants.

Lyman and O'Brien (2005) presented a case showing change in the number of variants coincident with environmental change. They examined the mandibular alveolar lengths of wood rats (*Neotoma cinerea* and *N. lepida*) in the Homestead Cave materials originally studied by Grayson (1998, 2000). They tested a version of the same hypothesis that Grayson tested but instead of monitoring NTAXA over time, they tracked NMORPHS. Coefficients of variation did not correspond well with moisture history, but the number of 0.4 mm size classes of mandibular alveolar lengths (a form of variants) did. There were more size classes when moisture was greatest and fewer size classes when moisture was least (Fig. 8.4). Part of this difference was the result of change from one species with longer mandibular alveolar lengths to another with shorter mandibular alveolar lengths. As might be expected, the number of variants was greatest when both species were present during the Pleistocene-Holocene transition, but taxonomic richness was not the only variable driving the number of variants. The desert wood rat (*N. lepida*) – the only species present during the middle and late Holocene – for example, had more variants when conditions were more moist (N = 4) and fewer when conditions were drier (N = 3). This likely reflects a narrowing of the realized niche forced by reduced primary productivity. Yet the species survived and a greater diversity of variants returned once moisture increased during the late Holocene, suggesting this taxon may be resilient with respect to modern global warming. Given that the collection of *Neotoma* mandibles at Homestead Cave was generated by non-anthropogenic processes, and the changes correspond to shifts in climate regimes, we must conclude that the changes in NMORPHS was driven by climate change.

8.5.2.3 Human Impacts

I have described three cases of change in biodiversity measured two ways (NTAXA and NMORPHS). All three have involved naturally accumulated and deposited faunal remains, the presence/absence status of species and of variants corresponds with shifts in climate and primary productivity, and hence all involve non-anthropogenic change in biodiversity. All three seem to document cases of normal background flux in biodiversity as a response to climate change. What about a case of change in biodiversity driven by human activities, either direct influences such as hunting or indirect influences such as habitat modification or the introduction of predators? One well-known and well-publicized case of such concerns the prehistoric impacts of human colonizers of Pacific Islands. As documented at some length by Steadman (1995, 2006), when humans first inhabited the numerous islands of the Pacific Ocean, those islands were occupied by dozens of bird species. But, exploitation of the bird populations by humans, habitat modification, and the introduction of dogs (*Canis familiaris*) and other exotic taxa resulted in the loss of many bird species. NTAXA of birds decreased significantly. A large variety of bird taxa was present when people first colonized the islands, but the rapid disappearance of that variety subsequent to human colonization, plus direct evidence of human exploitation of many of the species (butchered and burned bones of the birds in human waste middens), provides an unambiguous indication of an anthropogenic cause. Not all reported cases of prehistoric anthropogenic impacts are so clear-cut (Lyman 2010a).

One reason that documenting instances of anthropogenically driven changes in biodiversity is difficult concerns the steep data requirements; I have alluded to some of these above, things like solid chronological control and synchrony of key events, changes in technology, changes in climate that make ecological sense in terms of how fauna responded, and the like (see Grayson and Cannon (1999) for extended discussion). Another reason that detecting changes in biodiversity caused by prehistoric humans is difficult concerns the fact that there are no hard and fast, generally agreed upon rules for generating data (what kinds of data are necessary?) or for interpreting data (how should it be analyzed?) once they are generated.

Thus, for example, we have some who argue that prehistoric foragers depressed some populations of sea lions along the eastern Pacific Ocean (e.g., Hildebrandt and Jones 2002) and others who argue that the evidence is statistically ambiguous (e.g., Lyman 1995) or that a clear distinction between a local population and a metapopulation must be made in order to correctly categorize apparent instances of human depression of prey populations (e.g., Lyman 2003). An example will help make some of these points of contention clear.

Wildlife ecologist Charles Kay (1994, 1995; Kay et al. 2000) has long argued that predation by American Indians on North American elk or wapiti (*Cervus elaphus*) kept populations low until Euroamericans removed the Indians and other predators and began managing landscapes. Wapiti populations subsequently irrupted and as a result the now excessive number of wapiti has modified landscapes such as that of Yellowstone to the point that ecologies are being significantly modified, perhaps irreparably. There is little doubt about the fact that there seem to be too many wapiti in several national parks in the western United States and that there are too many based on the historically documented changes to vegetation from overgrazing and the like. What is of concern here is Kay's contention that predation by American Indians – a top-down process – depleted wapiti populations to a significant degree. If he is correct, then perhaps less restricted hunting of wapiti should be encouraged today, even on national park lands, to reduce the wapiti population to ecologically benign levels. Kay compiled paleozoological data from seven western states (Washington, Oregon, Idaho, Montana, Wyoming, Utah, and Nevada). In an earlier analysis I suggested there was minimal evidence among the paleozoological remains from the eastern half of Washington state that humans had depleted the local wapiti population (Lyman 2004a).

Kay (1994) lumped faunal data from archeological collections across the seven-state area regardless of age and concluded that since wapiti remains were not very abundant relative to remains of all other ungulates in the paleozoological sample, but wapiti were very abundant relative to other ungulates today in Yellowstone alone, then prehistoric human predation must have significantly depleted wapiti populations over the last 11,000+ years. I suggested (Lyman 2004a) Kay had done some analytical manipulations of data (spatial and temporal lumping, in particular) that no paleozoologist would do because it masked any indication of flux or variation in wapiti abundance and thus hindered identification of cause of flux. (This reflects the absence of a standard analytical protocol.) Since my earlier analysis, additional paleozoological data have been generated, and a new statistical procedure of analysis has been recommended (Cannon 2000). What does a new analysis suggest about anthropogenic impacts on the eastern Washington wapiti population?

I compiled data for the abundance of wapiti and other artiodactyl remains in 102 temporally and spatially distinct zooarcheological assemblages in eastern Washington. This is 16 more than in my (Lyman 2004a) original analysis (an increase of 18.6%). In addition, one of the original 86 assemblages has now been redated to about 1,500 radiocarbon years earlier than its age as understood a decade ago. I calculated an index of wapiti relative abundance by dividing the NISP of wapiti per 500 year bin by the total NISP of artiodactyls per 500 year bin. My reasoning in doing so is that because wapiti are one of the largest artiodactyl taxa in the region (second

Table 8.3 Abundances of artiodactyl remains (NISP) from 102 assemblages in eastern Washington state per 500 year bin. Wapiti index is calculated as: wapiti NISP/∑wapiti NISP + bison NISP + deer NISP + pronghorn NISP + bighorn NISP

Age	Wapiti	Bison	Deer	Pronghorn	Bighorn	Total	Wapiti index
0–500	465	4	2,982	471	669	4,591	0.101
501–1,000	126	108	2,068	930	839	4,071	0.031
1,001–1,500	167	41	1,106	114	196	1,624	0.103
1,501–2,000	93	31	349	431	22	926	0.100
2,001–2,500	62	375	579	18	36	1,070	0.058
2,501–3,000	41	3	3,483	61	297	3,885	0.011
3,001–3,500	23	5	1,335	29	252	1,644	0.014
3,501–4,000	54	1	230	110	21	416	0.130
4,001–4,500	2	1	645	2	82	732	0.003
4,501–5,000	2	0	29	0	14	45	0.044
5,001–5,500	32	10	1,481	121	335	1,979	0.016
5,501–6,000	0	0	93	37	12	142	0.000
6,001–6,500	0	0	0	0	0	0	–
6,501–7,000	36	0	108	79	0	223	0.161
7,001–7,500	63	0	116	2	1	324	0.194
7,501–8,000	0	0	0	0	0	0	–
8,001–8,500	0	0	0	0	0	0	–
8,501–9,000	11	0	56	24	1	92	0.120
9,001–9,500	0	0	0	0	0	0	–
9,501–10,000	2	0	4	2	0	8	–
10,001–10,500	28	183	27	6	18	262	0.107

only to bison (*Bison bison*) which occurred locally only intermittently over time and space (Lyman 2004b)), they would have been primary prey of human hunters, with deer (*Odocoileus* spp.), pronghorn (*Antilocapra americana*), and bighorn sheep (*Ovis canadensis*) being secondary prey. Summary data are presented in Table 8.3. Before interpreting those data, it is critical to consider bottom-up processes and top-down processes that might be influencing them.

With respect to bottom-up processes, there are three key environmental events that must be recognized. First is the Pleistocene-Holocene transition from about 12,000 to about 8,500 RCYBP, an era when local climatic conditions were cooler and more moist, and primary productivity was greater than today (Mehringer 1996; Chatters 1998). This was followed by the middle Holocene climatic era known locally as the Altithermal; during this period climates were warmer and drier than the earlier Pleistocene-Holocene transition and also warmer and drier than modern conditions. The Altithermal is typically characterized as extending from about 8,000 to 4,500 RCYBP, after which, with one small exception, climatic conditions were more or less like those of today. The exception is the Medieval Warm Period that extended from about 1,100 to 700 RCYBP (Cook et al. 2004; Nelson et al. 2011). As the name implies, conditions were relatively warm and dry with significant droughts being of greater magnitude and duration than any experienced during the historic era. All three of these climatic events – end of the Pleistocene Ice Age, Altithermal, Medieval Warm

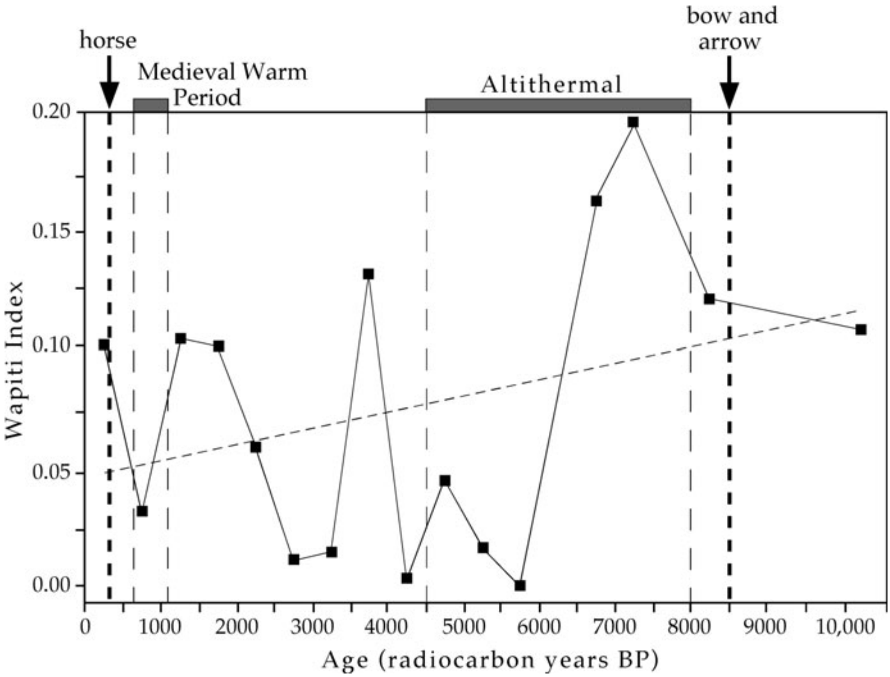

Fig. 8.5 Relative abundance of North American wapiti remains in eastern Washington per 500 year bin. *Dashed line* is simple best-fit regression line to show overall trend in abundance

Period – would have caused significant changes to local habitats and environments, and could have influenced wapiti abundance and size of individual animals, just as they seem to have influenced bison abundance and individual size (Lyman 2004b).

There are a plethora of changes in local human technology documented over the 11,000 or so radiocarbon years people are known to have lived in eastern Washington. Many of these, however, seem to be largely the result of cultural evolutionary processes that did not greatly affect adaptive fitness. The two changes that could well have influenced the procurement of artiodactyls, including wapiti, are the introduction of the bow and arrow about 8,500 RCYBP or earlier (Ames et al. 2010), and the appearance of the horse about 300 years ago (Haines 1938). Both would have likely had major influences on how efficiently large game such as wapiti were procured (e.g., Chatters 2004). The key analytical question, then, is do either the episodes of climatic change (bottom-up) or the episodes of technological change (top-down) correspond temporally with shifts in wapiti abundance?

The wapiti abundance index value for each 500 year bin for which data are available are plotted against time in Fig. 8.5. Also plotted there are the Altithermal, Medieval Warm Period, introductions of the bow and arrow and the horse, and a simple best-fit regression line that suggests overall the relative abundance of wapiti decreased from the end of the Pleistocene to modern time. A more appropriate statistical test is Cochran's test for linear trends, a form of chi^2 analysis (Cannon

2000). That test indicates that indeed there is a trend ($\text{chi}^2 = 44.25, p < .0001$); the proportion of artiodactyl remains per 500 year bin that represent wapiti is not equal over time but instead decreases. The key question thus becomes: What process or processes is driving that decrease?

Inspection of Fig. 8.5 suggests that wapiti were not very abundant at the end of the Pleistocene, and in fact the paleontological record suggests wapiti are a late Pleistocene immigrant to North America (Lyman 2010b and references therein). Perhaps the apparent upswing in abundance during the earliest Holocene reflects that early colonization, another hallmark of which is large body size (e.g., Geist 1987). The terminal Pleistocene wapiti of eastern Washington are larger than modern elk (Lyman 2010b), lending credence to the colonization scenario. The early Holocene upswing in wapiti abundance occurs despite the appearance of the bow and arrow. The subsequent drop in abundance of wapiti remains occurs during the peak of the Altithermal when primary productivity (in particular, grass; wapiti are primarily grazers) dropped. There is then an increase in wapiti, but some flux as well. The final drop in abundance corresponds in part with the Medieval Warm Period and the final increase occurs despite the appearance of the horse. In short, it appears that bottom-up processes driven by climate exerted major influences on wapiti in the Pacific Northwest; the evidence for anthropogenic impacts is minimal and basically comprises the overall trend of decrease over time, although this could also reflect the overall warming trend since the terminal Pleistocene and concomitant decreased primary productivity. On one hand, historic evidence in conjunction with zooarcheological data indicate that the early twentieth century distribution of wapiti in eastern Washington was the result of anthropogenic extirpation of local populations (Lyman 2011). It is unclear, on the other hand, what other sorts of archaeological evidence might be called upon to strengthen the case for an anthropogenic, top-down process.

8.6 Conclusion

Much recent conservation biology literature focuses on biodiversity, the diversity of life measured at one or more scales. The major concern is that the modern loss of biodiversity may well place the ecological health of the entire planet, including humanity, at risk. Numerous efforts have been aimed at determining what might happen to local and regional biodiversity in the face of increased global warming. Some of the most innovative of these have involved study of 100–200 year old natural history collections of animal specimens. Revisiting the locations where those specimens were collected in the nineteenth and earliest twentieth centuries to compare the extant fauna with the fauna represented by those museum collections has revealed instances of major change in biodiversity (e.g., Rowe et al. 2010; Johnson et al. 2011). Museum collections have their limitations, both in terms of spatial coverage and in terms of temporal coverage. Paleozoological collections provide means to fill both kinds of gaps.

The examples of change in biodiversity presented here tend to be of a piece; in particular, the major catalyst for change in biodiversity in each example is bottom-up, specifically, climate change in the form of greater warmth and aridity leading to decreased primary productivity and reduced faunal (taxonomic or variant) richness. This pattern holds in other areas as well (e.g., Faith (2011) and references therein), suggesting that if global warming is a real phenomenon (Barnosky 2009), then the rate of loss of taxa evident during the last 15,000 years or so will likely increase unless we significantly alter how we affect ecosystems. *That* is the real message of the preceding pages of this chapter. And it comes from paleozoological collections that are paleontological (non-archeological) as well as zooarcheological.

If we truly hope to conserve biodiversity, however it is measured, then we can ill afford to ignore the paleozoological record. But as noted, there are hurdles that must be cleared if that record is to meet demand. I have implied above that a key issue is going to be identifying whether bottom-up processes drove change in prehistoric biodiversity or top-down processes were responsible. This should assist us when it comes to making decisions about which changes in biodiversity warrant our attention and which may be benign in the sense that they represent little more than normal background flux. Further, though it is true the paleontological record allows more direct inference of non-anthropogenic processes, the zooarchaeological record does not a priori preclude such inferences. Finally, I have argued that the paleozoological record can provide indications of several of the scales of biodiversity with which we should be concerned. Examples presented above concern NTAXA and NMORPHS. With new technologies allowing study of ancient DNA, that scale of measurement of biodiversity should see greater attention. The future appears to be bright with respect to learning about the past in new ways. I believe those of us working on these issues need to also cast our eyes to the future occasionally and to use our data to assist with conservation biology. If we don't, our otherwise interesting but surely esoteric research endeavors may become devalued and eliminated, assuming a habitable planet still exists.

Acknowledgments I thank Julien Louys for asking me to write this chapter. It prompted me to go back to some old data that needed attention from a new perspective.

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Chapter 9
Long-Term Trends in Lineage 'Health' of the Australian Koala (Mammalia:Phascolarctidae): Using Paleo-diversity to Prioritize Species for Conservation

Gilbert J. Price

Abstract Understanding phylogenetic diversity over large temporal scales as afforded by the fossil record allows for the identification of the history of taxonomic diversity in extant taxa. Identification of such long-term trends in lineage 'health' is a critical, but commonly underutilized method for helping to prioritize species for conservation. The modern Australian koala (*Phascolarctos cinereus*) is a case in point. It is widely debated whether the modern koala should be an immediate candidate for conservation. Although modern populations have seen recent declines in some regions, in other areas koalas are overabundant, with translocation, contraceptive, and evening culling programs suggested as population control measures. The view from the fossil record is that koalas (family Phascolarctidae) have suffered a dramatic, progressive long-term decline in diversity (e.g., four genera and eight species in the late Oligocene, compared to only one genus and species at present). At no time in the known history of the Phascolarctidae has phylogenetic diversity been as low as today. Climate change, leading to enhanced variability in seasonality, increased aridfication, and habitat change has had a negative impact on phascolarctid diversity through time, and has been a determining factor in the geographic range of the modern koala. Do such observations warrant adding the modern koala to the list of threatened species? Although the answer to this question remains outside the scope of this chapter, it should be remembered that extinction of the extant koala would mark the loss of not only of a single species, but also of an entire family of endemic Australian marsupial.

Keywords Climate change • Extinction • Koala • Lineage health • Phascolarctos • Phylogenetic diversity

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9.1 Introduction

The ability to reliably identify species most at risk of extinction is a challenge of modern conservation. Typically, understanding changes in population size, genetic diversity and geographic range adjustments (Dunham et al. 1999; Celdran and Aymerich 2010; Richards et al. 2011; Ando et al. 2011) are but a few of the key factors that help inform the conservation status of extant forms. Ecological and biological monitoring of contemporary populations is the key to differentiating those species that may face extinction in the near future, versus those that are the least at risk. In a world of limited resources, developing priorities for conservation becomes critical.

The difficulty with existing approaches is that most species are poorly studied, especially on extended temporal scales. In some cases well-known animals (e.g., pandas) are the targets of intense conservation studies and their vulnerability to short-term environmental and climatic perturbations may be reasonably well understood (Isaac et al. 2007). However, population dynamics of the majority of known species remains comparatively poorly known due to a paucity of ecological and biological investigation (Leader-Williams and Dublin 2000). In fact, a large number of species lack significant ecological monitoring of any kind. Furthermore, several species are known only as specimens that have been curated in museum collections and hence their ecological role in nature is poorly understood (Burbidge et al. 2009). Therefore it is not possible to accurately determine either the conservation status or vulnerability of the majority of known species to even short-term environmental perturbations and climate change. Without such information, it is simply not possible to set reasonable goals for conservation or identify those species that are the most at risk of extinction.

The fossil record provides a powerful tool for understanding ecological change at varying spatial, and most importantly, temporal scales. A key research focus of several contemporary paleocological studies has been the investigation of how species respond, both on individual and community scales, to past environmental perturbations. For example, Blois et al. (2010) examined the response of a North American small mammal community to global warming associated with the late Pleistocene–Holocene transition. The results suggest that despite the fact that no extinctions were observed over that time period, the diversity of the local community changed dramatically in terms of evenness and richness. Several species, such as the mountain beaver (*Aplodontia rufa*) and pocket gopher (*Thomomys* sp. cf. *mazama*) underwent dramatic geographic range shifts and were not recorded locally in the younger deposits, and hence the time coinciding with the period where temperatures were at their warmest. Understanding such patterns of change in the past is critical for our ability to reliably predict how such species may respond to hypothesized future global warming.

The fossil record also allows for assessment of deep-time lineage ‘health’ of extant groups. It is widely recognized that the species amongst the most vulnerable to extinction are those that are found within the most taxonomically depauperate groups (Russell et al. 1998; Brooks et al. 2005; Isaac et al. 2007; Rolland et al. 2011). Indeed, phylogenetic diversity may actually be a better measure of biodiversity than species

Fig. 9.1 The only extant koala, *Phascolarctos cinereus*, is closely associated with open eucalypt woodlands

richness (Rolland et al. 2011). In any case, understanding phylogenetic diversity, not only today, but over longer temporal scales as afforded by the fossil record, allows the identification of extant taxa that might appear to be relatively abundant, but who have suffered long-term, progressive declines in taxonomic diversity. Understanding deep time trends in diversity is a critical, but commonly underutilized method for helping to prioritize candidates for conservation.

The modern Australian koala, *Phascolarctos cinereus*, may be a case in point (Fig. 9.1). Commonly a target of conservation measures and ecological monitoring (Penn et al. 2000), the koala has undergone significant geographic range contractions since European colonization in the late 1700s (Fig. 9.2). Multiple factors, such as habitat loss, disease (e.g., Chlamydia), vehicular traffic, and introduced predators (e.g., domestic dogs), are commonly cited as threats to modern koala populations (Dique et al. 2004). However, despite the apparently dramatic decline in geographic range, it remains difficult to reliably predict the number of wild koalas (Melzer et al. 2000), with recent estimates ranging anywhere from 43,000 to over 300,000 (The Australian Koala Foundation 2010; Parliament of Australia 2011). The ability to accurately determine the physical number of wild koalas is paramount to determining the conservation status of the species. In any case, the spatial pattern of modern koala population density is quite complex, with some populations being at historic lows in certain regions, but occurring in overabundance in others (Melzer et al. 2000). In fact, in those regions where koalas are in overabundance, contraceptive based management strategies have been introduced to limit population size (Middleton et al. 2003; Tanaka et al. 2009; Hynes et al. 2010). Such factors have, in part, been influential for policy makers declining recent nominations for the modern koala to be listed in the Australian Government's Environment Protection and Biodiversity Conservation Act 1999 (Natural Resource Management Ministerial Council 2009).

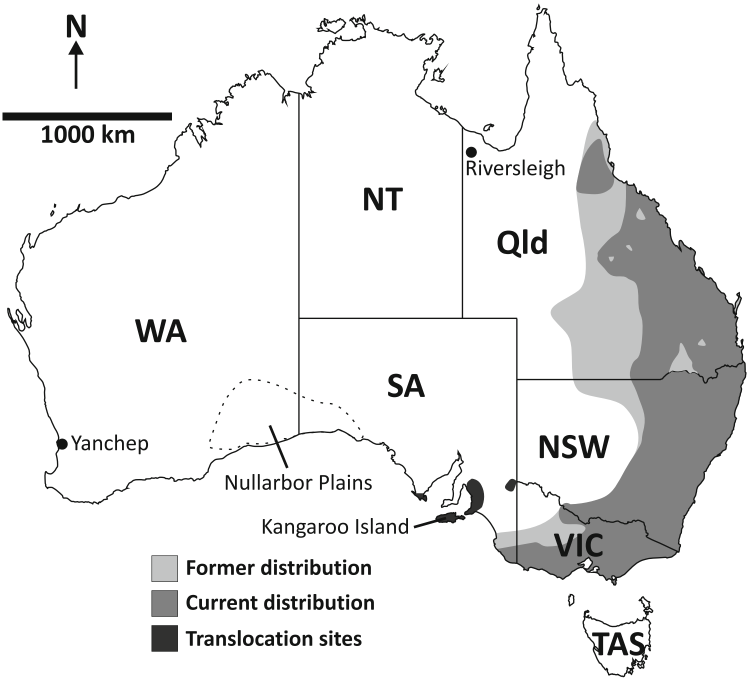

Fig. 9.2 Map of Australia indicating the modern and historic geographic distribution of the extant koala, *Phascolarctos cinereus*, as well as other sites mention in the text

Considering such a situation, and playing the role of 'Devil's Advocate', Flannery (1990, p. 174) asked the question, "What priority should we give koala conservation?" arguing that several other endemic Australian species are at higher immediate extinction risk than the koala and therefore deserving of greater attention. Archer et al. (1991) addressed the same question but from the view of the fossil record, and in particular, long-term trends in koala taxonomic diversity. On the basis of the completeness of the fossil record at the time of their study, they argued that koalas (members of the Phascolarctidae) are a taxonomically depauperate group with only a couple of species present at any one time during their 20+ million year history. Thus, Archer et al. (1991) suggested that the apparent low diversity of koalas today (i.e., one genus and one species) is not particularly unusual for the broader family and hence, the phylogenetic diversity of the group appears to be stable.

More recent fossil discoveries have drastically improved our understanding of prehistoric phascolarctid diversity. Since 1991, several new genera and species have been discovered, bringing the total number of known forms to at least 20. Coupled with improvements in our understanding of biostratigraphic relationships between geographically disparate fossil deposits, as well as new and improved dating methods, our understanding of the temporal occurrences of koalas has also greatly improved. The purpose of this study is to build on the approach of Archer et al. (1991) and provide a revised view of phascolarctid diversity through time.

Ultimately, an understanding of phascolarctid lineage ‘health’ may be useful for policy makers in determining emphasis, and the setting of priorities, for the conservation of the modern koala.

9.2 Members of the Phascolarctidae

Phascolarctids are typically medium- (ca. 3 kg) to large- (ca. 30 kg) bodied arboreal mammals. All known species, including both the modern koala and all extinct fossil forms, are interpreted to be folivores and endemic to Australian forests. The modern koala is a species that is closely associated with forests dominated by eucalypt trees (*Eucalyptus* spp.), where it relies almost exclusively on its leaves as a source of food (Fig. 9.1).

To date, eight phascolarctid genera and 20 species have been described. The fossil record dates back to at least the late Oligocene (>23 Ma). Although several relatively derived forms have been recorded from deposits of that age, earlier, more plesiomorphic phascolarctids are unknown due to a paucity of vertebrate-bearing pre-late Oligocene fossil deposits. On the basis of molecular studies, koalas are thought to have originated sometime in the middle-late Eocene (Beck 2008). However, a lack of appropriately aged fossil deposits from that Epoch precludes testing this hypothesis.

9.2.1 *Priscakoala Black et al., 2012*

Although the monotypic *Priscakoala* is considered to be the most plesiomorphic phascolarctid, it is not the geologically-oldest member of the family (Fig. 9.3) (Black et al. 2012). Represented by cranial and dentary remains, the type species *Priscakoala lucyturnbullae* is known only from early to middle Miocene deposits of the Riversleigh World Heritage area of northern Australia (Fig. 9.2). Its phylogenetic position, coupled with the geological age of the taxon and temporal relationship to other more derived koalas, suggests that older, more plesiomorphic ancestors of *Pr. lucyturnbullae* must have existed at least in the late Oligocene and possibly before.

9.2.2 *Koobor Archer, 1976*

The origins and familial relationships of *Koobor* have remained controversial since its discovery in 1976. Although Archer (1976, 1977) considered that *Koobor* was an undoubted koala, subsequent researchers have questioned its phylogenetic position within the Phascolarctidae, instead suggesting that it may either be better placed in the enigmatic extinct marsupial family, the Illiaridae (Pledge 1987a; Tedford and

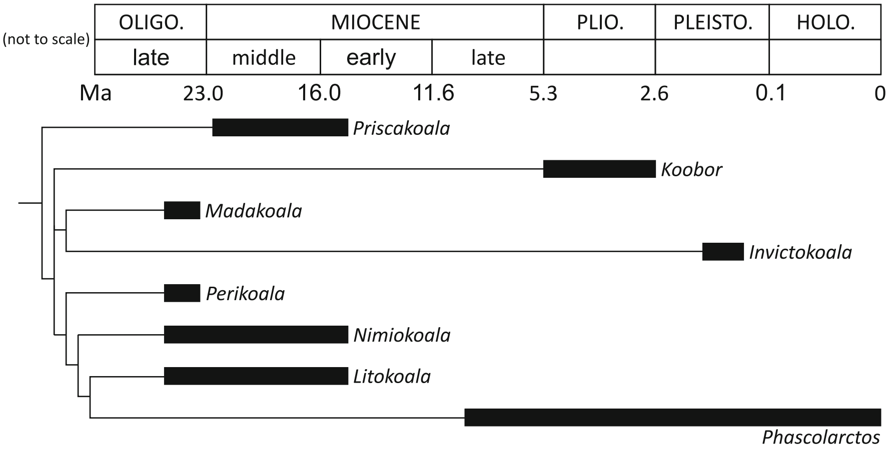

Fig. 9.3 Stratocladgram of phascolarctid inter-relationships (Modified from Black et al. in press)

Woodburne 1987), or may actually represent a new family altogether (Myers and Archer 1997). The most recent phylogenetic analysis of the broader Phascolarctidae suggests that *Koobor* is indeed a primitive koala, and second most plesiomorphic of the known genera (Fig. 9.3) (Black et al. 2012). In fact, Black et al. (2012) considered that *Koobor* may be a sister taxon to *Priscakoala*. If that interpretation is correct, then older, hitherto unknown and more plesiomorphic members of the clade must have been present between the Pliocene and at least the middle Miocene. *Koobor* is comprised of two species, *K. jimbaratti* and *K. notabilis*, from Pliocene deposits of central eastern and northeastern Australia (Archer 1976, 1977).

9.2.3 *Madakoala* Woodburne et al., 1987

Madakoala is thus far known only from late Oligocene deposits of central Australia. Three distinct species have been identified, *M. devisi*, *M. wellsi*, and an undescribed species, *Madakoala* sp. (Woodburne et al. 1987).

9.2.4 *Invictokoala* Price and Hocknull, 2011

The monotypic *Invictokoala* is known only from a maxillary specimen from the middle Pleistocene Mt. Etna fossil deposits of central eastern Australia . The type species *I. monticola* possesses a similar dental morphology to the geologically-older *Madakoala*, alluding to a close phylogenetic relationship between both forms (Price and Hocknull 2011). The implication of that interpretation is that the *Madakoala*-*Invictokoala* lineage represents a ‘ghost’ lineage within the broader Phascolarctidae.

That is, there are no known fossil representatives of the group between the late Oligocene and middle Pleistocene (Fig. 9.3). Consequently, if that interpretation is correct, there must be unknown transitional members of that lineage from intermediately-aged deposits (i.e., between the late Oligocene and middle Pleistocene).

9.2.5 *Perikoala* Stirton, 1957

Although the type locality of *Perikoala* was originally considered to be Pliocene in age (Stirton 1957), subsequent biostratigraphic and geochronological studies have supported a late Oligocene period for deposition (Woodburne et al. 1993). Two species have been recognized, *Pe. palankarinnica* and *Pe. robustus*, both known only from central Australian deposits (Stirton 1957; Woodburne et al. 1987).

9.2.6 *Nimiokoala* Black and Archer, 1997

Nimiokoala is one of the better and more completely preserved extinct members of the Phascolarctidae. Represented by isolated teeth, cranial and mandibular specimens, two species are presently recognized: *N. greystanesi* from early to middle Miocene deposits of Riversleigh, and the undescribed but distinct *Nimiokoala* sp. (Black and Archer 1997) from the late Oligocene of central Australia.

9.2.7 *Litokoala* Stirton et al., 1967

Litokoala is a diverse genus within the Phascolarctidae, second only to *Phascolarctos*. Four species are presently recognized: *L. kutjamarpensis*, *L. thurmerae*, *L. garyjohnstoni*, and *L.* sp. nov. (Stirton et al. 1967; Louys et al. 2007, 2009; Pledge 2010; Black et al. submitted). The poorly known *L. thurmerae* is represented by only a single worn molar tooth from a late Oligocene deposit of central Australia. *Litokoala garyjohnstoni* and *L.* sp. nov. are known only from early Miocene deposits of Riversleigh. *Litokoala kutjamarpensis* has the greatest geographic and temporal range of all *Litokoala* species, known from deposits of both central Australia and Riversleigh, spanning the early to middle Miocene.

9.2.8 *Phascolarctos Blainville, 1816*

Phascolarctos is the only extant member of the Phascolarctidae (Fig. 9.3). The oldest member of the genus, the undescribed *Phascolarctos* sp. from Riversleigh is thought to be late Miocene in age (Myers et al. 2001). *Phascolarctos maris* is a poorly represented species, known from only a single tooth from a probable Pliocene deposit in southern Australia (Pledge 1987b). The largest-bodied koalas, the 'megafaunal' *Ph. yorkensis* and *Ph. stirtoni*, are known from Pliocene and Pleistocene deposits of southern and eastern Australia (Pledge 1992; Archer et al. 1997; Price et al. 2009a, b). The extant *Ph. cinereus* has a fossil record extending back until at least the middle Pleistocene (Price 2008). *Phascolarctos cinereus* was originally considered to have been a late Pleistocene-Holocene dwarf of the extinct *Ph. stirtoni* (Archer 1984; Archer and Hand 1987; Murray 1984), thus implying that the later taxon did not suffer extinction in the late Pleistocene as a suite of other large-bodied 'megafauna' did (e.g., Price and Sobbe 2005; Price et al. 2011). However, Price (2008) demonstrated that the dwarfing hypothesis is not supported due to significant morphological differences between the two forms (and hence, warranting specific distinction), and the fact that the earliest known temporal occurrence of the supposed 'dwarf', *Ph. cinereus* (>350 ka), significantly predates the late Pleistocene. On the basis of those observations, the extant *Ph. cinerus* is considered to be a species distinct from the extinct *Ph. stirtoni* (Price 2008).

9.3 Phascolarctid Diversity Through Time

The combination of direct fossil records and an understanding of phylogenetic (Fig. 9.3) relationships between known forms, both coupled within a reliable geochronological framework, allows for the tracking of long-term trends in koala diversity. On the basis of the available evidence, it is clear that phascolarctids have suffered a dramatic long-term decline in diversity over the middle to late Cenozoic (Fig. 9.4). Phascolarctid diversity was greatest in the late Oligocene (ca. 22–24 Ma) with at least five genera present (*Litokoala*, *Nimiokoala*, *Perikoala*, *Madakoala*, and the hypothesised ancestor of the plesiomorphic *Priscakoala*). Eight species are evident from that time (*L. thurmerae*, *Nimiokoala* sp., *Pe. robustus*, *Pe. palankarinnica*, *M. wellsi*, *M. devisi*, *Madakoala* sp., and the ancestor of *Priscakoala*).

Leading into the early Miocene (ca. 16.4–23.0 Ma), the two central Australian taxa, *Madakoala* (three species) and *Perikoala* (two species), suffered extinction (Fig. 9.4). Overall, generic diversity decreased from five to four (with only *Litokoala*, *Nimiokoala*, *Priscakoala*, and the transitional member of the *Madkoala-Invictokoala* lineage present in the early Miocene). Species level diversity decreased from eight to six (including only *L.* sp. nov., *L. garyjohnstoni*, *L. kutjamarpensis*, *N. greystanesi*, *Pr. lucyturnbullae*, and the transitional *Madakoala-Invictokoala* taxon during the early Miocene).

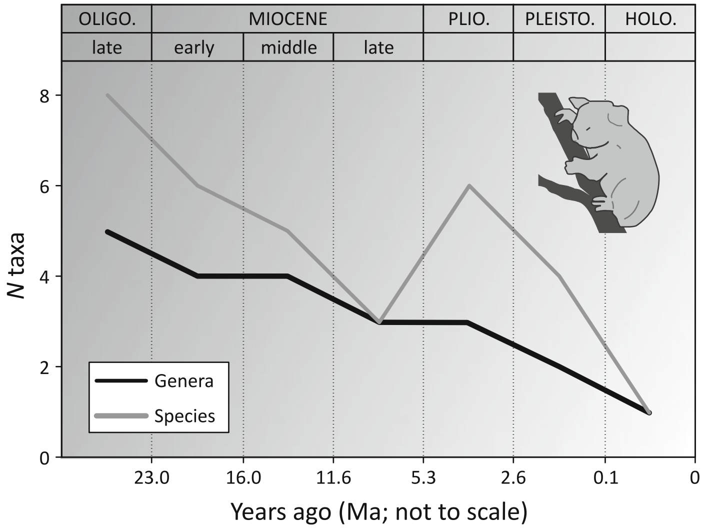

Fig. 9.4 Late Oligocene to recent trends in phascolarctid phylogenic diversity

Phascolarctid generic diversity remained steady between the early and middle Miocene (10.4–16.4 Ma) with no apparent extinctions (Fig. 9.4). However, species diversity decreased from six to five taxa (with *L. kutjamarpensis*, *N. greystanesi*, *Pr. lucyturnbullae*, transitional member of the *Madkoala-Invictokoala* lineage, and the ancestor of *Koobor* all present in the middle Miocene), including the apparent extinctions of *L.* sp. nov. and *L. garyjohnstoni*.

Our understanding of phascolarctid diversity in the late Miocene (5.3–10.4 Ma) is limited due to a paucity of appropriately-aged fossil deposits (Black 1999). At face value, diversity appears to have declined from four to three genera between the middle and late Miocene (earliest *Phascolarctos*, transitional member of the *Madakoala-Invictokoala* lineage, and the ancestor of *Koobor* present at that time). Three genera, *Priscakoala*, *Litokoala*, and *Nimiokoala* have not been recorded in post-middle Miocene deposits (Fig. 9.4). Species diversity appears to have decreased from five to three between the middle and late Miocene (taxa as for generic level above).

The fossil record of the Pliocene is much more extensive than that of the late Miocene and hence there is a better understanding of phascolarctid diversity during that Epoch. Significantly, koala diversity at the generic level is much lower than that of the better sampled middle Miocene, with only three taxa present (*Koobor*, *Phascolarctos*, and the transitional member of the *Madakoala-Invictokoala* lineage). Despite relatively low levels of generic diversity during the Pliocene, six species have been recognized (*K. jimbaratti*, *K. notabilis*, *Ph. maris*, *Ph. yorkensis*, *Ph. stirtoni*, and the *Madkoala-Invictokoala* member), making it comparable in species diversity to the early Miocene (Fig. 9.4).

The transition to the Quaternary (encompassing the Pleistocene – 2.6 Ma to 11 ka, and Holocene – last 11 ky) marked the beginning of a sharp decline in phascolarctid diversity that appears to have continued to the present day (Fig. 9.4). Only two genera have been recorded (*Phascolarctos* and *Invictokoala*) in Pleistocene deposits. *Koobor* has not been recorded in deposits younger than Pliocene, implying its pre-Quaternary extinction. Diversity decreased from six to four species between the Pliocene and Pleistocene (with only *Ph. cinereus*, *Ph. stirtoni*, *Ph. yorkensis*, and *I. monticola* present).

The Pleistocene–Holocene transition represents the largest loss of diversity, at least at the species level, in the known history of the Phascolarctidae (Fig. 9.4). The rainforest-adapted *Invictokoala* has not been recorded after ca. 320 ka anywhere on the continent. The 'megafaunal' *Ph. stirtoni* has not been recorded in deposits after 53 ka (Price et al. 2009b), therefore pre-dating the hypothesised time of intense 'megafaunal' extinctions (e.g., Roberts et al. 2001). The extant *Ph. cinereus* is the only member of the Phascolarctidae that appears to have persisted through the Holocene to the present day.

9.4 Discussion

9.4.1 Driving Factors of Koala Diversity Through Time

The exact mechanisms and processes of prehistoric koala extinctions and broader changes in diversity is by no means clear, but almost certainly involved significant climate change, principally, a long-term trend towards aridification, enhanced seasonality and habitat change. The earliest known koalas thrived during warm and wet periods, and appear to have preferred habitats consisting of well-wooded vegetation including rainforest. Dental and cranial anatomy of the early koalas demonstrates a specialty for feeding on soft foliage, rather than the tough, leathery leaves of eucalypts – the near exclusive diet of the modern koala, *Ph. cinereus* (Louys et al. 2009).

Significant post-middle Miocene declines in rainfall and cool temperatures were largely responsible for a major reorganization of the distribution of Australia's central forests, leading to a major contraction of such habitats to the coastal fringes (Black et al. 2012). It was also at this time (i.e., late Miocene) that saw the origin of the extant genus, *Phascolarctos*, a taxon that is closely associated with the open, dry sclerophyll eucalypt forests of modern Australia. The teeth of *Phascolarctos* possess well-developed crenulations in molar enamel and are significantly higher-crowned than the ancestral koalas.

Although the traditional view is that koalas suffered extinction from rainforests in the late Miocene (Archer and Hand 1987), more recent discoveries of koalas in rainforest fossil deposits have suggested that koalas may have actually always been closely associated with such habitats (Price and Hocknull 2011). A paucity

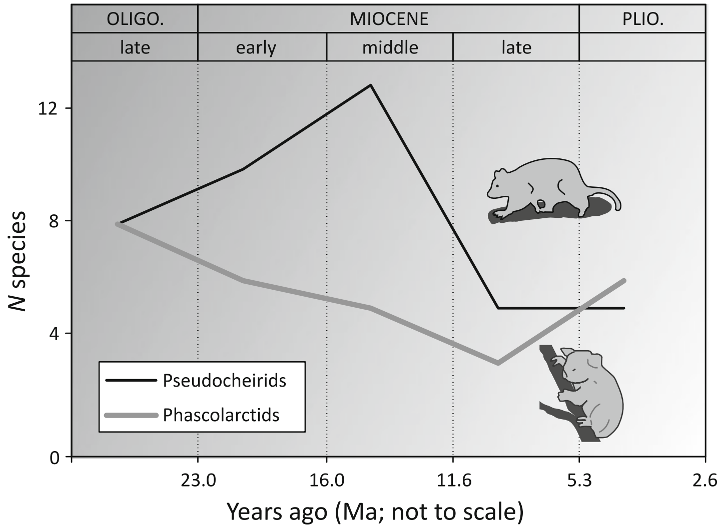

Fig. 9.5 Late Oligocene to Pliocene trends in phascolarctid and pseudochierid species diversity (see Long et al. (2002) for additional information on pseudochierid palaeodiversity)

of rainforest fossil deposits may reflect their post-Miocene rarity, and hence, may influence our understanding of koala-rainforest ecological relationships after that time. It is clear however, that koalas suffered extinction from rainforests of the continental fringe after the middle Pleistocene (Price and Hocknull 2011).

Archer and Hand (1987) also speculated that the loss of koalas from rainforests was associated with competition from other arboreal herbivores such as ringtail possums (Pseudochiridae), and principally, the large-bodied *Pseudokoala*. Again, a more complete picture of koala and ringtail possum diversity through time now allows the testing of such a hypothesis. At face value, fossil data suggests that while koalas suffered a long-term decline in diversity between the late Oligocene and Pliocene, ringtail possums diversified significantly at least until the middle Miocene (Fig. 9.5). However, significant differences in dental morphology and body size between those early koalas and possums suggests that both groups would have filled significantly different niches in the Oligo-Miocene forests, such it is likely that competition would have been minimal (similar factors also explain the niche partitioning of sympatric modern koalas and ringtail possums; Smith and Ganzhorn 1996). In any case, the giant ringtail *Pseudokoala* is thus far known only from Pliocene and Pleistocene deposits, and there is no evidence that it competed directly with the earlier rainforest koalas. The only post-Miocene rainforest koala known, *Invictokoala monticola*, has been recorded sympatrically with *Pseudokoala* from the middle Pleistocene rainforest deposits of Mt. Etna, central eastern Australia (Hocknull 2005; Hocknull et al. 2007; Price and Hocknull 2011). Neither taxon has been recorded from younger deposits locally, or anywhere else on the continent, after that time.

9.4.2 Climate Change and Influence on the Geographic Distribution of the Modern Koala

The modern koala, *Ph cinerus*, has a fossil record dating back to at least 350 ka. Strikingly, it is the only koala that survived through the period of intense late Pleistocene megafaunal extinctions (hypothetically 50–40 ka); earliest human arrival (ca. 45–50 ka); enhanced seasonality over the last 50 ky; intense aridification associated with the last glacial maximum (30–18 ka); post-glacial global warming (18–11 ka); and through the period of European colonization (late 1700s). Yet the fossil record demonstrates that it was not entirely resilient to such impacts through the Pleistocene–Holocene transition. Fossil records demonstrate that the modern koala once had a near continent-wide distribution (Price 2008), being found not only through eastern and southeastern Australia (including its modern geographic range), but also across southern central and southwestern Australia (e.g., Archer 1972; Lundelius and Turnbull 1982; Prideaux et al. 2010). For example, late Pleistocene fossils of *Ph. cinereus* have been recorded from Madura Cave, part of the Nullarbor Plains ('the treeless plains') (Lundelius and Turnbull 1982) (Fig. 9.2). The occurrence of the extant koala in the late Pleistocene indicates the former existence of local eucalypt woodlands. In contrast, the modern Nullarbor Plains is dominated by chenopod shrubs (Morton et al. 2011). Independent paleohabitat evidence from nearby offshore pollen cores has demonstrated a progressive, long-term reduction in eucalyptus forest in the region (Van der Kaars et al. 2007). Although forests appear to have been locally widespread at Marine Oxygen Stage (MIS) 5E (around 130 ka), and hence, implying an episode of high effective precipitation, *Eucalyptus* decreased significantly after this time. A considerable decline in charcoal abundance at the MIS 5–4 boundary (around 74 ka), and depressed charcoal-pollen counts after that time also suggests a progressive decline in the biomass available for burning. A paucity of charcoal and decline in *Eucalyptus* abundance strongly suggests a more open, sparser habitat after 74 ka (Van der Kaars et al. 2007), similar to today (e.g., Morton et al. 2011). Other southern Australian palynological records demonstrate similar MIS 5–4 declines in eucalypt forest (Singh and Geissler 1985; Harle 1997; Harle et al. 1999). It is those late Pleistocene changes – tending towards greater seasonality, droughts, a decline in rainfall, aridification and habitat change (see also Hesse et al. 2004) – that likely contributed to the demise of the region's late Pleistocene koala populations. It is also important to point out that such changes pre-date human colonization of the continent by >20,000 years, thus humans cannot be instigating factors in such long-term trends. Pre-human climate changes leading to the decline of local forests may also be implicated as the cause of extinction of numerous forest mammals, such as browsing kangaroos, arboreal tree kangaroos, and forest wallabies, recorded from older middle Pleistocene deposits of the region (e.g., Prideaux et al. 2007).

This newly refined understanding of late Pleistocene climatic changes, its influence on the decline of eucalypt forest habitat, and subsequently, local koala

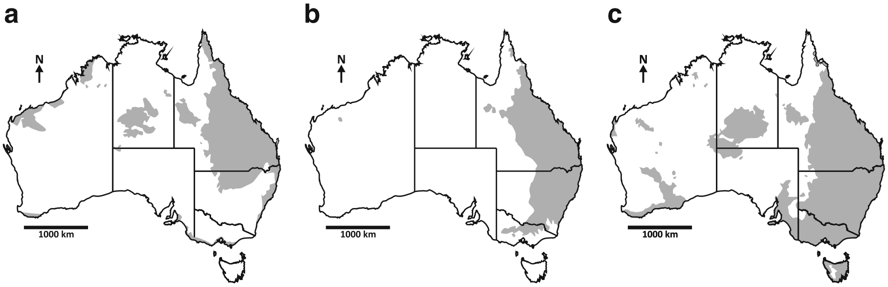

Fig. 9.6 Bioclimatic models based on the distribution of the modern koala. (**a**) potential koala distribution with a 6°C drop in temperature and 20% decline in rainfall; (**b**) potential koala distribution with an additional 40% decline in rainfall; and (**c**) regions that today fall within the bioclimatic envelope of the extant koala (Modified from Adams-Hosking et al. 2011)

range contractions, is also supported by independent bioclimatic modeling. Adams-Hosking et al. (2011) developed a bioclimatic envelope for the modern koala and explored a variety of scenarios mirrored to reflect the actual hypothesized changes in late Pleistocene temperature and rainfall. The resulting models suggest that a decline in temperature by 6°C and reduction in rainfall by 20% (relative to today) would result in the total loss of koala habitat in southern central Australia (Fig. 9.6a); a subsequent decline in rainfall by 40% is predicted to result in the total annihilation of koala habitat in the southwest (Fig. 9.6b). Although bioclimatic modeling based on modern conditions suggests that the extant koala could persist in southwestern Australia today (Fig. 9.6c), potential connective corridors (e.g., Nullarbor Plains) are too sparsely vegetated to allow natural koala dispersal into the region. In other potentially favorable areas, such as Kangaroo Island off southern central Australia (Figs. 9.2 and 9.6c), koalas, introduced from the mainland by Europeans in the 1920s, have thrived so successfully that they are now considered to be a pest species (Masters et al. 2004). Significant population control measures for the Kangaroo Island koalas such as culling have been considered (Tyndale-Biscoe 1997; Ross and Pollett 2007), while fertility contraceptive measures and translocations have been introduced (Duka and Masters 2005). Conversely, in regions that are not considered to be suitable for the modern koala today, such as Yanchep of southwestern Australia (approximately 300 km to the north of the southwestern favorable zone; Figs. 9.2 and 9.6c), introduced populations have failed to become established. In fact, the original population introduced to Yanchep in 1938 died out by 1941; and numerous other introductions have since occurred (Congreve and Betts 1978). Failure of the population to become well established may be explained, in part, by both inbreeding effects (Congreve and Betts 1978) and bioclimatic unsuitability.

Rainfall and availability of permanent sources of freshwater, in addition to general tree suitability, continues to have a strong influence on the distribution and survival of the modern koala. For example, Munks et al. (1996) noted that koalas more frequently used those trees that grew proximal to permanent water bodies versus those from more distal areas. Gordon et al (1988) observed that numerous koalas (ca. 63% of the population) from southwestern Queensland suffered mortality during a major drought and heat wave in the summer of 1979–1980. A later, extended drought between 2001 and 2009 from the same region resulted in an 80% decline of the local population (Seabrook et al. 2010). During the 1978–1980 event, mortality was greatest in those areas where food trees suffered leaf-fall and browning of the foliage, which, significantly, included those trees that were growing along dry stretches of the local watercourses. The cause of individual mortality was likely a combination of malnutrition and dehydration; the survivors from those areas were commonly observed in poor condition with anemia and high tick loads (Gordon et al. 1988). Gordon et al. (1988) also identified differential rates of mortality in the region during the 1979–1980 drought. High rates of survivorship were observed for those areas where the food trees grew adjacent to sources of permanent water (hence, such trees were least affected from drought conditions; a pattern also later observed by Seabrook et al. (2010) in the 2001–2009 drought). Demographically, mortality was greatest amongst younger animals that were excluded from optimal sites by older individuals (Gordon et al. 1988). Thus, a lack of recruitment into the breeding population, as well as ongoing local drought conditions over the subsequent few years drastically impeded the recovery of the population. During the 2001–2009 drought, despite a major population crash, there was only a minor change in overall koala distribution in the region. The ability of populations to migrate from the drought affected areas appears to have been significantly impeded by regional land clearing, thus reducing potential migratory connective habitat corridors (Seabrook et al. 2010).

Although such population crashes may be rare events (Gordon et al. 1988), it is easy to imagine a scenario where late Pleistocene koala populations of southern and central Australia were regularly exposed to similar drought conditions associated with the last glacial cycle. Where such climate events occurred frequently and populations were not able to adequately recover before the next event, local population extinctions would have been imminent, progressive and repetitive across the landscape, leading to a massive geographic distributional range shift.

Collectively, the view from the fossil record, independent paleoclimatic evidence, bioclimatic modeling, and observations of modern populations clearly demonstrates the vulnerability of koalas to prehistoric and recent changes in precipitation regimes, moisture availability, habitat change, and short and long-term variations in seasonality. Significantly, such climatic changes mirror those that are predicted to occur in the future, particularly in those regions where koalas currently persist (Intergovernmental Panel on Climate Change 2007; Dunlop and Brown 2008; Hamin and Gurran 2009; Seabrook et al. 2010). Thus, the long-term view is that climate change, associated with increased aridification, increased variability in seasonality, and habitat change, has had, and will likely to continue to have, detrimental impacts on the persistence of koala populations.

9.5 Should the Modern Koala Become an Immediate Priority for Conservation?

At present, koalas are listed as being of 'least concern' on the 2011 International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN 2011). Within Australia, they are not listed in the Environment Protection and Biodiversity Conservation Act 1999 (Natural Resource Management Ministerial Council 2009), although a ministerial position on a recent nomination to be included as 'vulnerable' in the Act is pending and will be announced in 2012 (Minister for Sustainability, Environment, Water, Population and Communities 2011). On a State-by-State level, koalas are: listed as 'regionally vulnerable' in the Southeast Queensland Bioregion, but 'of least concern' in other areas as per Queensland's Nature Conservation Act 1992; listed as 'vulnerable' under the Threatened Species Conservation Act 1995 for New South Wales; protected wildlife under Victoria's Wildlife Act 1975 but not listed under the Victorian Flora and Fauna Guarantee Act 1988; and protected under the National Parks and Wildlife Act 1972 of South Australia (Natural Resource Management Ministerial Council 2009). The key challenge faced by policy decision makers and their advisors is to determine whether the modern koala is truly a species on the brink of extinction, and therefore whether or not it should become a priority for conservation.

At a time of widespread confusion and concern on the possible fate of the koala, it may be useful to consider the deep-time history of another iconic family of Australian marsupial, the Thylacinidae, which includes the recently extinct *Thylacinus cynocephalus* (variously known as the Tasmanian tiger, Tasmanian wolf and thylacine). Strikingly, the long-term view of the Thylacinidae has many parallels with the patterns of diversity changes as seen in the Phascolarctidae. Nine genera and thirteen species have so far been described, with a fossil record dating back to the late Oligocene (Long et al. 2002). For at least the first 15+ million years of the known history of the Thylacinidae, there were a minimum of two distinct genera present at any one time (Fig. 9.7). Both genus and species diversity was greatest in the middle Miocene, before declining steadily, such that by the Pliocene, only one genus (*Thylacinus*) and one species (*Thylacinus* sp.; Mackness et al. 2003) remained (Fig. 9.7). The modern Tasmanian tiger has a fossil record dating back to the Pleistocene (Dawson 1982), and leading into the Holocene, was the sole survivor of the previously diverse family. The Tasmanian tiger was widespread across mainland Australia (e.g., Price and Webb 2006; Prideaux et al. 2010), Tasmania (Mooney and Rounsevell 2008) and New Guinea (Sutton et al. 2009), at least until the mid Holocene. The Tasmanian tiger suffered extinction from the Australian mainland and New Guinea following the introduction of the dingo (*Canis lupus dingo*) by humans around 3.5 ka (Gollan 1984). Although it is possible that additional factors other than competition with the dingo also contributed to the extinction of the Tasmanian tiger from such regions (Johnson and Wroe 2003), it is clear that Tasmania was its last refuge prior to European colonization.

During the 1800s and following the colonization of Tasmania by Europeans, the Tasmanian tiger was regarded as a significant killer of sheep, although this

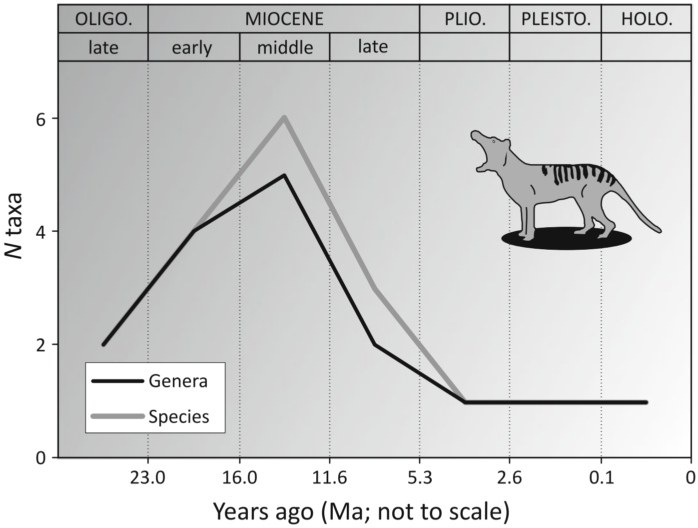

Fig. 9.7 Late Oligocene to recent trends in thylacinid phylogenic diversity (see Long et al. (2002) for a summary of key taxa)

reputation was greatly over-exaggerated (Paddle 2000). In addition to farmers killing Tasmanian tigers to protect their stock, a bounty scheme was also established to control their numbers (Paddle 2000). In addition to hunting, competition with introduced domestic dogs, habitat loss and disease played a significant role in the decline of thylacine populations (Paddle 2000). Although the Tasmanian tiger was recognized as a species vulnerable to extinction as early as 1901, it wasn't until the 10th of July 1936, that it became an officially protected species by the Tasmanian State Government. As Penn et al. (2000, p. 630) pointed out in relation to establishing policy-based conservation strategies for the modern koala, "the best time to consider conservation management is before the population has become so small that options are limited"; in the case of the Tasmanian tiger, the last known living individual died in captivity on the 7th of September 1936, just 59 days after the species became officially protected by legislation (Paddle 2000).

The long-term decline in diversity of the Thylacinidae coincided in time with intense late Cenozoic climate-driven environmental changes; humans, both directly (e.g., hunting) and indirectly (e.g., land clearing and introduced competitors) contributed to their ultimate extinction. Thus, the passing of the last Tasmanian tiger in captivity marked not only the extinction of a single species, but an entire family of endemic Australian marsupials. It remains tempting to speculate how the deep-time knowledge of lineage 'health' of the Thylacinidae may have influenced the decision of policy makers of the 1800s and 1900s in terms of prioritizing the Tasmanian tiger as candidate for conservation sooner; however this is outside the scope of this chapter.

Although the long-term trend in lineage 'health' of phascolarctids points to a steep, downward decline in diversity, does this alone warrant adding the modern koala to the list of threatened species? The answer to this question is far more complex than simply understanding the history of its phylogenetic diversity and must consider other external factors as well. However, it may be critical for environmental managers, conservationists, and perhaps most importantly, policy makers and advisers, to consider the following facts:

1. Koalas have declined dramatically in diversity over the last 20+ million years (four genera and eight species in the late Oligocene, compared to only one genus and species today);
2. At no time in the known history of the Phascolarctidae has phylogenetic diversity been as low as what it is today;
3. Climate change, principally a long-term trend towards increased aridification and seasonality, has not only shaped our past and present ecosystems and influenced the evolution of our biota, but has had detrimental impacts on koala diversity through time;
4. Climate change and associated habitat changes of the Quaternary – the last 2.6 Ma in the history of life on our planet, including the time period in which we currently live – has strongly influenced and caused major geographic range contractions and localized population extinctions of the modern koala;
5. Similar patterns of past Quaternary climate change are also predicted to occur in the future; and
6. Extinction of the modern koala will mean the loss of a species that has survived on the continent for at least the last 350 millennia; it will mark the demise of a genus that persisted for close on 9 Million years; and ultimately, it will result in the decimation of yet another endemic family of marsupials that previously ruled Australia's forests for over 23 Million years.

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Chapter 10
The Past and Future of the Mammoth Steppe Ecosystem

Sergey A. Zimov, N.S. Zimov, and F.S. Chapin III

Abstract During the Last Glacial Maximum (LGM) the mammoth steppe was the planet's biggest biome. Ice rich loess-like soils of this biome covered vast northern territories. These soils are currently one of the biggest carbon reservoirs. It is likely that in this century the bigger part of these soils will thaw. This would lead to massive erosion, destruction of modern ecosystems and a large emission of carbon dioxide and methane into the atmosphere, which are produced from the decomposition of Pleistocene organics. Minimizing these effects is possible only through the restoration of ecosystems similar to the Pleistocene mammoth steppe. Skeleton densities in the permafrost show that the mammoth steppe was a highly productive ecosystem similar to African savannas. Biomass of animals in the north of Siberia was ~10 t/km^2. Herbivores enhanced biocyclicity, trampled moss and shrubs and maintained pastures. Therefore this ecosystem was only partially dependent on climate. Analyses of climate dynamics, vegetation and animals shows that today the climate in the north of Siberia, Alaska and Yukon are close to the optimum of the mammoth steppe, and that climate warming did not destroy this ecosystem. Rather, humans are the more likely cause. After the LGM, climate warming allowed humans to penetrate the north, where they decreased animal densities to the point where they became insufficient to maintain pastures. In this chapter we discuss questions of preservation of bones and artifacts in the permafrost, physiology and evolution of pasture ecosystems and the role of humans in this ecosystem.

Keywords Extinction • Global warming • Humans • Mammoth steppe • Permafrost

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> *'If one had not seen this with one's own eyes, it would be impossible to believe that in these desolate areas there could exist such a large number of animals, congregating sometimes in herds of thousands. Only by wandering from one place to another could these large groups find enough feed on the meager grasslands of the wastelands. But the animals do not know their major enemy – humans, and the animals live wild and free, far away from bloodthirsty pursuit.'*
>
> N.M. Prjevalskii
> Mongolia and Tangut country (1873)

10.1 Introduction

According to IPCC reports, in this century alone the climate on the planet will become warmer by 2–7.5°C (Solomon et al. 2007). In the Arctic this change in temperature will be even greater, which will have a massive impact on northern ecosystems. Specifically, tundra ecosystems will give way to forests and polar deserts will in turn give way to tundra. But this will not be the only outcome. In the northern parts of Siberia, Alaska, and the Yukon, glaciers are few. In these areas vast plains, river valleys and mountain slopes have accumulated massive strata of loess or loamy soils. Sedimentation is slow – usually less than millimeters per year, but over the course of tens of thousands of years this has resulted in an accumulation of several tens of meters of loess (Schirrmeister et al. 2002; Sher et al. 2005; Zimov et al. 2006a). These layers are frozen and on average contain 50% ice, although in the far north of Siberia ice content can reach 90%. The biggest part of this ice is a polygonal network of ice wedges, which form as a result of frost cracking of sediments (Yershov 1998). The local name of such massive Pleistocene loess with ice wedges is *yedoma* (Fig. 10.1).

During interglacial periods the depth of the summer thaw increased and these ice wedges began to thaw. Depressions appeared, water filled these depressions, ponds appeared, which interflowed and migrating lakes (thermokarst lakes) were formed (Zimov et al. 1997; Walter et al. 2006). During the course of the Pleistocene-Holocene transition (PHT) this process eroded half of the yedoma (Walter et al. 2007). During the migration of thermokarst lakes creeks, ravines and rivers were encountered. When this happened, water escaped from the lakes, creating canyons. The lakes dried out and refroze, and new nets of polygonal ice wedges began to form.

With increased global warming the permafrost layer will again begin to thaw. It could be assumed that this will first occur next to southern permafrost boundary, where the temperature of permafrost is close to 0°C, rather than in northern Siberia, where permafrost temperatures are as low as −5°C to −10°C, such that global warming is not a thread to northern Siberian ecosystems. But that is not so. The top of the ice wedges in the north usually lay at a depth of only 0.5–1.8 m, with the depth of summer thaw (active layer) being 0.2–1.6 m (pers. obs.). Therefore in

Fig. 10.1 Part of Duvanii Yar, where the ice-wedge thaw is active. In June the river water level is high and the beach absent

some cases if the depths of the summer thaw increases by only 0.1–0.2 m, ice wedges will begin to melt, and the permafrost layers will begin to erode.

It can be imagined that the soils of northern Siberia are a subsurface "glacier" 10–50 m thick, which is protected from the summer sun with a thin soil layer. As one moves north the permafrost gets colder, but simultaneously the ice content increases and the thickness of heat-insulating soil cover decreases. For this region, it makes no sense to discuss the vegetation response to climate change – all vegetation would be destroyed. Modern soils would be mixed with yedoma soils; some would slide down to thermokarst lakes, some to creeks or rivers; this would increase their turbidity, and river and estuary ecosystems would be destroyed. Substantial portions of organics and mineral soils would be transported to the ocean, which would in turn accelerate sea ice thawing.

Besides regional effects, permafrost degradation will also affect global climate. Carbon storage in the top layer of permafrost is estimated to be $1,672 \times 10^{15}$ g (1,672 Pg) of carbon (Tarnocai et al. 2009). This is more than the amount stored in the terrestrial biomass and atmosphere combined. Permafrost is the biggest organic carbon reservoir. And the yedoma is especially carbon rich, with hundreds of kilograms C per m^2 (Schirrmeister et al. 2002; Zimov et al. 2006a). When the yedoma thaws microbes quickly transform this carbon into greenhouse gases. In aerobic conditions CO_2 is produced (Zimov et al. 2006b) and in anaerobic conditions (e.g. in the bottoms of thermokarst lakes, ponds and rivers) CH_4 is produced (Zimov et al. 1997; Walter et al. 2006). Microbial oxidation of carbon is accompanied by heat production, therefore when the organic rich systerm starts to thaw, the process becomes hard to stop (Chuprynin et al. 2001; Khvorostyanov et al. 2008), and the heat produced by microbes is enough to thaw the entire system. Greenhouse gas emissions from thawing permafrost would strengthen global warming which would in turn increase permafrost thawing; and the probability that bigger portions of the yedoma will thaw in this century is already high. Is there is a way to slow down permafrost thawing? Theoretically it is possible, but there are few options. In this chapter we discuss the reasons why one such option, namely the rewilding of extensive areas in northern Siberia, may hold the answer to the loss of this unique ecosystem.

10.2 Observations and Experimentations on Permafrost Thaw

Figure 10.2 shows our experimental permafrost thaw site. Initially a mossy forest was situated on this inclined slope, 8 km to the southeast from our station (Fig. 10.3). The depth of the summer thaw varies from 0.3 to 0.8 m. The tops of ice wedges are situated as deep as 1.6–1.8 m beneath the surface. In the beginning of the experiment the temperature of permafrost was −6°C to −7°C. In 2001, in an area covering 3 ha, the top organic layer of soil with a thickness of 0.2–0.3 m was removed with the help of bulldozer. The next year an additional 0.3–0.4 m of soil was removed over 1 ha. The removed soil acted as a heat insulating "coat" for the permafrost underneath, and the removal of this coat caused permafrost degradation. On the territory where only the top layer was removed 1.5–2 m of permafrost thawed over 10 years, however where there was additional removal, the permafrost thawed by 4–4.5 m.

Mechanical treatment in our experimental site is equivalent to 2–3°C of warming. This would not be enough for all the permafrost to thaw; however a substantial portion would. If the climate stays stable then the permafrost thawing in our experiment would slow down with time, as the ground slough would create an insulating cover for ice wedges over time. But summer temperature increases over the last years (more than 2°C for 20 years) accelerated the thawing of permafrost on our site.

If we were to repeat our experiment on a flat surface, then the permafrost would equally degrade; however there would be no drainage and the area would be covered with water – i.e., a thermokarst lake would appear. And if the slope were steeper then the thawing soil would flow down, sliding on slippery ice wedges. Frozen soil and ice would appear on the surface, which might accelerate thawing by up to 0.1–0.2 m per day. The zone of erosion would quickly occupy the entire slope. Down the slope a ravine would appear while up the slope a vertical, rapidly retreating cliff would appear. Active erosion would stop only when inclination of entire slope declined or when all ice wedges thawed.

The loamy soils and loess found in the north are very texotropic – the wet mineral soil can look solid, but subject to disturbance it quickly turns into a liquid mud. Figure 10.4 shows images of the inclined slope of the Filipovka River basin, 50 km to the northeast from our station. In 2002 there was natural fire, which increased the depth of the summer thaw. The top horizons of the ice-rich permafrost thawed, started moving and turned into a torrent. As a result all the thawed soil from

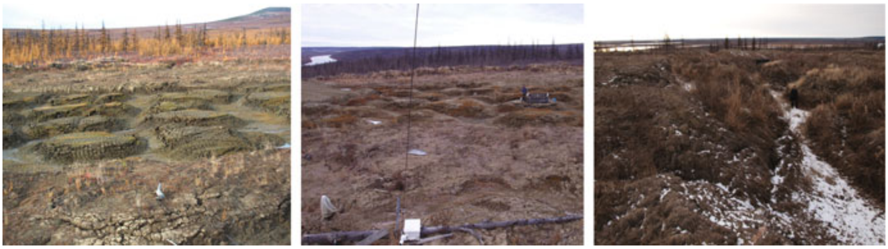

Fig. 10.2 On this gentle slope the organic layer of soil was removed with the help of a bulldozer. This has provoked degradation of permafrost and polygonal net of ice wedges. In 10 years 4–5.5 m of permafrost have thawed and the flat surface has turned to badland

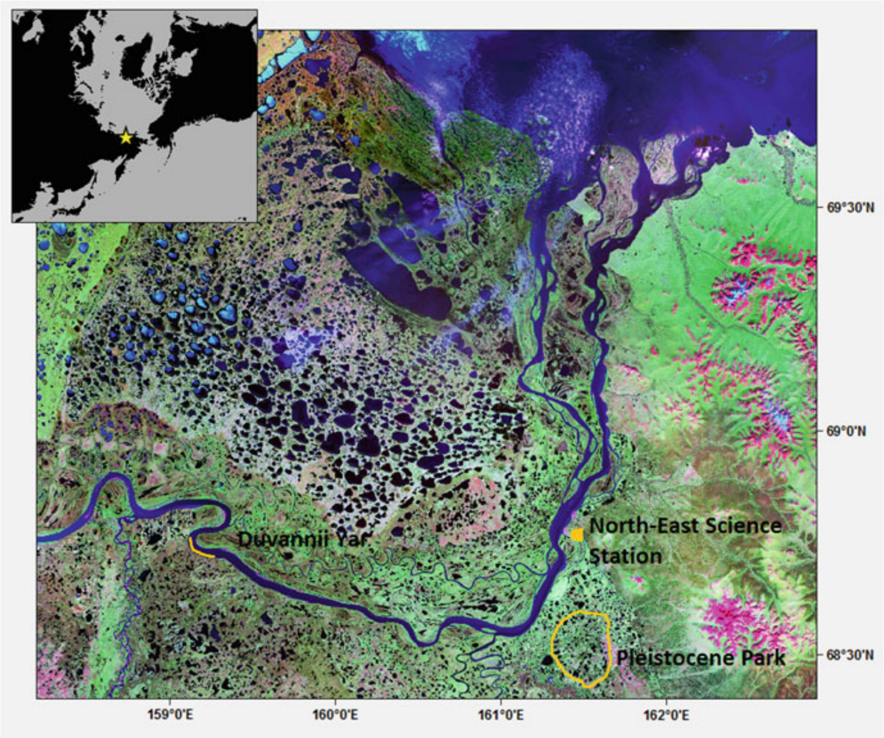

Fig. 10.3 Location of the North-East Science Station, Duvanii Yar and Pleistocene Park

this slope flowed down the Filipovka Tributary. This slope is only 0.1% of the watershed area but all the water in the Filipovka River turned into a mudflow.

The landscape shown in Fig. 10.2 is not unique. If ice wedges are covered with a thin layer of soil, then after a fire polygonal depressions appear. If, for example, the depth of the soil layer were only 0.7 m, and summer thaw depths increased to 1 m, then each year 0.3 m of ice would thaw. Previously this was a rather rare phenomenon. Now due to global warming it is becoming much more common in northern

Fig. 10.4 Gentle slope in the basin of Filipovka River, where the year before the image was taken, fire provoked permafrost degradation, and finally the entire soil layer has slid down to the river. In the next year herbs appeared (*yellow* color) on this slope and their roots have stopped the erosion

Siberia, and even in undisturbed places such reliefs can appear. And if the climate warms up by an additional 3°C, then the entire yedoma region would look like those in Figs. 10.1, 10.2, or 10.4.

10.3 Halting the Permafrost Thaw

Regional climate might be cooled via a change in landscape albedo. During summer dark green forests and shrubs absorb more heat compared to light green grasses and herbs (Foley et al. 1994; Lee et al. 2011). If dark forest and shrubs were removed, then from autumn to spring (8 months per year) northern landscapes would be white, reflecting the heat from the sun. This solution is extreme, and another solution exists. Soil surface is warmed in the summer and cooled in the winter. But at a depth of ~10 m there are no seasonal amplitudes of temperature, and it is roughly equal to the mean annual temperature of the soil's surface, which in turn depends on the mean temperature of the air. But this dependency is complicated. In the summer, soil temperature is roughly equal to air temperature, while in the winter a layer of snow exists between the soil and air, which is a good heat insulator. During such times air temperature can reach −50°C, while soil surface temperatures stay at −10°C. A decade ago the mean annual temperature near our station was −11°C. In the absence of snow the permafrost temperature would also be −11°C. But owing to the snow temperatures of permafrost are −6°C to −7°C. If we were to press this snow then it would lose most of its heat insulating abilities, and the permafrost would cool.

To artificially change vegetation and snow density on such a huge scale is near impossible. However it can happen naturally, through the trampling actions of large mammals, in particular herbivores. Currently, northern Siberia's mammalian biomass is too small for such trampling. However, as we argue below, this was not always the case.

10.4 Current Biodiversity in Northern Siberia

If one were to travel through the entirety of Siberia from south to north using winter roads, or drive on the boat along the Kolyma River (2,000 km) one would likely not meet any big animals. Using snowmobiles, boats, helicopters, we have travelled tens of thousands of kilometers along the Siberian north, and although looking carefully we have seen only eight bears, two wolves, two lynxes and one wolverine. It could be assumed that this territory is too severe to sustain many large mammals. But that is not true.

The East Siberian Sea is even more northerly and severe than Siberia. It is clear from ice only for 1–2 months of the year. However, when we boated on it, from the mouth of Kolyma River to Wrangel Island and back (roughly 1,600 km), we observed ~3,000 seals, ~300 walruses, 11 whale herds and 23 white bears. Admittedly these animals are not herbivores: they are positioned on the top of the trophic pyramid. However their total biomass, despite severe conditions, is several tons per km^2. Wrangel Island is the most severe wild nature reserve in Russia. Of the herbivores, only lemmings, as well as reindeers and musk ox reintroduced in twentieth century live there. However it is one of the richest Russian reserves based both on animal density and total biomass.

Northern Siberia has become a desert due to human action. In the seventeenth century when sable trappers reached Kolyma, up to 18,000 sables were trapped per year. At the same time snow geese were so abundant that tundra in the summer would appear to be covered with snow (Syroechkovskii 1986). However shortly after this both sable and snow goose disappeared completely. At the beginning of the nineteenth century, not far from our station each autumn around 100,000 wild reindeer crossed the Kolyma River (Syroechkovskii 1986). Today none of the locals remember this. For reindeer herders wild reindeer are major pests, and are actively killed, such that they have vanished from the area. Moose were rare in the region for a long time, but after the USSR collapse poaching control has been substantially reduced, and the populations of moose have declined ten-fold.

However the picture is not all bleak. Last century work was started on the reintroduction of sable. Current prices on sable fur can’t cover the expenses connected with trapping, and today on the Kolyma the sable population has recovered. Muskrats were also introduced to the Kolyma in the twentieth century, and now this species is widespread. On the Taimyr Peninsula, Wrangel Island, mouths of Lena, Indigirka and Kolyma Rivers, musk-ox were introduced and they have adapted everywhere and actively increased their populations. Due to economic reasons the Taimyr Peninsula lost its domestic reindeer herds, and a 100,000 domestic reindeer have been replaced with a million wild reindeers (Syroechkovskii 1986).

10.5 The Climatic Hypothesis and the Ecosystem Hypothesis

The current low density of animals in northern Siberia is not connected with severe climate. During glacial epochs the climate was more severe, yet mammoths, wooly rhinos, horses, bison, elk, musk-ox, antelopes (saiga), and cave lions thrived (Sher et al. 2005). During the Pleistocene the glacial mammoth steppe was the planet's biggest biome. It spanned from France to Canada and from Arctic Islands to China (Adams et al. 1990; Guthrie 1990). During interglacial warming forests took over, and the north of Siberia, Alaska and the Yukon Territory were refugia for this psychrophilic ecosystem. Trees and shrubs would also have penetrated to these places, but they were not the dominant vegetation cover (Sher 1997). It is only during the last interglacial, in the Holocene, that the mammoth steppe has vanished. Instead it has been replaced by moss forest and tundra. Many lakes and wetlands have appeared. It has been assumed that, during the Holocene, in contrast to other previous interglacials (Sher 1997), a cold dry steppe-like climate switched to a warmer wetter climate that, in turn, caused the disappearance of grasslands and their megafauna (Guthrie 1990; Vereshchagin and Tikhonov 1990; Velichko and Zelikson 2001; Schirrmeister et al. 2002; Sher et al. 2005). This is often referred to as the Climatic Hypothesis.

In contrast to the Climatic Hypothesis we propose an Ecosystem Hypothesis (Zimov and Chupryninm 1991; Zimov et al. 1995; Zimov 2005), which assumes that the mammoth ecosystem was relatively insensitive to climatic variation and that numerous animals maintained highly productive grasslands over a wide range of climates. Under such a strong disturbance regime, mosses and shrubs were trampled, and highly productive, actively transpiring graminoids and herbs dominated (Zimov and Chupryninm 1991; Zimov et al. 1995; Zimov 2005). During the PHT the rise in precipitation was accompanied by increased temperatures, so climatic aridity did not change substantially. The Ecosystem Hypothesis proposes: "In some places, such as sandy and stony ground, trees and shrubs would have appeared. This might have caused changes in the relative proportion of horses and moose. But overall, if climate was the only controlling factor, the total grassland productivity and the number of herbivores should have increased in the Holocene" (Zimov 2005, p. 798). We propose that the disappearance of the mammoth steppe was caused by an increase in hunting pressure. The resulting decline in abundance of animals would have reduced forage consumption, causing an accumulation of surface leaf litter, insulating the soil, and reducing summer soil temperatures. This would have initiated a cascade of other ecosystem changes, including a decline in productivity and transpiration, wetter soils, and lower nutrient availability. These, in turn, would have altered the competitive balance among species, promoting the growth of mosses and shrubs and reducing the abundance of grasses. The net effect would be a decline in forage quantity and quality, leading to continued decline in animal numbers (Zimov and Chupryninm 1991; Zimov et al. 1995; Zimov 2005). An important implication of the Ecosystem Hypothesis is that the grassland ecosystem could be regenerated in the north if one could increase the density and diversity of animals.

10.6 Chronological Support for the Ecosystem Hypothesis

Recent publication of many new ^{14}C dates of animal fossils from Alaska and Yukon provide an opportunity to clarify the relative chronologies of animal extinction, vegetation dynamics, and human colonization (Guthrie 2006). In this section we compare these data with chronologies assumed by the Ecosystem and Climatic Hypotheses. We presented the data in a form of probability distribution (each ^{14}C data is presented as a bell-curve with a 400 year base). The total ^{14}C data density curve is sum of area of all the bell-curves (Fig. 10.5).

Greenland ice cores show abrupt temperature and precipitation fluctuations at the PHT. At 14,650 calendar years BP (approximately 12,500 ^{14}C years BP (Reimer et al. 2004)) the average Greenland temperature rose sharply (up to Holocene levels), and precipitation doubled (the Bolling Warming Event (BWE)). During the Younger Dryas (11,600–12,800 calendar years BP) climatic parameters returned to their initial state, and at the end of the Younger Dryas temperatures rose sharply again (Severinghaus and Brook 1999). Similar climatic dynamics were recorded at both high and low latitudes of the northern hemisphere (Severinghaus and Brook 1999), and similar dynamics should also be recorded for Alaska.

If the Climatic Hypothesis explained vegetation and animal dynamics, steppe-like vegetation would have been replaced by tundra vegetation during the BWE, and the steppe would have been reestablished during the Younger Dryas, when the climate returned to glacial conditions. We propose that in fact, the opposite happened. Glacial climate was not favorable for the mammoth steppe ecosystem in Alaska and the Yukon, and during the LGM nine animal species went extinct (Guthrie 2006). When the climate warmed from 15,000 to 12,400 radiocarbon years BP there was a substantial rise in abundance of grasses and sedges, and animal densities increased (Fig. 10.5). Pollen influx of *Artemisia*, a drought-adapted species, rose even more than the influx of other species. This suggests that aridity did not decrease at the PHT.

The BWE did not affect plant species composition but affected animals. Data on Fig. 10.5 indicates that strong warming and increases of snow depth during the BWE was not accompanied by the extinction of any species. On the contrary animal populations grew. During glaciations the elk (*Cervus*) population was very small (only two ^{14}C dates (Guthrie 2006)). This population increased sharply by ~12,600 ^{14}C years BP. The Elk peak is statistically the most reliable (50 dates). Its right slope is very steep. The ^{14}C dating represented by this slope has a standard deviation of ± 90–240 years (Guthrie 2006). We did additional smoothing (± 200 year) in building the figures of ^{14}C date density. Thus in reality this slope is almost vertical- there was a sharp population rise. Reintroduction of musk-ox to Wrangel Island is a contemporary example of such a rise. Their population grew 100 times in 35 years (Vartanyan 2007).

Approximately 12,400 years ago an abrupt change occurred: horses vanished, bison disappeared for over 300 years, and mammoth and elk populations began to decrease sharply (Fig. 10.5). It is clear that this abrupt faunal change was not triggered

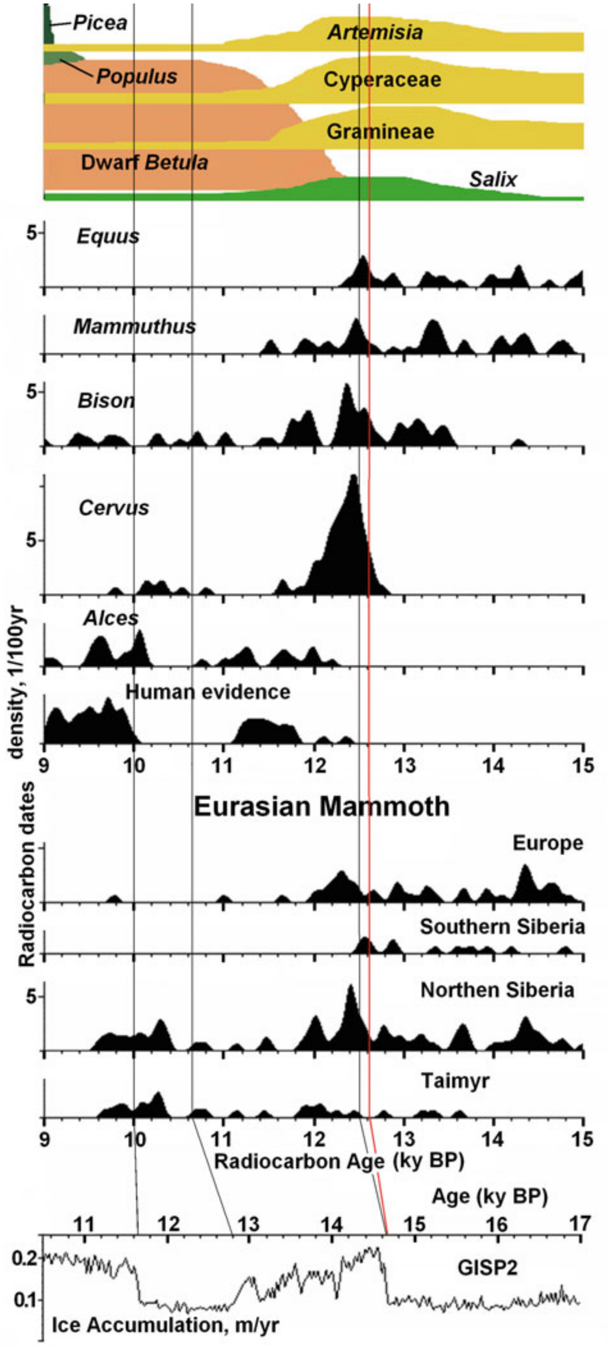

Fig. 10.5 *Upper part*: generalized pollen record, density of ^{14}C dates of animals, and human evidence for Alaska and Yukon (from Guthrie 2006). *Lower part*: density of ^{14}C dates of mammoths for Europe, southern Siberia and China (Vasil'chuk et al. 1997; Kuzmin et al. 2001), the entire Siberian Arctic (Vasil'chuk et al. 1997; Kuzmin et al. 2001; Sher et al. 2005), and the

by vegetation change, because vegetation was stable during this period. The only thing corresponding with these massive extinctions was the first evidence of humans (12,370 ^{14}C years BP) (Fig. 10.5). It therefore appears plausible that a relatively small number of hunters triggered the collapse of several herbivore populations (Martin 1984).

After the first appearance of humans, some of the species recovered their populations (which is in accord with mathematical modeling results (Alroy 2001)), but human population continued to increase and this led to herbivores' extinction. It was only well after that that pastures degraded and dwarf *Betula* appeared. The appearance of moose (*Alces)* at 12,200 radiocarbon years BP closely corresponds with a decrease in *Salix* and rise in dwarf *Betula*, which is not the usual forage for the moose. One possible explanation for this shift is that, as long as there were abundant bison, elk, and mammoth, which actively ate willow sprouts, willow shrubs would not have grown above the snow cover. Moose (tallest hoofed animal) may have appeared in large numbers only when populations of other animals had decreased, creating a new feeding niche–tall willow shrubs.

The increase in ^{14}C dates of mammoths at the BWE (Fig. 10.5) can also be observed in Europe and the Siberian north (Vasil'chuk et al. 1997; Sher et al. 2005). During the Holocene the mammoth population on Wrangel Island increased substantially. There were five-fold more Holocene dates there (3,730–7,710 years BP range) than Pleistocene dates (Vartanyan 2007). This occurred despite the fact that, in contrast to Alaska where loess accumulated throughout the Holocene (Muhs 2003), in Siberia sedimentation stopped (Schirrmeister et al. 2002; Sher et al. 2005), and most of the bones remained on the surface, where weathering would have destroyed them.

10.7 The Mammoth Steppe Climatic Envelope

The essence of the Climatic Hypothesis is as follows: mammoths, other extinct animals, and their pastures (i.e., the mammoth steppe) required a certain range of climatic parameters that defined their climatic envelope. In the Holocene, climate changed radically, and territories with suitable climate for the mammoth steppe disappeared throughout the planet. To further assess the Climatic Hypothesis, we define the mammoth steppe climatic envelope, i.e., the optimal and peripheral climatic space of the mammoth steppe.

Here we discuss two climatic characteristics – heat and moisture, as aridity level is determined by these two factors. We characterize moisture by annual precipitation (P) and heat by annual radiation balance (R), which correlates closely with mean summer temperature. We consider a two-dimensional climate space with

Fig. 10.5 (continued) Taimyr Peninsula (Sher et al. 2005); snow accumulation for Greenland (Severinghaus and Brook 1999). *Vertical black lines* represent Younger Dryas boundaries based on IntCal04 (Reimer et al. 2004); the *red line* is a corrected (elk peak correction) Bowling radiocarbon boundary

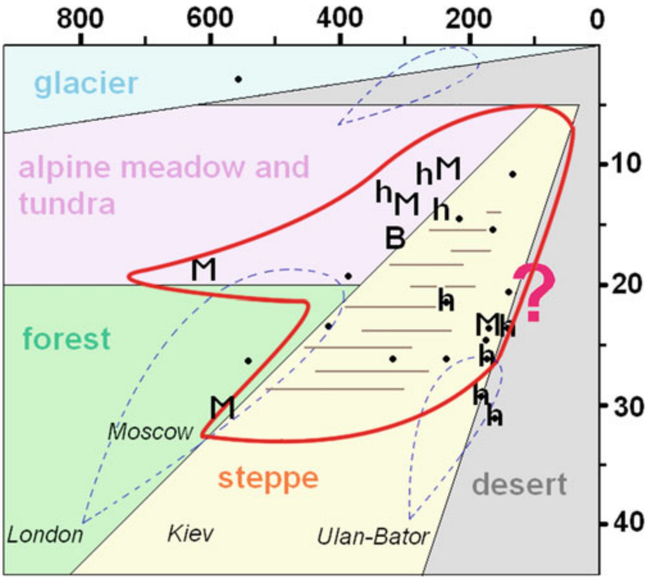

Fig. 10.6 Climatic space with the most important landscape boundaries shown. The axis R could also represent average summer temperatures (20 kkal/cm^2/year approximately corresponds to 10°C). *Black dots* are the meteorological stations of northeast Siberia (see Fig. 10.7). *h* represents Holocene and modern horse grasslands in Siberia; *M* and *B* are Holocene grasslands of mammoths and Siberian bison. *Brown cross-hatching lines* represent Holocene natural bison habitat of interior Alaska and northwestern Canada. Question mark (‘?’) is the presumed locations of the mammoth steppe climatic envelope that are consistent with the Climatic Hypothesis. The *red solid line* is our estimate of the boundary of the continuous climatic envelope of mammoth steppe. *Dashed blue lines* enclose areas where climatic trajectories lie, during the last glacial cycle, in three geographical locations: London, Ulan-Bator and top of the 1,700 m mountains near the Oymyakon region. Today’s snow line of the Oymyakon Mountains is situated on 2,300 m

these two parameters (coordinates). Aridity can be assessed using Budyko’s radiation aridity index (Budyko 1984), which is the ratio of R (in this case energy received by the landscape) to the energy needed to evaporate an amount of water equal to P. If this index is less than 1, the climate is humid; if greater than 1, the climate is arid: with values between 1 and 2 equivalent to steppe, 2–3 semi-desert, and >3 desert environments (Budyko 1984).

Such a two-dimensional climate space is illustrated in Fig. 10.6, which shows the most important boundaries for desert, arid and humid climates (Budyko 1984). Beside those we show the approximate position of three additional boundaries: the snow line where R equals the energy needed to melt an amount of ice equivalent to annual precipitation; the northern (altitudinal) forest border; and the boundary of polar desert. Vertical movement in this climate space is equivalent to latitudinal movement in real (geographical) space. Movement to the right of this climate space is equivalent to movement from the ocean to the continental interior. Movement to the upper left quadrant is equivalent to moving upward in elevation: colder with more precipitation.

On the basis of this envelope, we make five arguments: (1) Similar to geographical space, in climatic space the mammoth ecosystem should have an optimal zone and a peripheral zone where conditions for survival are severe; (2) The mammoth steppe existed in different climates on a huge territory for a long period of time. Mammoths lived simultaneously in Spain, England, Mongolia, China and Arctic Islands (Vasil'chuk et al. 1997; Kuzmin et al. 2001; Sher et al. 2005; Alvarez-Lao and García 2011). It is obvious that climate differed between these regions, therefore, it can be assumed that the mammoth steppe climatic area was spacious; (3) If mammoths became extinct in the Holocene everywhere because of climate then there is currently no place on the planet where the climate would still be suitable for the mammoths. It then follows from the Climatic Hypothesis that mammoths were living under a unique combination of R and P, which are not met anywhere today; (4) It seems that the mammoth steppe optimum must be situated in the colder part of the steppe sector (Fig. 10.6), and their range should move smoothly into temperate climate steppe; (5) The range of climatic optimum for mammoth steppe was approximately 150–300 mm of precipitation and 8–10°C summer temperatures, which corresponds to climatic reconstructions for Eastern Europe, where the mammoth ecosystem received 250–300 mm of precipitation annually (Velichko and Zelikson 2001).

In the PHT the previously arid climate in the north of Siberia did not become humid (Zimov and Chupryninm 1991; Zimov et al. 1995). Figure 10.7 shows the meteorological stations of northeastern Siberia, where radiation balance observations are conducted (all circumpolar, including islands and continental); these are also shown on Fig. 10.6 with black points. We see that even though this region has abundant lakes and wetlands its climate is arid. The most arid part is in the Pole of Cold in Oymyakon (Budyko's index = 3.28; the most right and lowest black dot on Fig.10.6), and most humid is in mountains near the glacier, not far from Oymyakon (Budyko's index = 0.1; the most upper and left dot). We can use another known climatic index, in which potential evaporation is calculated by summer temperatures, but we get the same results – the climate is arid (Sokolov and Konyushkov 1998). Around 400–500 mm of precipitation evaporates from lake surfaces or high productive grasslands in these territories; this is twice precipitation this region receives (Zimov and Chupryninm 1991; Zimov et al. 1995). Lakes persist only because of drainage from slowly transpiring forests and tundra. In Central Yakutia vast steppe territories grazed by horses do not have any river drainage (Pavlov 1984). Nevertheless, proponents of the Climatic Hypothesis suggest that the climate of northeast Siberia and Alaska is too wet for the mammoth steppe (Guthrie 1990; Vereshchagin and Tikhonov 1990; Velichko and Zelikson 2001; Sher et al. 2005). If correct, the climatic envelope of the mammoth steppe would be restricted to a small area between the upland cold deserts of Tibet and the polar deserts of the Canadian Arctic (indicated with a red question mark in Fig. 10.6). The Climatic Hypothesis assumes that this small envelope occupied a huge territory of Eurasia and Northern America during both the LGM and the BWE. This climate space was

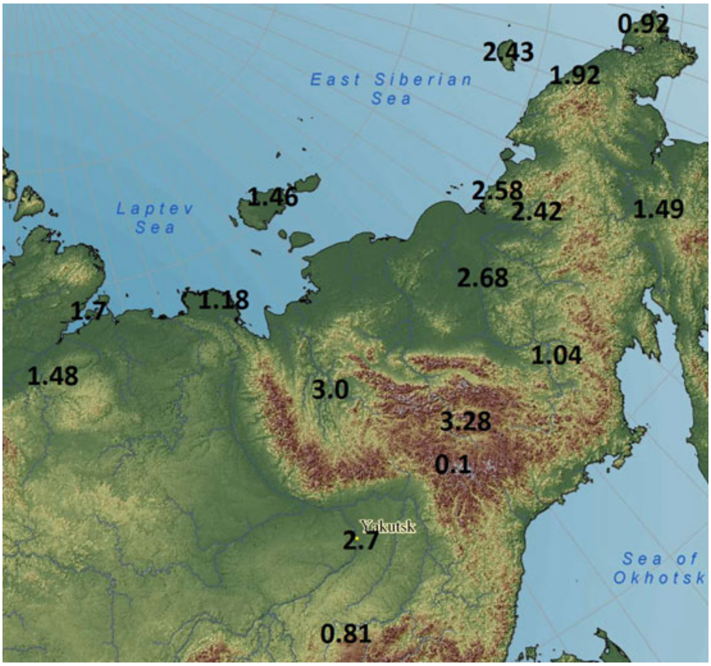

Fig. 10.7 Budyko's radiation aridity index in different locations North-Eastern Siberia

characterized by only ~100 mm of precipitation, raising questions of how the glaciers of Europe could have developed and persisted.

The last mammoth refuge on the continent was the north of Taimyr Peninsula, where they persisted until the Holocene (Sher et al. 2005). If the Climatic Hypothesis holds, then the entire climatic envelope of mammoths should be situated in even more severe conditions than on the Taimyr Peninsula (polar desert). However mammoths lived in the Iberian Peninsula (Alvarez-Lao and García 2011), which would suggest that summer there (40°N) was colder than in Taimyr today (i.e., 25–30°C colder than today). This is not possible. We suggest that the Climatic Hypothesis as currently stated (i.e., "colder and dryer") is unrealizable. The mammoth steppe could exist at 100 mm precipitation and with northern Taimyr summer temperatures, but it's unlikely that this represented optimal conditions.

It is possible to amend the Climatic Hypothesis by assuming that R and P changed very quickly, and that every region had its own subspecies of mammoth that were adapted to local conditions. Hence mammoths wouldn't have had time to adapt to fluctuations or migrate to more suitable regions. However this would not explain why in Europe, Northern Siberia and North America mammoths sustained bigger climatic jumps yet vanished under relatively stable climate (see Fig. 10.5). A better explanation is that the mammoth steppe did not disappear due to climate.

10.8 Climatic Envelope of Mammals of the Mammoth Steppe Ecosystem

In this section we revisit the numerous radiocarbon dates for bones of animals that used to live in the mammoth steppe ecosystem. Many of these bones date from the Holocene and therefore experienced a climate similar to the modern climate. By looking on climatic maps at the modern climate (R and P) of these locations, we can directly estimate the climate experienced by Holocene populations of these species. These points in climate space are shown in Fig. 10.6.

The lack of horses in Alaska during the Holocene has been lead to suggestions that the modern Alaskan climate is not suitable for them (Guthrie 2006). However, in Siberia, where the climate is similar, horses persisted well into the Holocene (up to 2,200 ^{14}C years BP) in the arid far north (Lena delta and New Siberian Islands) and in humid climates (the Taimyr) (Sher et al. 2005). The semi-wild Yakutian horses today occupy a more southern and warmer climate (Fig. 10.6).

With bison, the situation is the reverse, with only one Holocene bison date in northern Siberia (9,300 ^{14}C years BP) (Sher et al. 2005), but extensive bison distributions in interior Alaska and the Yukon throughout most of the Holocene. They occurred along the arctic coast as far north as Victoria Island and as far south as southern Alaska near Anchorage (Stephenson et al. 2001). The climatic envelope of the American bison is shown in Fig. 10.6 with a dotted line.

Reindeer now live on the far north and in Mongolia. In historical times their southern boundary passed through Germany along the steppes of Eastern Europe (Syroechkovskii 1986). Therefore the climatic envelope of reindeer occupies almost the entire climate space of Fig. 10.6. In many regions of Siberia and North America musk-ox have lived until historical time (Sher et al. 2005), and as a result of recent reintroductions they currently live in Norway, Siberia, and Alaska.

We have no Holocene dates for the wooly rhinoceros, but their bones tend to occur in regions that are more arid than those of mammoths. For example, the northwestern portion of Eurasia to the north of 62°N including Taimyr is a humid part of the mammoth steppe. Many mammoth remains were found there but no rhinos (Garrut and Boeskorov 2001). On the other hand, wooly rhinos were common in the most arid regions of mammoth steppe, south of Central Siberia and Mongolia (Garrut and Boeskorov 2001), where mammoths are rare (Kuzmin et al. 2001).

Mammoths existed in the arid zone in the Holocene (Wrangel Island (Fig. 10.8), with the most recent date of 3,730 ^{14}C years BP) (Vartanyan 2007), in the humid zone on the north of Western Siberia (Gydan peninsula, 9,730 ^{14}C years BP), in the northern Taimyr (9,670 ^{14}C years BP) (Sher et al. 2005), in the very humid St. Paul Island in the Bering Sea (5,700 ^{14}C years BP) (Yesner et al. 2007; Guthrie 2004), and on the coast of Gulf of Finland (9,780 ^{14}C years BP) (Vasil'chuk et al. 1997). While the early Holocene climate may not have been the same as today; it is indisputable that on Wrangel Island and on St. Paulo Island mammoth lived in a late Holocene climate.

On the climatic space (Fig. 10.6) these sites are situated very far from each other. Wrangel Island is a dry polar desert, and St. Paulo has a very humid climate with no

Fig. 10.8 Wrangel Island was the last mammoth refugium. This picture shows grassland near the Ushakovskaya weather station, where the average July temperature is 1°C. The territory is characterized by high animal nitrogen inputs. It is the middle of September, but photosynthesis continues

permafrost. And the fact that mammoth lived on these two islands genetically isolated for the long time suggests that the mammoth's climatic envelope was very wide.

The ^{14}C data indicated that during the LGM mammoths lived on the climatically severe archipelago of New Siberia (79–80°N) (Sher et al. 2005) and Wrangel Island (Vartanyan 2007). They continued to live there in the Holocene. Today summer temperatures on these islands are approximately 0°C, and the vegetation would not feed a mammoth population. The paradox is that under the current climate, the same place can be a polar desert (in the absence of animals) or grassland (if animals are present). During the last 50 years, after the reintroduction of herbivores on Wrangel Island, ungulate biomass has exceeded the intended density (calculated maximum) by almost an order of magnitude (Vartanyan 2007). We suggest this happened because the biomass of forage has increased as herbivores maintain their grasslands. This is only the beginning of ecosystem succession. The potential grassland productivity on the island is shown in Fig. 10.7. Biological productivity in the north is limited less by photosynthesis than by nutrients (Chapin et al. 1995). Nutrient cycling is limited by slow decomposition and nutrient release from soil organic matter. Only in the warm stomachs of animals can this process be substantially accelerated.

In summary, the animals of the mammoth steppe occupied a broad climatic envelope. Similarly the distribution of modern tundra does not depend on aridity but occurs in sites ranging from 50 to 1,000 mm of annual precipitation. Based on the above information, we tried to reconstruct the boundary for a continuous climatic envelope for the mammoth steppe (Fig. 10.7). In geographical areas that now lie inside the envelope, the mammoth steppe ecosystem would not vanish because of R and P changes during PHT. The next important question is whether animal population densities in the mammoth steppe were high enough to prevent expansion of moss, shrubs, and trees.

10.9 Mammalian Population Density of the Mammoth Steppe

Animal density for the mammoth steppe can be estimated from the number of bones found in permafrost. However, from most of the skeletons, few to no bones are preserved (Guthrie 1990; Sher et al. 2005). We have reconstructed animal densities using several methods for different sites. We have done this most precisely based on data collected at Duvanii Yar in the Kolyma River lowland (68°38′N, 159°07′E), the largest yedoma exposure (Vasil'chuk et al. 2001; Zimov et al. 2006b) (Fig. 10.1). During the time of yedoma accumulation, this territory, remote from mountains and hills, was a flat plain, and animal density in the area was likely determined by forage availability.

The bone concentration in the Duvanii Yar yedoma (as for most other yedoma and loess) is small, only one bone (or its fragment) for each ~500 m^3, therefore it is difficult to find bones on the cliffs (exposure). However accounting for the 50 m height of exposure, the density of bones is 1 bone per 10 m^2 or 100,000 bones per km^2. Observing this high density is only possible on the exposed shores, where sediments slide or crumble and are washed from the area by waves and streams. Well-washed bands several meters wide appear on the Duvanii Yar only rarely. After a storm the water level in the rivers drops abruptly, and mud flowing down the exposures don't have enough time to cover all exposed (washed) bones. For minor rivers, where there are no big waves, large exposures and beaches are absent.

Bones are initially deposited at the location of an animal's death. Predators can disperse some of the bones, although this is unlikely for the tusks and molars of mammoths. On the large beaches at Duvanii Yar mammoth bones occur in groups several tens of meters from one another and belong to one animal (one skeleton), making it possible to directly calculate the density of mammoth skeletons. On average, each accumulation is 8–10 bones (up to 19). Fragments of tusks and/or molars are present in most of the accumulations (Fig. 10.9). On three occasions (1998, 2009 and 2011) the beach was well washed and we were able to count the density of mammoth skeletons on four transects. Densities were 1,030, 1,170, 1,380 and 1,450 per km^2. This density was calculated as the number of bone accumulation centers falling into the bands of well-washed shore (width of the bands multiplied by length) (Zimov et al. under review).

The number of tusks can also be used to calculate the density of mammoth skeletons in the yedoma. Average annual commercial collections of mammoth tusks from Duvanii Yar are about 250 kg/year, and range from 70 to 450 kg/year. Due to the length of the exposure (10 km) and the rate of erosion (2.5 m/year), the density of the tusks is equal to 10 t/km^2. The average weight of a tusk in this region is 25 kg (39 kg for males and 11 kg for females) (Vereshchagin and Tikhonov 1990). Thus, the density of commercial tusks is 400/km^2. However most of the tusks are disintegrated by being on the surface and in the yedoma are preserved only as small fragments without commercial value. If we assume that only 20% of tusks (by weight of all tusks) are preserved in permafrost and appear in the collection, then we obtain 1,000 skeletons/km^2, the same mammoth density that we calculated from skeleton density at Duvanii Yar.

In order to obtain a precise estimate of hoofed animal density, we used full bone collections gathered in 2007 and in 2009 over the area of ~0.01 km^2. The collection is shown in Fig. 10.10. Not shown are 23 woolly rhinoceros bones (that were found in 6 accumulations), 4 musk-ox bones, 3 elk bones, 2 moose bones, 1 hare bone, 4 wolf bones, 2 cave lion bones, and 61 unidentified mammoth bone fragments. The distribution of fossils from different species on Duvanii Yar was very similar to the distribution of bones obtained from the ~3,000 bones collected in the entire region

Fig. 10.9 August 2011 in the central part of the Duvanii Yar. Width of the well-washed band in the central part of the shore was on average 6–10 m. Here, in 1,570 m transect, 169 bones and bones fragments of mammoths were found: 5 bones were isolated, 4 accumulations with 2 bones, and 32 accumulations with 3–10 bones or their fragments. In 29 accumulations particles of molars and tusks were present. The diameter of each accumulation is ~10 m. In this image we show all four accumulations with mammoth jaws

of northern Siberia (Sher et al. 2005). So the species distribution on Duvanii Yar is typical of the Siberian north. Massive bones dominate for each species (Fig. 10.10) with thin bones, for example ribs, being very rare, and the smallest bones absent.

To compare the skeletal densities of different species, we used the dependence (proportion) of the relative probability of bones to persist (to be found) to bone weight. To correct for the influence of bone shape (length), we used a reduced weight (bone weight (g)/bone length (cm)$^{3/2}$). Linear dependence was recorded for all species and holds true for a range of bone weights from grams to kilograms (Fig. 10.11). The same dependency (linear) was recorded for the mammoth collection gathered from the entire Siberian north (Fig. 10.11). The number of bones in the collection is also proportional to the number of dead animals. Assuming that all four graphs reflect the same functional dependence on bone weight, we determined a relative density of skeletons for four species (using the ratio between equation coefficients (Fig. 10.11)). We determined (rounding) that bison skeletons were 20 times more abundant than mammoth skeletons, horses 30 times and reindeer 80 times. These estimates are close to those obtained by using the average number of bones in the accumulations (Zimov et al. under review).

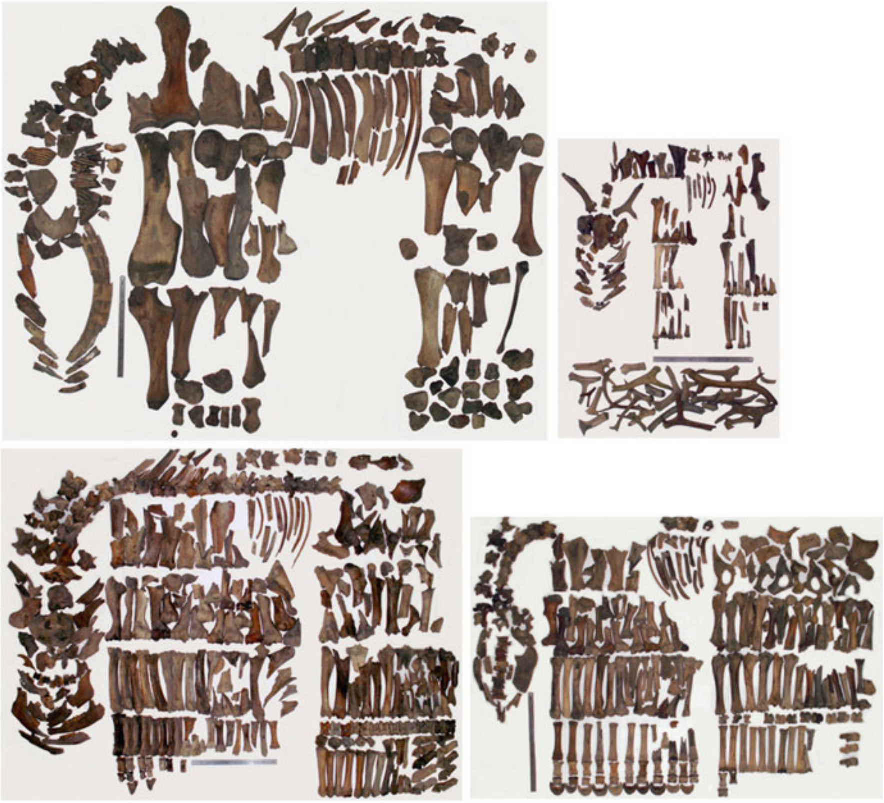

Fig. 10.10 Bones of mammoths, horses, bison and reindeers collected on the shore of Kolyma river on the western part of Duvanii Yar exposure on the area of ~1 ha. Bones are positioned to be consistent with their anatomical position. Mewed reindeer horns presented separately

Duvanii Yar loess accumulated from 42,000 to 13,000 years BP (there are 40 ^{14}C dates from this exposure (Vasil'chuk et al. 2001)). In collections gathered from northern Siberia, ~10% of all of the mammoth bones were older than 45,000 years (Sher et al. 2005). Therefore, we took a more conservative estimate that all bones accumulated for ~40,000 years. The average age for a dead mammoth, calculated based on annual rings on tusks, was 40 years (maximum age ~80 years) (Vereshchagin and Tikhonov 1990). We are making a conservative evaluation of the density of dead mammoths at 1,000/km^2. From this we determined that the average adult mammoth density was about 1/km^2.

There were very few bones of young ungulate animals; they are relatively soft and therefore are often eaten by predators. By accounting for high predator pressure, and the maximum age of modern animals, we assumed that the average longevity of mature horses, bison, and lions was 10 years, 7 years for reindeer, and 5 years for wolves, which gave us an average animal density per square kilometre of 5 bison (total weight of 3 t), 7.5 horses (3 t), 15 reindeer (1.5 t), 0.25

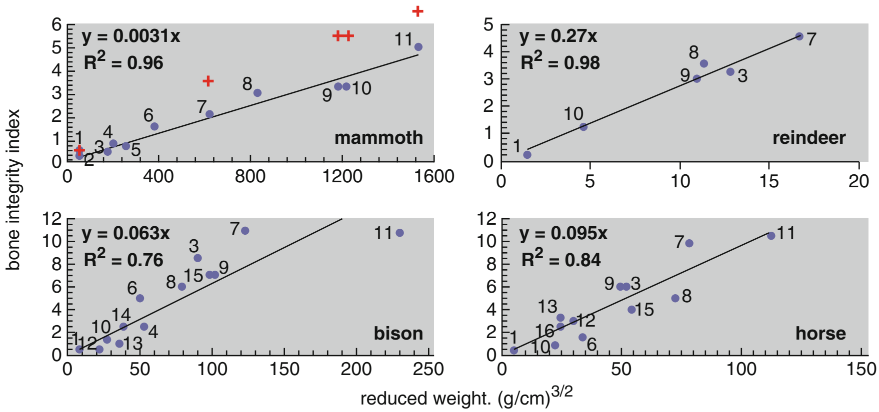

Fig. 10.11 Dependency of bone integrity on reduced weight. Bone integrity index is the ratio of the number of bones of a specific type in a collection (Fig. 10.10) to the number of such bones in an entire skeleton of a species. 1 – rib; 2 – caudal vertebra; 3 – metapodial; 4 – carpal and tarsal; 5 – vertebra; 6 – calcanea; 7 – radius and tibia**;** 8 – mandible; 9 – scapula and pelvis; 10 – molar; 11 – humerus and femur; 12 – phalanx I; 13 – phalanx II; 14 – ulna; 15 – talus; 16 – phalanx III (hoof). *Red* “+” – data from big mammoth ^{14}C collection gathered in all of Siberia (Sher et al. 2005)

lions (0.05 t), and 1 wolf (0.05 t). By adding the weight of the mammoths (=2.5 t (Vereshchagin and Tikhonov 1990)) to the rest of the more uncommon herbivores (0.5 t), we calculated a total herbivore biomass of 10.5 t, enough to feed wolves. All of these estimates were averaged over a period of 40,000 years. Mammoth density dynamics are illustrated on Fig. 10.12 (Kuzmin et al. 2001; Sher et al. 2005; Vartanyan 2007; Nikolskiy et al. 2009). During the LGM, the number of mammoths was at their lowest; it increased as the climate became warmer.

Similarly, we obtained equivalent estimates of animal density for the Lena river delta, New Siberian and St. Paulo Islands (Zimov et al. under review). These estimates are approximate. Many parameters (animals weight, shore width, etc.) were rounded, but the accuracy of these estimates is probably similar to the accuracy of the estimates of animal densities in modern ecosystems. Our roughest estimate was for predators, but considering that almost all of the vertebrae of horses were eaten, and that predator action broke all of the humeral bones, we believe that the predator population was large enough to eat most things.

We also see large number of herbivores in the north today. Semi-wild horses inhabit northern Siberia. Their biomass in Yakutia exceeds the biomass of reindeer (Agricultural Atlas of Yakutia 1989). The modern density of wild and semi-wild reindeer in the forest and tundra of the north-eastern Siberia is only 60 kg/km^2 (1 per km^2 (Agricultural Atlas of Yakutia 1989)). In contrast, the current biomass for horses in the Aleko-Kuel region, (300 km west of Duvanii Yar) on the most productive low-lying meadow, is 200 times this value (30 horses/km^2), which is close to the above estimate of 10.5 t. The same density of ungulate animals is maintained on the grasslands of Pleistocene Park (100 km of east of Duvanii Yar) (Fig. 10.13).

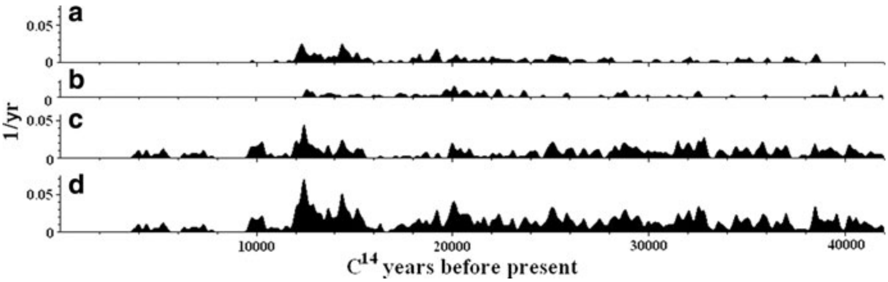

Fig. 10.12 Density of ^{14}C dates of Siberian mammoths

Fig. 10.13 Horses, bison and musk-ox inhabit Pleistocene Park. There are also three species of deer. This represents the highest diversity this area has seen in the last 12,000 years

10.10 Mammoth Steppe Physiology

Although the accuracy of any single calculation might be questioned, as with any paleo-reconstruction, the consistency of patterns that we obtained from many independent data sources and approaches suggest that the following inter-related conclusions are robust:

1. Plant, herbivore, and predator productivity in mammoth steppe was close to the theoretical maximum for a northern ecosystem. The ecosystem very efficiently utilized all resources. The density of animals and their community structure was similar to that of an African savanna. To feed animals, plants utilized all available water.
2. Vegetation was dominated by palatable high-productivity grasses, herbs and willow shrubs (Guthrie 1990; Sher et al. 2005). No other vegetation could maintain 10 t/km^2 of herbivore biomass.

Fig. 10.14 Part of the Duvanii Yar exposure. The soils (yedoma) are fertile, so even though it's a cold northern-faced slope, highly productive grasses appear in locations of permafrost erosion. In this part of the exposure, grasses prevent erosion through root reinforcement of the soil. In conditions of cold and dry climate with herbivores absent, thermally insulating litter accumulates on the surface, fertility declines, and in several years grass productivity also declines. If herbivores appear on the site they maintain meadow productivity and also decrease permafrost thawing

3. The soils were fertile. The content of bio-available phosphorus in the yedoma is an order higher than in modern soils (Zhigotsky 1982). If soils of the mammoth steppe appear on the surface due to erosion, they are immediately overgrown by highly productive grasses and herbs (Fig. 10.14).
4. Winters were much longer than summers, and winter forage was a limiting resource. Therefore, summer overgrazing was not possible. In the summer animals could eat only half of all available forage. During winter herbivores ate all the rest (Fig. 10.15); however, without long-term damage to the grass community, since all living parts are preserved in the soil. Therefore, all of the insulated snow cover was trampled, and the soils cooled significantly during winter. A change in snow depth of ~10 cm changes the temperature of the permafrost by 1°C (Yershov 1998). Soils were fully trampled throughout the year, preventing the establishment of a moss layer and the expansion of slowly growing shrubs and trees into grasslands (Zimov et al. 1995). The albedo of the mammoth steppe was significantly higher than the albedo of forests and shrublands, especially during the snow season (Foley et al. 1994). Litter did not accumulate in the ecosystem. Therefore, at the beginning of the summer, until new grass had grown bare soil surface (Fig. 10.15) was intensively heated by the sun.
5. Moderate summer grazing stimulated the regrowth of grasses. As a result, grasses had no time to finish their life cycle and were covered with snow still having a high nutritional value. Plant species assemblage is usually determined from pollen records that are collected from loess strata. These records often consist of species that are not common in grasslands (Guthrie 1990;

Fig. 10.15 Pleistocene Park in spring after snowmelt. Ten years prior, the area was a continuous community of 2–3 m tall willow shrubs. Due to erosion and long-term active grazing, the plot developed into a meadow with fertile soils and nutritious grasses. Herbivores therefore graze in this area several times per winter, trample down snow, and eat all the vegetation that grows during the summer. The winter temperature of the soil surface at this site is 15–20°C colder than for grasslands without grazing. We presume that during herbivore population peaks in spring all of the mammoth steppe grasslands looked similar to this

Sher et al. 2005). If on some territory several meters of loess accumulated, it would indicate that another territory with sparse vegetation cover and strong winds would erode the same amount of dust, and that all of the spores and pollen (and everything aerodynamically lighter than sand including insect remains) from deflated areas would appear in pollen-poor grasslands and, in the end, in loess strata. These inferences can be applied to all mammoth steppes that formed on loess-dominated soils. In areas with poor stony or sandy soils, the productivity of palatable plants would be smaller and grazing and trampling would be weaker. Therefore, slow-growing unproductive plants were able to survive and persisted in the regional flora. Mammoth steppe biomes consist of different ecosystems: unproductive deflation areas, productive grasslands on loess or loamy soils, and tundra and forests (savanna) on poor soils. These patterns explain the complicated composition of the pollen spectrum.

6. Due to high productivity and corresponding plant transpiration, water was often a limiting resource; grass roots competing for water penetrated the entire depth of the active layer. This is additionally suggested by the fact that in the yedoma numerous thin grass roots are preserved (Sher et al. 2005). Near the permafrost table soils were thawed just for few weeks per year, and temperatures never rose substantially above zero, therefore organic decomposition was low, and labile carbon accumulated (Zimov et al. 2009). Hence the mammoth steppe was an ecosystem with a high rate of decomposition for aboveground biomass (in animals' stomachs), and a very low rate of decomposition in deeper soils.

7. The similarity of density and the assemblage of species on the northern and southern parts of the lowlands suggest that regular massive migrations of herbivores with regional differences in mortality were unlikely.
8. Mammoth steppe would only be stable under conditions of very high animal densities, as they had a strong impact on the environment. An expansion of the high-albedo psychrophilic steppe biome, whose dry soils and permafrost accumulate carbon (Zimov et al. 2006a, b; Zimov et al. 2009) and do not produce methane (Rivkina et al. 2006), would promote climate cooling and permafrost expansion, whereas a degradation of the ecosystem and permafrost in response to recent warming would amplify climate warming (Zimov and Zimov under review).
9. Mammoth steppe on the Siberian north was the coldest and driest part of the biome. In other grassland ecosystems, where there was 2–4 times more precipitation, and grass and herb productivity and animal densities were correspondingly higher. An analysis of paleovegetation maps indicates that during the LGM forested areas were 10 times smaller than in the Holocene, and that an area of grass-herb dominated ecosystem reached 70×10^6 km^2 (Adams and Faure 1998). If similar animals to the mammoth steppe consumed all forage, assuming average herbivore density of 20 $\mathrm{t/km}^2$ (twice more than in the north of Siberia), we obtain global animal biomass values (1.4 billion tons) close to that obtained via methane emission by herbivores (Zimov and Zimov under review). During the LGM, wetlands were rare. For that period no ^{14}C basal peat initiation dates are know. They appeared in abundance only in the Holocene (Yu et al. 2010). Furthermore, during the LGM methane concentration in the atmosphere was almost half of Holocene values, and herbivores were the main source of methane due to a total herbivore biomass exceeding total modern biomass of humans and domestic animals combined (Zimov and Zimov under review). In the Holocene the density of herbivores declined by an order of magnitude (Zimov and Zimov under review).

10.11 The Pasture Ecosystem

During glacial periods ecosystems were different from that found today. Among plants grasses and herbs dominated. The main characteristic of grassland ecosystems was the abundance of herbivores, which maintained wet or dry pastures. In the spring these ecosystems looked like those on Fig. 10.15. Only bones and excrements were left on the surface. We propose to call these ecosystems pasture or grazing ecosystems. With the help of herbivores pasture ecosystems were dominant and could compete with forests even in humid climates.

On a geological timescale pasture ecosystems are amongst the youngest. These ecosystems have the highest rates of biocycling, with some of the most fertile soils. Unlike evergreen plants, fast growing grasses encourage grazing and trampling as it stimulates their growth. Grasses do not spend energy on toxins and thorns, and they maximise sunlight and water resources. The grazer's niche in this ecosystem is to eat everything that has grown during summer (rain season) and return all the nutrition back to soil through defecation. Predators in this ecosystem maintain herbivore population densities.

On different continents pasture ecosystems have different biological species, but similar assemblages of functional types. For example, the African antelopes and the cervids of Eurasia occupy similar functional types in pasture ecosystems. Pasture ecosystems are very dynamic: where forests or mossy tundra may need many years to recover after natural disasters (e.g., fires), pasture ecosystems may recover in several weeks. Over the course of the last million years, under the dynamic Pleistocene climate, the mammoth steppe and other pasture ecosystems replaced forests and occupied large parts of the world.

10.12 The Mammoth Steppe Ecosystem and Humans

Mathematical modelling indicates that for the current climate in north-eastern Siberia, two stable states of nature exist: in the presence of strong hunting pressure mossy-shrub plant communities exist, while in the absence of hunting pressure grass dominated communities prevail (Zimov and Chupryninm 1991; Zimov et al. 1995). To shift environment from one state to another, there is no need to exterminate all animals. However, in the north of Siberia little evidence of humans during the PHT exists, and in Russia the overkill hypothesis (Martin 1984) is not popular. We have shown that there were around 100 million large animals living in the north. In Africa and Asia humans did not exterminate the megafauna (Barnosky et al. 2004; Louys 2008). Why then did this happen in the north with mammoths? We can't provide definitive proof that humans drove the mammoths extinct. However we can show that humans could do it, both physically and mentally. And we show that the density of artefacts in the north does not contradiction that.

Initially *Homo sapiens* appeared in the southern part of the mammoth steppe and for many thousands of years was part of that ecosystem. Animals were so abundant in the mammoth steppe that humans would not need to look for animals. However, many of the animals were dangerous. Humans were the slowest species with the most defenseless young. Biologically, humans are least adapted to cold and long winters. Therefore, the survival of humans and possibilities for expansion into the vast woodless plains of the north were not limited by animal density, but by severe climate conditions, the absence of natural shelters, and their level of technology. Every new dwelling type, weapons, clothes, and fire-making techniques all contributed to increased human efficiency and survival, and therefore the expansion of the human climatic envelope. Humans learned how to build shelters, where they could retreat and store food and animal grease for fire, and thus they became the main predator. At the end of PHT humans had already learnt how to hunt all species and how to survive in any environment. The most striking example of this is an early Holocene archeological site on the small island of Johovo, 500 km north of the

Arctic coast (76°N, 153°E). Armed with bone tools, these people lived in those extreme conditions, mostly hunting polar bears (Pitul'ko 1993), which are three times larger than the cave lion, and 10 times larger than the hunters themselves. If humans could regularly (i.e., with little risk) hunt the biggest and most dangerous predators, in the most severe environments, it means they could hunt mammoths everywhere.

Human expansion north in geographical space reflected climatic changes. People were likely absent or rare in the homogeneous northern Siberian plains in the cold epochs before the BWE. During the BWE the climate in northern Siberia and Alaska became similar to the glacial climate of Eastern Europe, and these territories became more suitable for human occupation.

The BWE also sharply changed the landscape. Permafrost degradation led to numerous badlands (see Fig. 10.2), thermokarst lakes with steep cliffs (Fig. 10.1) and canyons. These changes would not have affected most animals; however they provide huge advantages for hunters. Heterogeneous landscapes provide better opportunities for hunters to closely stalk their prey. The landscape also became better for cliff hunting. Falling from a cliff of only a few meters is sufficient for big herbivores to break their legs. Permafrost degradation would have created such cliffs every kilometer, such that chances for successful hunting were substantially increased. In the south for a long time humans were in equilibrium with other animals, but during extensive migration to the north and to America, experienced hunters met numerous animals that were likely unafraid of people and were potentially easier to kill.

Human expansion to the northern mammoth steppe occurred under conditions of unlimited resources. In such cases prey are often consumed irrationally. For example, bears that encounter abundant salmon, even being sated continue to hunt but eat only fattest part of the salmon head (pers. obs.). Our experiments on the Kolyma region have shown that if voles or ground squirrels have unlimited access to grains, they store them without limit. Evidence exists of reindeer extermination in northeastern Siberia in nineteenth century. When numerous reindeer herds were crossing big rivers, each hunter killed 70–100 animals daily. Only minor portions of the harvested meat were consumed, and reindeer carcasses that were killed only for skins were piled together into ramparts up to half kilometer long (Syroechkovskii 1986). At the same time in North America 50 million bison were exterminated. Why would one suggest that the ancestors of modern humans used prey more efficiently?

Animals in the mammoth steppe were very numerous, and if humans exterminated a substantial portion, then the north should preserve the evidence of that. However, calculating the probability of finding such evidence suggests otherwise. Assuming that on average over each square kilometer humans killed 1–2 mammoths and 10 bison. However on the same territory 1,000 mammoth and 20,000 bison skeletons that died over the course of the late Pleistocene through natural causes are also preserved. In a collection such as presented in Fig. 10.10, finding bones from animals killed by humans is unlikely.

The yedoma plains do not have lithic resources. Therefore, it is likely that for hunting (similarly to Zhokhov Island) bone tools were mostly used. Assuming that killing and dressing 10 animals required ~100 bone tools. Bone tools are “small bones” – similar in size to bison ribs; so the probability that they persisted in permafrost is low – one out of hundreds (Fig. 10.11) – leading to the persistence, on average, of no more than several bone artefacts per square kilometre. Even specialists can overlook these artefacts among mudflows and millions of other bones. To find one such artefact it would be necessary to gather tens or even hundreds of collections such as ours (Fig. 10.10). Also it should be mentioned that in contrast to Alaska, in northern Siberia, in the BWE accumulation of loess stopped (Sher et al. 2005) and any evidence of human activity remaining on the surface would have decayed.

Predators in the mammoth steppe used all of the herbivores (including soft bones) and therefore they could exist in high densities; however only few of their bones are preserved in permafrost. In all of the collections gathered from the Siberian north, there were only several tens of bones from wolves and lions. Human bones are similar in size to those of wolves and lions, but periods of active animal extinctions were 100 times shorter than the time of yedoma accumulation. Therefore even at rational resource consumption rates by humans the probability of finding a mammoth hunter bone is hundreds of times smaller than the probability of finding wolves’ or lion’s bones, and human bones should be absent in these collections.

If we assume that the bigger part of mammoths in PHT died during cliff hunts, and under every cliff suitable for hunting 50 mammoths died (in the Berelyokh mammoth graveyard are the remains of over 160 mammoths, on Achchaghyi-Allaikha graveyard over 28 mammoths (Nikolskiy et al. 2009)) then on the Siberian plains there should be on average one such cemetery for every 50 km^2, and roughly the same density of archaeological sites should be found. What is the probability of encountering such sites? Annually, 20–30 t of tusks are collected on the yedoma plains (Boeskorov et al. 2008), and the density of tusks in the yedoma is 10 t/km^2, indicating that on average 2–3 km^2 of eroded yedoma would be surveyed annually. From this we calculate that the probability of encountering a mammoth graveyard is very small, only one graveyard discovery every 17–25 years. Since 1947 scientists have discovered three mammoth graveyards (Nikolskiy et al. 2009), in line with such estimates.

The highest density of ^{14}C mammoth dates in the Siberian north is recorded for the BWE (after 12,600 ^{14}C years BP) (Figs. 10.5, 10.12). But it is interesting to note that all of the dates that were found to the south of 73°N are found either in mammoth cemeteries or in archeological sites (Kuzmin et al. 2001; Sher et al. 2005; Nikolskiy et al. 2009). This data indicates that to the south of 73°N mammoths died because of humans and became extinct during the BWE, while to the north of 73°N (western Siberia, Taimyr and northern islands) mammoths died of natural causes and persisted (Kuzmin et al. 2001; Sher et al. 2005). And humans arrived there only after the sharp climate warming subsequent to the end of the Younger Dryas cold period. All our estimates are very rough, but they indicate that in northern Siberia there were enough people to cause a decline in the herbivore population, thereby decreasing pastures and ecosystem productivity, with the eventual extinction of mammoths and bison.

The modern climate of north-eastern Siberia, central Alaska and Yukon Territory is likely the climatic optimum for the mammoth steppe (Fig. 10.6). In colder and dryer conditions pasture productivity declines, while in warmer and wetter conditions, it would be harder for animals to excavate deep snow while grazing for forage, and it would be harder to prevent trees and shrub expansion. Holocene climate warming became fatal for the mammoth ecosystem, because with warming humans penetrated the north.

10.13 The Future of the Mammoth Steppe

It was in the rich pasture ecosystems that modern humans first appeared, and civilizations were born in this ecosystem. The mammoth ecosystem was one of the first victims of the exploitation of grasslands. Humans reduced animal numbers, and mossy forests and tundra replaced grasses. Different megafauna species became extinct with arrival of humans or new technology on different continents (Barnosky et al. 2004). In many places animal biomass decreased and pastures ecosystems turned to woodlands. We suggest that because grasses were no longer grazed they began to reproduce via seeds more aggressively. By exterminating animals humans may have lost a source of meat, but a new feeding niche opened up. The appearance of agriculture and the domestication of animals and the artificial control of biocycling negatively impacted pasture ecosystems. From an ecological point of view these agricultural ecosystems are simple: they have few species, and biological competition is suppressed. However one could consider that there is direct competition between agricultural ecosystems and their wild counterparts for territory and fertile soils. Today almost all meadows, steppes and prairies are tilled or converted into domestic pastures and hayfields. In Africa grassland ecosystems have been moved to nature reserves. Near civilization only those animal species that can hide in forests, mountains or in dry deserts have survived.

It is frequently stated that in the past people lived in harmony with nature. For example, when native Siberian hunters, Yukagirs, drove reindeers to the lakes, they always let one reindeer go (Syroechkovskii 1986). But only one and the rest were killed. Reindeers persisted there only because Yukagir weapons were primitive. It wasn’t a harmony it was equilibrium. The majority of people have forgotten about grassland ecosystems and their associated animals outside of Africa. For most, wild nature is a forest with songbirds or desert with lizards, and tundra is considered an untouched habitat. However in Russia, for example, the majority of tundras are pastures for domestic reindeers. Wild reindeer are the primary pest of domestic herds and regardless of prohibitions are actively killed by reindeer herders. Besides lemmings and hares, of the wild herbivores found in the Russian tundra only geese have persisted, but even they are losing places for wintering and have been substantially reduced in number. Lemmings and hares cannot maintain active biocycling on the tundra; therefore lichens and mosses now dominate these ecosystems.

Only 100 years ago, hunters were killing hundreds of animals in Africa for sport and in Europe were treated like Olympic champions. The famous explorer Prjevalskii was one of the last to see the wild pasture ecosystems (see epigraph). But he not only discovered new animal species, he also exterminated them. Based on his reports he shot every single animal or bird he met during his journeys. “Usually, I placed on the boat nose and continuously sent greeting all creation I have met on my way either from fowling piece, or from carbine depending on distance.” (Przhevalsky 1947, p. 10). A few hundred such explorers could exterminate all animals in any pasture ecosystem. Now everyone is ready to preserve nature; however there is almost nothing left of the wild. Most commonly it is some form of plant assemblage, with no or very few big animals or birds in it, who have a minimal impact on the environment. Therefore to preserve nature one should first recover biological diversity.

Atmospheric content and the planet’s climate is changing, and pollution to ecosystems increases. The population of the planet has just reached seven billion people. Many existing ecosystems can’t be preserved in their current locations, as they would change. It is easiest to preserve that which is of no interest to anyone, like polar deserts. But it is most important to preserve the most precious. The basis of our civilization is grasses and herbivores. The majority of domestic plants and animals, as well as humans, originated from pasture ecosystems. This is the motherland of civilization. These ecosystems should be under the biggest protection. But how do we protect something that doesn’t exist anymore? Today many of the species that are considered native to pasture ecosystems exist only in zoos and on farms. In these places we can preserve what the animals looked like in the wild, but not how the animals migrated, how they defended themselves from predators, how they competed with others, how they resisted parasites and various toxins. Animals should be preserved in ecosystems. But first these ecosystems must be recovered.

Can complex, self-regulating grassland ecosystems be recovered in the mid-latitudes? Technically yes. In a region with a suitable climate reserves should be delineated, and as many species which had previously lived in similar conditions should be assembled there. These animals would then fill the niches in the reserve according to their functional groups. In such a scenario, all the animals need not be from one regional community. Currently, many of the species in wild ecosystems are immigrants from other regions: e.g., horses moved to Siberia from America. Nor need it be purebred species. They could be of various breeds, feral or domestic animals. For example wild horses became extinct in America 12,000 years ago, but mustangs subsequently successfully occupied their niche. Right now we are not capable of constructing new ecosystems. But components of pasture ecosystems are capable of self-construction and evolution.

The question is only where to do that. Pasture ecosystems can be sustainable only on very big territories. Good agricultural land is very expensive. In Europe one probably place where pasture ecosystems can be revived is the region around

Chernobyl'. In the United States on the west of Great Plains agriculture is experiencing serious problems and the possibility of reconstructing pasture ecosystems there is being seriously discussed (Donlan et al. 2006).

Wild nature should be preserved from poachers. On the other hand, truly wild ecosystems could threaten nearby agricultural and pastoral land. For example, it is enough for one diseased bison to escape and an entire region would be closed for quarantine. Reliable fences are needed for the harmonious co-existence of civilization and wild nature.

The vast plains of northern Siberia, Alaska and Yukon are reliably fenced from agricultural land and pastures with snowy ridges. The climate of these territories is close to the optimum for northern pasture ecosystems, and they can be revived there. Modern soils there are poor in nutrients, but the underlying mammoth soils are an order richer in nutrition. As soon as mammoth soils thaw they are overgrown by grasses. Grasses prevent erosion, but they cannot prevent permafrost degradation. However if other grasslands exist somewhere nearby with abundant herbivores, then herbivores will migrate to the thawing permafrost. In the winter they would excavate snow looking for forage, and would strongly compress it, promoting permafrost cooling. Already there is enough forage for millions of bison, horses, musk-ox, elk, reindeers, moose and snow goats. All that is needed is to gather and settle them in their former areas and to maintain their conservation, and with time animals would fill all existing ecological niches. Animals would increase grassland productivity, and finally would densely fill these grasslands, as back in the Pleistocene.

The rebirth of pasture ecosystem is probably the only way to preserve the permafrost. Moreover, during the peak of the last glaciations, pasture ecosystems dominated the planet, and the biggest of these was the mammoth steppe ecosystem. Atmospheric concentration of CO_2 and CH_4 was substantially lower than in Holocene (Solomon et al. 2007). Albescent pasture ecosystems promote the planet's cooling. They can be very useful to combat current climate warming. They can absorb more carbon from the atmosphere than forests and can reliably preserve this carbon from fires in the deep soil. These ecosystems must be returned to nature.

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Chapter 11
The Future of Mammals in Southeast Asia: Conservation Insights from the Fossil Record

Julien Louys

Abstract The Pleistocene zoogeographic history of Southeast Asian megafauna are examined in order to determine if any patterns of extinction vulnerability can be discerned, and if so determine which extant megafauna species may be in need of heightened conservation effort. Sites in Southeast Asia were examined for three time periods: Early, Middle and Late Pleistocene, and compared with modern distribution patterns. Taxa were divided into one of four conservation statuses: extinct, critically endangered, endangered and vulnerable. One pattern clearly observable for the species in the extinct and critically endangered categories was a widespread distribution throughout the Pleistocene, only to suffer extreme range reductions or extinctions between the Late Pleistocene and today. At least three species in the endangered category display similar distribution patterns: the giant panda (*Ailuropoda melanoleuca*), the tiger (*Panthera tigris*) and the Malayan tapir (*Tapirus indicus*). Although the panda, and to a more limited extent the tiger are well recognised as conservation priorities, this is less true for the tapir. If the zoogeographic patterns observed for extinct or critically endangered species are any guide, the outlook for the panda, tiger, and tapir, independent of stepped-up conservation efforts, are bleak.

Keywords Conservation • Giant panda • Malayan tapir • Paleo-distribution • Pleistocene • Tiger • Zoogeography

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11.1 Introduction

Southeast Asia is one of the richest regions on Earth in terms of its biodiversity. It is home to the highest proportion of country-endemic mammal species (Sodhi et al. 2010) as well as over half a billion people. Over the last 2 million years it has hosted a wide variety of large-bodied mammals, including rhinoceroses, giant tapirs, giant pangolins, and many elephants and elephant-like stegodons, only some of which are now extinct (Louys et al. 2007). However, the continued existence of many species in Southeast Asia is severely under threat from over-hunting, urbanisation and especially deforestation (Sodhi et al. 2004; Corlett 2007, 2010; Woodruff 2010). Currently Southeast Asia has the highest proportion of endangered species across all taxonomic groups except amphibians (Sodhi et al. 2010). Wildlife is being removed from hunting and the illegal pet trade at six times sustainable rates (Sodhi et al. 2004), such that the density of large mammals even in protected areas is much lower than expected (Steinmetz et al. 2006; Corlett 2007). It has been estimated that 24–63% of Southeast Asian endemic taxa are at risk of extinction due to deforestation alone (Sodhi and Brook 2006).

During the world's last great extinction event, the Late Quaternary megafauna extinctions, over 100 genera of large-bodied mammals became extinct (Barnosky 2008). Climate change and human over-hunting are the two primary factors often debated as producing these extinctions (Barnosky et al. 2004). Compared to other continents, the extinction event in Southeast Asia appears relatively minor, with only 28 genera of megafauna becoming extinct over the entire Pleistocene – equivalent to the extinctions experienced by North America in the late Quaternary alone. Although hominins have been in Southeast Asia since the Early Pleistocene (Louys and Turner 2012), there are no indications that they have adversely affected megafauna until the end of the Late Pleistocene (Louys et al. 2007; Louys 2008). Evidence from Borneo, where arguably the best zooarcheological record exists for the region, shows that only one species became extinct during the Late Pleistocene; all other extinctions occur well into the Holocene (Cranbrook 2010).

The extinction of most megafauna in Southeast Asia through the Pleistocene is likely to have been primarily driven by extreme changes in habitat, in turn driven by regional and global changes in sea-level, precipitation, hydrology and temperature (Louys 2008). Most paleoecological data suggest that during the Last Glacial Maximum (LGM), Southeast Asia was a complex mosaic of grasslands, open woodlands and closed forests (Bird et al. 2005). This came as a result of the exposure of the low-lying Sunda shelf as well as changes in the latitudinal extent of the Inter-Tropical Convergence Zone and the intensity of the Asian monsoon. Although the exposure of the Sunda shelf was greatest during the LGM, heterogeneous environments were also present in Southeast Asia throughout Pleistocene glacial periods, with conditions returning to more homogenous, forested habitats during interglacials (Louys and Meijaard 2010).

As a result of the prevalence of more open habitats during the Pleistocene, many Southeast Asian megafauna were ecologically adapted to these types of environments (Louys 2008; Pushkina et al. 2010). Southeast Asian mammals show a significant shift in diet over the Pleistocene, from more C4-based diets during the Middle Pleistocene to more C3-based in modern individuals, suggesting that the loss of open habitats during interglacials drove open-adapted mammals into more forested landscapes (Pushkina et al. 2010). Those species unable to effectively migrate to more suitable habitats or adapt ecologically experienced range reduction and/or eventually became extinct (Tougard et al. 1996; Jablonski and Whitford 1999; Louys et al. 2007; Louys 2008; Woodruff and Turner 2009).

Of all the extinctions suffered by large-bodied mammals in Southeast Asia throughout the Quaternary, the majority were lost during the Early Pleistocene (Louys et al. 2007). Most of the extinctions recorded during this time were of Mio-Pliocene species that had been in decline through the Neogene. A drop-off in extinction intensity is observable over the Middle Pleistocene, although the number of extinctions suffered during this time is still significant (Louys et al. 2007). Finally the Late Pleistocene saw the smallest extinction signature of the Pleistocene. In fact, Southeast Asia experienced very few generic-level extinctions during this period, and of these only four represent global extinctions: the giant tapir (*Megatapirus*), two proboscideans (*Stegodon* and *Palaeoloxodon*) and the giant hyena (*Pachycrocuta*), with at least three of these probably surviving into the Holocene. However, an examination of only global extinctions of megafauna in this region is misleading, and range reductions need to be examined to fully appreciate the extent of losses (Louys et al. 2007; Corlett 2010).

This chapter will examine the Pleistocene distribution of those Southeast Asian taxa that became extinct, as well as those currently considered critically endangered, to determine whether any major zoogeographic patterns through time are discernable. Philosophically, this chapter follows similar studies conducted by Jablonski and Whitford (1999) and Tougard et al. (1996), who studied the paleo-distribution of select Southeast Asian species through the Pleistocene. This study differs in that I examine paleo-distributions of extinct or critically endangered megafauna species in order to determine if deep time patterns indicative of extinction threat exist. I then extend the study to endangered and vulnerable species to see if such patterns are repeated in these groups, and hence if any endangered and vulnerable species should be prioritised in conservation efforts.

11.2 Methods

I used published species lists from select Southeast Asian sites spanning the Early to Late Pleistocene (Table 11.1). These sites are not suggested as being exhaustive of the paleo-distribution of species in Southeast Asia; however they are indicative of the ranges that were occupied by the species under consideration. Several sites were

Table 11.1 The sites from which species in Figs. 11.1–11.4 were drawn, listed in alphabetical order. Sites where only *Pongo* sp. were found are indicated by * next to the site names

Early pleistocene	Middle pleistocene	Late pleistocene
Djetis, Java	Ban Fa Suai, Vietnam	Duoi U'Oi, Vietnam
Gongwangling, China	Chenjiawo, China	Hang Hum, Vietnam
Irrawady beds, Myanmar	Daxin, China*	Jiande, China
Jianshi, China	Guanyindon, China	Keo Leng, Vietnam
Liucheng, China*	Hexian, China	Lang Trang, Vietnam
Mohui, China	Hoshantung, China	Lida Ajer, Sumatra
Trinil, Java	Hsingan, China	Liujang, China
Yuanmou, China	Kao Pah Nam*	Ma U'Oi, Vietnam
	Kedung Brubus, Java	Maba, China
	Koloshan, China	Niah, Borneo
	Mogok, Myanmar	Pubu, China
	Phnom Lang, Cambodia	Punung, Java
	Tam Hang, Laos	Sibrambang, Sumatra
	Tambun, Malaysia	Tongzi, China
	Tangshan, China	
	Tham Hai, Vietnam	
	Tham Khuyen, Vietnam	
	Tham Om, Vietnam	
	Tham Phra Khai Phet, Thailand	
	Thum Wiman Nakin, Thailand	
	Wuming, China	
	Wuyun, China	
	Xuetangliangzi, China	
	Yenangyuang, China	

very close geographically and for the sake of clarity were grouped together when shown on the maps (Figs. 11.1–11.4). The grouped sites are Pubu, Wuyun and Mohui; Keo Leng, Tham Khuyen and Tham Hai; Lang Trang, Ma U'Oi and Duoi U'Oi; Thum Wiman Nakin and Thum Phra Khai Phet; Lider Ajer and Sibrambang; and Trinil and Djetis. Species lists were compiled from Antoine (2012), Bacon et al. (2011), Han and Xu (1985), Louys et al. (2007, 2009), Louys and Meijaard (2010), Meijaard (2004), Norton et al. (2010), Piper et al. (2007), Rink et al. (2008) and Wang et al. (2007).

Southeast Asia is herein defined as the area west of Wallace's line, including both Sundaic (Borneo, Java, Sumatra, Malaysia and Thailand south of the Isthmus of Kra) and Indochinese (Thailand north of the Isthmus of Kra, Cambodia, Laos, Vietnam, Burma and southern China) biogeographical subregions. The northern extent of the Indochinese subregion fluctuated throughout the Pleistocene (Louys et al. 2009; Norton et al. 2010), but is herein roughly delineated by the Qinling Mountains and the Yangtze River. The most northern site included in this analysis is that of Gongwangling, Lantian, an Early Pleistocene site situated on the northern slopes of the Qinling Mountains.

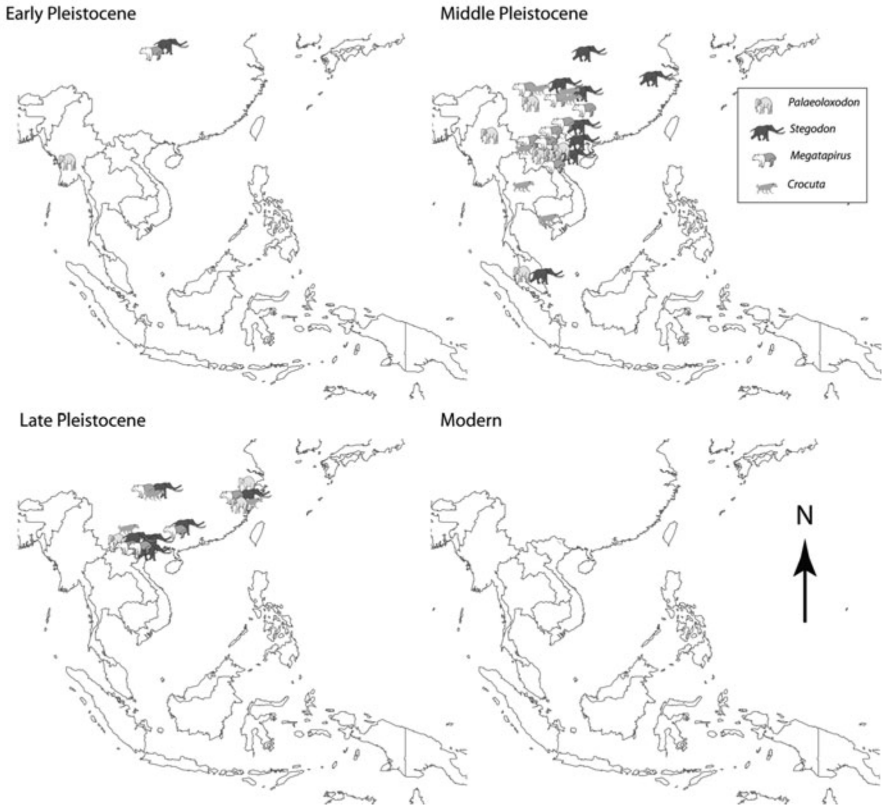

Fig. 11.1 Paleo-distribution of globally or regionally extinct species in the Early, Middle and Late Pleistocene of Southeast Asia

Taxonomy of many Pleistocene Southeast Asian faunas is in need of revision (Bacon et al. 2011). Here, I used the taxonomy of Louys et al. (2007), which largely follows that of Nowak (1999), with revisions to Rhinocerotidae following Antoine (2012). *Pongo pygmaeus* is considered as one species here, as it is not readily distinguished as two separate species in the fossil record. In three sites, *Pongo* was only identified to genus level, however these occurrences were also plotted (these sites are indicated in Table 11.1). Modern species distributions were obtained from Antoine (2012), Lekagul and McNeely (1988) and the IUCN Red List (IUCN 2011). Threatened species from SE Asia were obtained from the IUCN Red List (IUCN 2011), with the addition of *Stegodon orientalis, Palaeoloxodon namadicus, Megatapirus augustus* and *Crocuta crocuta*, Pleistocene Asian species which are either extirpated from the region (in the case of *C. crocuta*) or became extinct sometime in the Holocene (in the case of the other three species). I examined only large-bodied species that had at least three fossil occurrences in at least one time period.

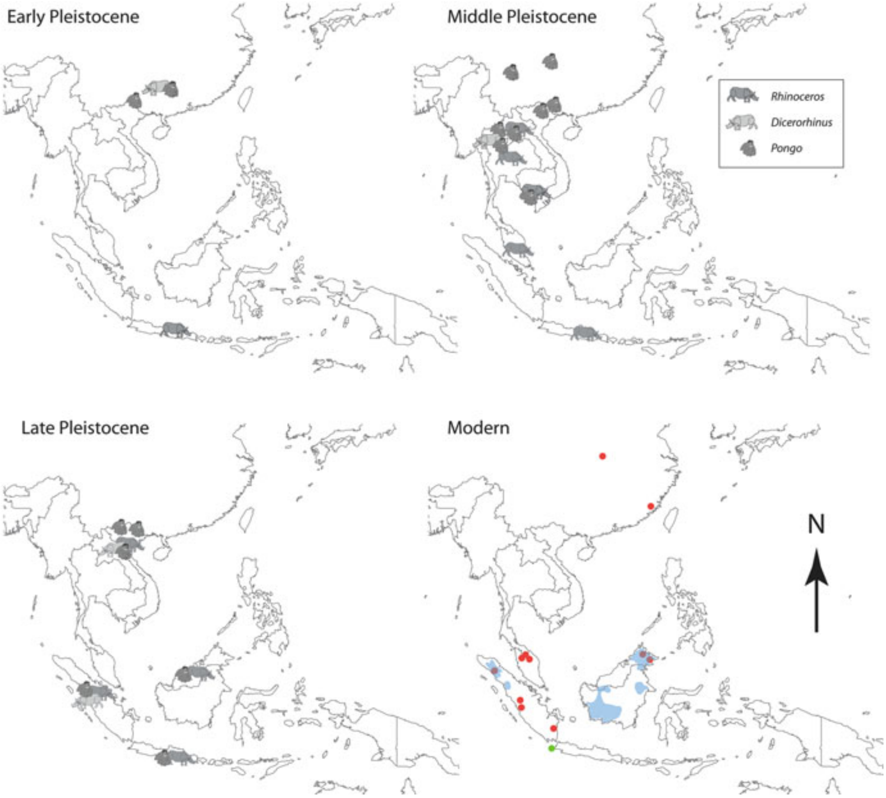

Fig. 11.2 Paleo-distribution of critically endangered species in the Early, Middle and Late Pleistocene of SE Asia; and current distributions: *Rhinoceros sondaicus* green; *Dicerorhinus sumatraensis* red; *Pongo pygmaeus* blue

11.3 Results

11.3.1 Extinct Species

The following extinct species are considered (Fig. 11.1): archaic elephant (*Palaeoloxodon namadicus*), stegodon (*Stegodon orientalis*), giant tapir (*Megatapirus augustus*) and the spotted hyena (*Crocuta crocuta*). Both elephants see an expansion from Indochina (Early Pleistocene) to maximum distribution in both Indochina and Sundaland (Middle Pleistocene), back to an Indochinese distribution in the Late Pleistocene. Both probably survived into the Holocene (Tong and Liu 2004; Li et al. 2011). The hyena makes its first appearance in the Middle Pleistocene where it is found throughout Indochina, but appears restricted to southern China by the Late Pleistocene. Currently, it is restricted to Africa, although it persisted in China until the Holocene (Tong and Liu 2004). The giant tapir shares a similar distribution history,

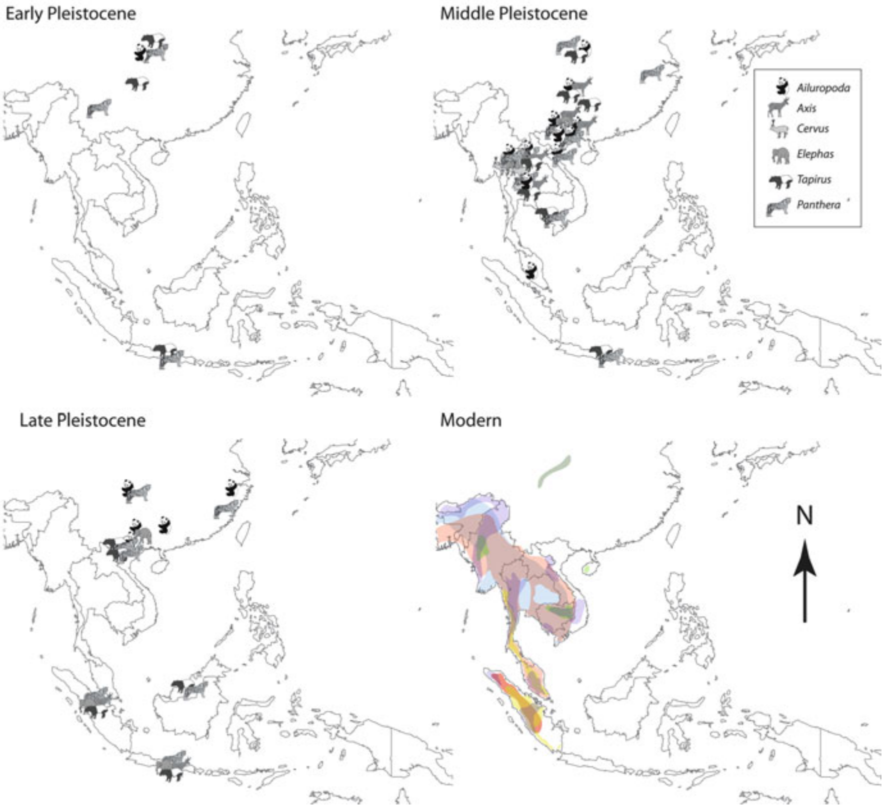

Fig. 11.3 Paleo-distribution of endangered species in the Early, Middle and Late Pleistocene of SE Asia; and current distributions: *Ailuropoda melanoleuca* dark green; *Axis porcinus* blue; *Cervus eldii* green; *Elephas maximus* red; *Tapirus indicus* yellow; *Panthera tigris* purple

with a widespread presence in Indochina by the Middle Pleistocene, and apparent restriction to southern China in the Late Pleistocene. It also persisted in China until the Holocene (Tong and Liu 2004).

11.3.2 Critically Endangered Species

Three critically endangered species are considered (Fig. 11.2): the Javan rhino (*Rhinoceros sondaicus*), the Sumatran rhino (*Dicerorhinus sumatraensis*) and the orangutan (*Pongo pygmaeus*). The Javan rhino is well represented in Java in the Early Pleistocene, and from that point on is found throughout both Sundaland and Indochina well into the Late Pleistocene. It continues to be found throughout Southeast Asia well into historical times (Antoine 2012). Since then, its

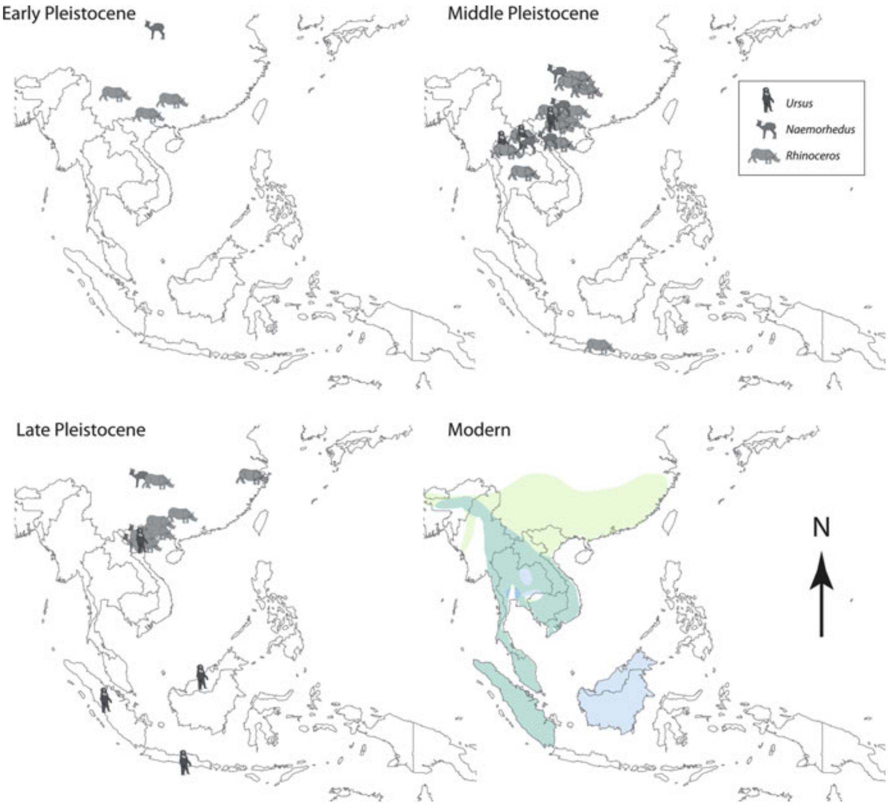

Fig. 11.4 Paleo-distribution of endangered species in the Early, Middle and Late Pleistocene of SE Asia; and current distributions: *Ursus malayanus* blue; *Naemorhedus sumatraensis* green

geographical and population decline has been the result of loss of habitat, as well as massive poaching and over-killing, a practice that sadly continues today (Milliken et al. 2009; Antoine 2012). Since its extinction in Vietnam (Kinver 2011), it is now restricted to a tiny (~40 individuals) population in west Java, and is perhaps the most endangered large-bodied species in the world. The Sumatran rhino shares a similar fate. It is recorded from southern China in the Early Pleistocene, Vietnam in the Middle Pleistocene, with a pan-Southeast Asian distribution by the Late Pleistocene, which extended well into historical times (Antoine 2012). Like the Javan rhino, it has suffered heavily from loss of habitat, poaching and hunting over the last 200 years. The orangutan is found in the Early Pleistocene of southern China, with a widespread Indochinese distribution by the Middle Pleistocene, extending well into the Late Pleistocene and perhaps even the Holocene (Kahlke 1972). It is currently found in isolated populations restricted to Borneo and Sumatra, and is critically threatened due to loss of habitat to palm oil plantations (IUCN 2011).

11.3.3 Endangered Species

The following endangered species are examined (Fig. 11.3): the giant panda (*Ailuropoda melanoleuca*), the hog deer (*Axis porcinus*), Eld's deer (*Cervus eldii*), the Asian elephant (*Elephas maximus*), the Malayan tapir (*Tapirus indicus*) and the tiger (*Panthera tigris*). The giant panda had a much greater distribution throughout the Pleistocene compared to today, where it is restricted to several protected areas in China. The hog deer makes its first appearance in the Middle Pleistocene, where it is found throughout northern Indochina. By the Late Pleistocene it is restricted to Sundaland, however is currently only found in Indochina. This is probably a collection/identification issue, as fossil cervid taxonomy is notoriously poor for Southeast Asia (Bacon et al. 2011). If real, this palaeo-distribution pattern is unique for Southeast Asian mammals. The Eld's deer's fossil record is poor – it is found in northern Indochina in the Middle Pleistocene, is absent from Late Pleistocene and is currently found in parts of Indochina. Regardless of its paleo-distribution, however, its range has alarmingly decreased since historical times (Lekagul and McNeely 1988). The Asian elephant is found in Indochina in the Middle Pleistocene; by the Late Pleistocene it is found through most of Southeast Asia, mirroring its current distribution. The Malayan tapir is found throughout Southeast Asia from the Early to the Late Pleistocene. However in recent times it has undergone a significant range reduction and is restricted to the western portions of Sundaland. Likewise, the tiger, which shares a near pan-Southeast Asian distribution throughout its Pleistocene history experienced significant range reductions in Southeast Asia during historic times.

11.3.4 Vulnerable Species

Three vulnerable species are examined (Fig. 11.4): the Indian rhino (*Rhinoceros unicornis*), the sun bear (*Ursus malayanus*) and the serow (*Naemorhedus sumatraensis*). The Indian rhino shows a strong presence throughout Pleistocene assemblages in Indonchina, and also makes a presence in Java in the Early and Middle Pleistocene (Antoine 2012). Currently it is restricted to South Asia (namely India, Nepal and Bhutan). The sun bear is found throughout Indochina in the Middle Pleistocene, and spreads through to Sundaland by the Late Pleistocene. This is similar to its current range, except for its extinction from Java. The serow is restricted to southern China and the northern parts of Vietnam and Laos for most of the Pleistocene. It currently has a broad Southeast Asian distribution.

11.4 Discussion

The analysis above highlights that the species that underwent considerable range reductions from Pleistocene to current distributions are some of those under the most critical threat of extinction, or are those that have already become extinct. Of particular note in the extinct category are two species of proboscidean (the archaic elephant and stegodon), the giant tapir, and the Indian rhino – currently found only in South Asia, but which previously had a wide Southeast Asian distribution. Of the critically endangered SE Asian megafauna, both species of rhino (Javan and Sumatran) as well as the orangutan suffered considerable range reductions; for the rhinos at least this occurred during historic times. As argued elsewhere (Sodhi et al. 2004; Corlett 2007; Louys 2008), this Holocene-recent extinction signature is largely a result of massive habitat loss, but also over-hunting, either for subsistence but increasingly for the traditional medicines market (Corlett 2007).

While the Indian rhino shows complete extirpation from Southeast Asia between the Late Pleistocene and current distributions, no other vulnerable species examined shows the same level of range reduction. However, three species in the endangered category clearly do. These are the giant panda (*Ailuropoda melanoleuca*), the tiger (*Panthera tigris*) and the tapir (*Tapirus indicus*). Although Eld's deer (*Cervus eldii*) has a spotty fossil record, its alarming range decline in historical times indicates that this species may also have a zoogeographic pattern similar to those of the tapir, tiger and panda. These latter species share the extreme range reductions between the Late Pleistocene and today that many extinct or critically endangered large-bodied species experienced. While the plight of the panda and tiger are well known internationally, that is less true of the tapir and Eld's deer. The paleontological record suggests that if conservation efforts towards the tiger, in particular the four Southeast Asian subspecies, the Malayan tapir and Eld's deer are not stepped up, then they will likely suffer the same fate as the stegodon, the giant tapir and the archaic elephant.

11.5 Final Comments

Environmental changes in Southeast Asia over the Pleistocene primarily affected more open-adapted species, and many surviving megafauna are likely to be those best adapted for forested conditions, such that even reduced rates of deforestation in the region will likely have devastating effects on many species' survival. However, surviving megafauna may well be those that show some level of ecological flexibility. An understanding of the ecology and biology of the past factors that detrimentally influenced the survival of mammals in the region is paramount in any attempt to prevent further extinctions. In particular, it is important to understand the ecology of fossil Southeast Asian mammals, and the factors that have previously contributed to their extinction. If just those megafauna species experiencing any range reduction during the Late Pleistocene become extinct, a very likely possibility given current trends, then this would bring the intensity of extinction commensurate with that of other continents during the Late Quaternary. This projection is in line with estimates based on the species-area relationship, which predicts that up to 85% of mammals in the region could be extinct by the end of the century (Sodhi et al. 2010). Southeast Asia is a region of critical importance to matters of biological conservation and to human long-term sustainability during an era of global climate change. There is an urgent need to intensify local and international conservation efforts and to address both biological and socio-economic issues if we are to avoid a megafauna extinction event within our lifetime.

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Chapter 12
Conservation Implications of Fossil Roan Antelope (*Hippotragus equinus*) in Southern Africa's Cape Floristic Region

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Abstract Southern Africa's Cape Floristic Region (CFR) is a global priority for conservation action, with 41 native large mammal species considered in ongoing conservation schemes. This study reviews historic and paleozoological evidence suggesting that an additional species – the roan antelope (*Hippotragus equinus*) – is native to the region and warrants consideration in conservation efforts. A single observation in 1778 suggests that a population of roan antelope formerly inhabited the CFR in the vicinity of Plettenberg Bay (Western Cape, South Africa). The fossil record is consistent with this observation, showing that roan antelope inhabited the southern coast of the CFR for the last ~20,000 years. Roan antelope were likely extirpated from the CFR during the late 1700s, broadly corresponding to the extinction of the blue antelope (*H. leucophaeus*) and the near-extinction of the bontebok (*Damaliscus pygargus pygargus*). If the goal of conservation efforts is to establish viable populations of extant species that are native to the region, then roan antelope is a prime candidate for conservation action and reintroduction to the CFR.

Keywords Blue antelope • Cape Floristic Region • Conservation biogeography • Native species • Roan antelope • South Africa

12.1 Introduction

There is a small yet growing body of literature demonstrating the value of paleozoological data to conservation biology (e.g., Lyman 1996, 2006; Lyman and Cannon 2004; Grayson 2005; Grayson and Delpech 2005; Faith, in press).

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The conservation applications of paleozoological data are numerous (reviewed in Lyman 2006) and stem from the potential to provide long-term biogeographic histories of animal populations. One such application concerns the determination of whether or not a species is native to a region. Such insight is essential to informing species translocations and to restoring biodiversity in disturbed habitats (i.e., restoration ecology). To illustrate how fossil data can be used to establish baseline biodiversity in disturbed habitats, this study examines the fossil history of roan antelope (*Hippotragus equinus*) in southern Africa's Cape Floristic Region (CFR) and discusses its implications for large mammal conservation efforts in the region.

Comprising an area of ~88,000 km^2 along the southern and western coast of South Africa (Cowling and Heijnis 2001), the CFR is a global priority for conservation action (Myers et al. 2000; Cowling et al. 2003). The CFR is best known for its spectacular floristic diversity, including the world's highest frequency of endemic plant species (69%) (Goldblatt and Manning 2002; Linder 2003). Mammal diversity is likewise impressive; historic accounts document at least 24 ungulate species in the CFR, with the Cape mountain zebra (*Equus zebra zebra*), Cape grysbok (*Raphicerus melanotis*), bontebok (*Damaliscus pygargus pygargus*), and extinct blue antelope (*Hippotragus leucophaeus*) regarded as endemic or near-endemic to the region (Skead 1980; Kerley et al. 2003). Although the CFR flora remains the focus of conservation planning, the larger mammals (>2 kg) are also the subject of ongoing conservation efforts (Kerley et al. 2003). Many species are in need of conservation action (e.g., Cape mountain zebra) and large herbivores are known to play an important ecological role in the dynamics of the plant communities (Johnson 1992; Radloff 2008).

Development of a conservation plan for the CFR large mammals requires baseline information on their potential geographic distributions and abundances (Kerley et al. 2003). This is problematic, however, as many species have been extirpated or undergone massive range reductions following European colonization of South Africa (Du Plessis 1969; Skead 1980). To overcome this issue, Boshoff and Kerley (2001; see also Boshoff et al. 2001) estimated the potential distributions of large mammals in the CFR on the basis of habitat requirements and historic records. The limitations of historic data are recognized. Boshoff and Kerley (2001) note that although reviews of early historic records (Du Plessis 1969; Skead 1980; Rookmaaker 1989) are useful in determining the presence or absence of most species in the CFR, they are often unclear about the specific locations and habitats occupied by different species. In addition, there are doubts about the accuracy of identifications for some species (reviewed in Skead 1980). Historic descriptions of rainbow-colored zebras in the CFR (Skead 1980) provide ample reason to exercise caution.

There are 41 native mammal species included in the range maps developed by Boshoff and Kerley (2001) and considered in the CFR conservation plan (Cowling et al. 2003; Kerley et al. 2003). Below, I review historic and paleozoological evidence suggesting that a 42nd species – the roan antelope – is native to the CFR and warrants consideration the large mammal conservation plan.

12.2 Distribution of Roan Antelope in South Africa

Roan antelope are among the largest African bovids, with males standing ~1.4 m at the shoulder and weighing ~270 kg (Skinner and Chimimba 2005). They favor open grasslands or lightly wooded savannas with stands of medium-to-tall grass and freestanding water (Kingdon 1982; Skinner and Chimimba 2005). Roan antelope are predominately grazers and prefer to feed on medium to tall grass, avoiding overgrazed areas with short grasses. Like other tall-grass grazers in the CFR (e.g., Cape mountain zebra), *Themeda triandra* is among the preferred species of forage (Joubert 1976).

Today, roan antelope are rare in South Africa, limited to the northeastern edge of the country (Fig. 12.1), with a key population in northern Kruger National Park (Grant et al. 2002). Historic records, however, suggest a more expansive range in South Africa. Du Plessis (1969) found evidence that roan antelope once extended into northern and central South Africa in the early 1800s (Fig. 12.1). He found no accounts of roan antelope as far south as the CFR. Two years earlier, however, Mohr (1967) suggested that an animal documented and illustrated in 1778 by Robert Gordon near Plettenberg Bay (Fig. 12.1) was likely a roan antelope. More recently, Grubb (1999) provided a compelling argument that the antelope

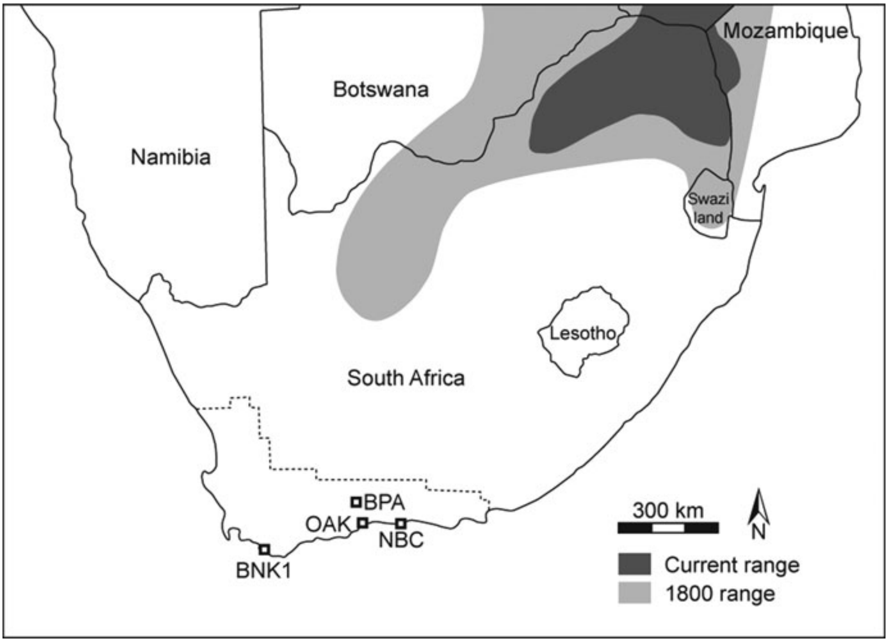

Fig. 12.1 The geographic range of roan antelope in the 1800s (Du Plessis 1969) and today (IUCN SSC Antelope Specialist Group 2008). The dashed line encompasses the CFR conservation planning domain. *BNK1* Byneskranskop 1, *BPA* Boomplaas Cave, *NBC* Nelson Bay Cave, *OAK* Oakhurst shelter. The 1778 sighting of roan antelope took place near NBC

documented by Gordon is not only a roan antelope, but also happens to be the holotype for the species. What follows is a brief summary of his work.

Believing the animal seen near Plettenberg Bay to be a hybrid of blue antelope and oryx (*Oryx gazella*), Gordon prepared several illustrations, one of which shows a complete skin pegged out for drying. It is understandable that roan antelope could be mistaken for a hybrid of those particular species, as the posteriorly curved horns are similar to those of blue antelope (straight in oryx) and the black and white markings of the face resemble oryx (unmarked in blue antelope). In the annotations of one painting, Gordon notes that the specimen was collected in the forests near Plettenberg Bay. Grubb (1999) reviews historic records tracing the skin from Gordon to The Hague in 1779, and then on to the Muséum national d'Histoire Naturelle in Paris in 1795. In the early 1800s, E. Geoffroy Saint-Hilaire (1803) compiled a list of specimens at the museum, including in it a detailed description of a skin attributed to a new species, *Antilopa equina* (now *Hippotragus equinus*). Although Geoffroy Saint-Hilaire reports the type locality as unknown, it is most likely that the holotype is the same specimen collected by Gordon from Plettenberg Bay. If correct, then there is good reason to believe that roan antelope inhabited the CFR in the late eighteenth century and that Gordon was the only European to document one before its extirpation. The paleozoological record provides an opportunity to further assess the history of roan antelope in the CFR.

12.3 Fossil Roan Antelope in the CFR

Klein (1974) first documented the presence of both roan antelope and blue antelope in late Quaternary fossil samples from the CFR. He noted that at Nelson Bay Cave and Oakhurst (Fig. 12.1) fossil teeth of *Hippotragus* are characterized by a heterogeneous mixture of small and large specimens, with the former attributed to blue antelope and the latter to roan antelope. The presence of roan antelope at Nelson Bay Cave is particularly noteworthy, as the site is located on the Robberg Peninsula at Plettenberg Bay, near Gordon's probable historic sighting.

In his initial study, Klein (1974) did not separate the mixed fossil samples into discrete roan antelope and blue antelope subsamples. This renders the biogeographic significance of the fossil roan antelope unclear since both Nelson Bay Cave and Oakhurst contain deposits from the latest Pleistocene, when an expansion of grassland habitats favored an ungulate community dominated by large grazers (Klein 1980, 1983; Faith 2011a, c, in press). Due to past climate and vegetational shifts, the presence of roan antelope during the latest Pleistocene or early Holocene should not be taken as evidence that it could survive in the CFR today. Rather, fossil evidence indicates that a large mammal community similar to the historic community emerged only within the last ^{14}C 5,000 year BP (radiocarbon years ago) (Klein 1980, 1983; Faith in press). Definitive records of roan antelope within this time frame would lend strong support to the contention that they could survive under the current climatic regime.

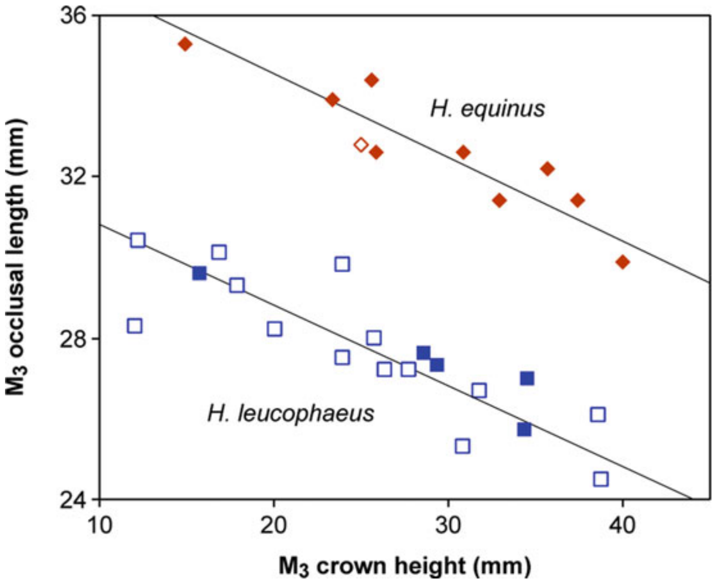

Fig. 12.2 The relationships between mandibular M_3 crown height and M_3 occlusal length for blue antelope (*squares*) and roan antelope (*diamonds*). Filled symbols are from Nelson Bay Cave and open symbols from other CFR fossil localities. The *solid lines* represent the RMA regressions for each taxon

Reconstructing the fossil distribution of roan antelope requires a means of reliably distinguishing its remains (primarily isolated teeth) from blue antelope. In 2009, the *Hippotragus* teeth from Nelson Bay Cave were studied to determine whether the two species could be distinguished from each other. Analyses of dental measurements from Nelson Bay Cave indicate that the *Hippotragus* teeth fall into one of two non-overlapping size groups, with the larger specimens belonging to roan antelope and the smaller to blue antelope (Faith 2011b). To provide one example of these results, which are reported in more detail elsewhere (Faith 2011b), Fig. 12.2 plots occlusal length against crown height for the mandibular M_3 (measurements follow Klein and Cruz-Uribe 1984). Two patterns are immediately clear. First, as the M_3 wears (i.e., crown height declines) its occlusal length increases. Second, at any given crown height, roan antelope have greater occlusal lengths than blue antelope. Measurements of *Hippotragus* teeth from other CFR sites, including Blombos Cave (Henshilwood et al. 2001), Boomplaas Cave (Klein 1978; Deacon 1979), Byneskranskop 1 (Schweitzer and Wilson 1982), Die Kelders Cave 1 (Klein and Cruz-Uribe 2000), Klasies River Mouth (Klein 1976; Singer and Wymer 1982), Pinnacle Point (Rector and Reed 2010), and Swartklip 1 (Klein 1975), confirm the observations from Nelson Bay Cave and demonstrate that the two species can be reliably distinguished on the basis of size alone (Faith 2011b) (Fig. 12.2). Figure 12.3 shows the occlusal outline of maxillary M^3s for both taxa, demonstrating the marked size difference.

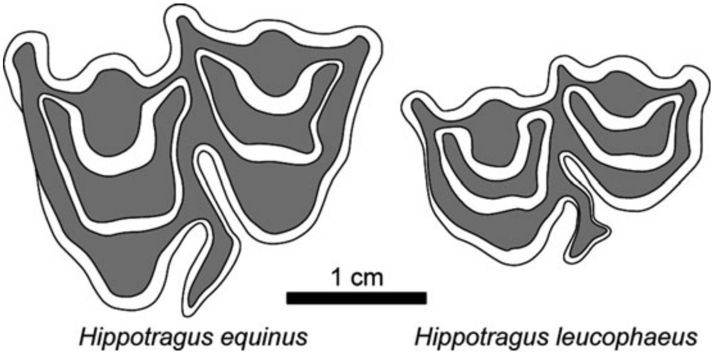

Fig. 12.3 Occlusal outline of the *left* maxillary M^3 of roan antelope (Nelson Bay Cave, BSJ/27D4) and blue antelope (Klasies River Mouth, KRM1-15: 27208), illustrating the marked difference in size between species

Dental remains attributed to roan antelope are known from four fossil sites in the CFR: Boomplaas Cave, Byneskranskop 1, Nelson Bay Cave, and Oakhurst (Fig. 12.1). Below, I discuss the biogeographic significance of the roan antelope from each site.

12.3.1 Boomplaas Cave

Excavations conducted from 1974 to 1979 by Deacon (1979) at Boomplaas Cave, located on the flanks of the Swartberg Mountains (Fig. 12.1), uncovered a stratified archaeological sequence dating back around 80,000 years (Deacon 1984). *Hippotragus* fossils were reported by Klein (1978), although these were identified only to genus. Table 12.1 provides the stratigraphy, chronology, and distribution of roan antelope for the upper part of the stratigraphic sequence, dating from the end of the Last Glacial Maximum through the Holocene. Radiocarbon dates from Boomplaas Cave are calibrated with the CALIB 6.0.1 radiocarbon calibration program (Stuiver and Reimer 1993) using the IntCal09 calibration curve (Reimer et al. 2009). Roan antelope are found only in the Pleistocene units, disappearing from the sequence just before the Pleistocene-Holocene transition at stratum BRL6. Previous studies demonstrate that the Pleistocene-Holocene transition at Boomplaas Cave is characterized by a major turnover event (Klein 1978; Faith 2011b, in press) characterized by the disappearance of several taxa from the sequence, including roan antelope, bontebok/blesbok (*Damaliscus pygargus*), springbok (*Antidorcas* cf. *A. marsupialis*), extinct long-horn buffalo (*Syncerus antiquus*), and extinct Cape zebra (*Equus capensis*). These open-habitat taxa were replaced by small browsers that prefer dense and shrubby vegetation (e.g., *Raphicerus*, *Oreotragus*). The absence of roan antelope throughout the Holocene sequence at Boomplaas Cave

Table 12.1 The stratigraphy, chronology, and distribution of roan antelope in the upper units at Boomplaas Cave. Radiocarbon dates from Deacon (1984)

Unit	Radiocarbon date (^{14}C years BP)	2σ calibration (cal years BP)	Roan antelope
BLD3	1,955 ± 65	1,726–2,059	–
BL	–	–	–
FBL	–	–	–
BLA	6,400 ± 75	7,171–7,433	–
BRL	–	–	–
BRL1	–	–	–
BRL2	9,100 ± 135	9,866–10,595	–
BRL3	–	–	–
BRL4	–	–	–
BRL5	–	–	–
BRL6	10,425 ± 125	11,954–12,613	X
BRL7	–	–	X
CL1	12,060 ± 105	13,668–14,186	X
	12,480 ± 130	14,094–15,119	
CL2	–	–	X
CL3	–	–	–
CL4	14,200 ± 240	16,846–17,881	–

implies that the taxon was absent from the local faunal community and is not likely to survive there today.

12.3.2 Byneskranskop 1

Located near the coast in the southwestern CFR, excavations conducted by Schweitzer at Byneskranskop 1 uncovered fossil remains dating from the end of the Pleistocene through the Holocene (Schweitzer and Wilson 1982). *Hippotragus* fossils were reported by Schweitzer and Wilson (1982) at the genus level. The stratigraphy, chronology, and distribution of roan antelope at Byneskranskop Cave 1 are indicated in Table 12.2. Roan antelope fossils are found sporadically throughout the Holocene sequence, with one specimen found in uppermost unit 1, which is associated with radiocarbon dates spanning the last ~3,000 years and also includes domestic sheep (*Ovis aries*). The presence of roan antelope within the last 5,000 ^{14}C years provides reason to believe that roan antelope could have survived in this region historically and – if reintroduced to protected areas with suitable habitat – could survive there today. Although Boshoff and Kerley (2001) do not consider roan antelope in their range maps, they predict that other large grazing ungulates, including buffalo (*Syncerus caffer*), bontebok, hartebeest (*Alcelaphus buselaphus*), and Cape mountain zebra, could find adequate habitat and forage in the vicinity of Byneskranskop 1. Two of these taxa, buffalo and hartebeest, are also found in association with roan antelope in unit 1 (Schweitzer and Wilson 1982).

Table 12.2 The stratigraphy, chronology, and distribution of roan antelope at Byneskranskop 1. Radiocarbon dates from Schweitzer and Wilson (1982)

Unit	Radiocarbon date (^{14}C year BP)	2σ calibration (cal year BP)	Roan antelope
1	255 ± 50	265–466	X
	535 ± 50	504–568	
	1,880 ± 50	1,705–1,930	
	3,220 ± 45	3,365–3,513	
2	3,400 ± 55	3,552–3,735	–
3	–	–	–
4	–	–	–
5	3,900 ± 60	4,152–4,445	–
6	–	–	–
7	–	–	–
8	–	–	X
9	6,100 ± 140	6,653–7,306	–
	6,370 ± 90	7,155–7,442	
10	6,540 ± 55	7,411–7,522	X
11	–	–	–
12	7,750 ± 90	8,376–8,777	–
13	–	–	X
14	9,760 ± 55	11,061–11,353	–
15	–	–	–
16	–	–	–
17	–	–	–
18	–	–	–
19	12,730 ± 185	14,162–16,115	–

12.3.3 Nelson Bay Cave

Nelson Bay Cave is located on the Robberg Peninsula at Plettenberg Bay (Fig. 12.1) and has been excavated by Klein (1972) and Inskeep (1987). Fossil remains are preserved in stratigraphic units spanning the last ~20,000 years (Table 12.3). Although Klein (1974) initially did not separate roan antelope from blue antelope, in a subsequent study (Klein 1983) he provided taxonomic counts showing that roan antelope are present only in the Pleistocene units (BSBJ and below). However, metric analyses of the *Hippotragus* teeth suggest a different pattern and confirm its presence in the Holocene (Faith 2011b). Table 12.3 shows that roan antelope persist throughout most of the Pleistocene and Holocene sequence, being absent only from uppermost unit RRI. Confirmation is provided in Fig. 12.4, which plots the basal length and width of maxillary M^1s of blue and roan antelope recovered from CFR fossil sites. There is clear separation between the larger roan antelope and the smaller blue antelope. The specimen indicated with a star in Fig. 12.4 was recovered from Inskeep's unit 91, which corresponds to Klein's unit IC, dated to 4,860 ± 65 ^{14}C years BP. Additional dates from Inskeep's excavation (not reported in Table 12.3) bracket the specimen between 4,520 ± 60 ^{14}C years BP and 5,320 ± 220 ^{14}C years BP (Inskeep 1987).

Table 12.3 The stratigraphy, chronology, and distribution of roan antelope at Nelson Bay Cave. Radiocarbon dates from Deacon (1984) and Inskeep (1987)

Unit	Radiocarbon date (^{14}C years BP)	2σ calibration (cal years BP)	Roan antelope
RRI*	455 ± 30	478–536	–
	3,600 ± 50	3,820–4,008	
IC	4,860 ± 65	5,465–5,742	X
BSC	5,825 ± 150	6,305–6,988	X
	5,830 ± 115	6,398–6,936	
	6,020 ± 160	6,499–7,254	
	6,050 ± 80	6,730–7,160	
RA	6,070 ± 125	6,662–7,252	X
	9,080 ± 185	9,658–10,701	
RB	8,070 ± 240	8,429–9,486	X
	8,570 ± 170	9,239–9,972	
J	8,990 ± 80	9,885–10,280	X
BSBJ	10,256 ± 210	11,309–12,564	X
	10,540 ± 110	12,096–12,651	
CS	10,150 ± 90	11,388–12,105	X
	10,180 ± 85	11,397–12,144	
	11,505 ± 110	13,143–13,622	
GSL	11,080 ± 260	12,425–13,467	X
	11,950 ± 150	13,430–14,140	
BSL	10,600 ± 150	12,037–12,800	X
YSL	16,700 ± 240	19,420–20,360	X
YGL	18,100 ± 550	20,195–22,976	X

A series of 18 dates bracket the uppermost unit (RRI) between 3,600 ± 50 and 455 ± 30 (Inskeep 1987)

The presence of roan antelope in unit IC is significant, as the ungulate species found here and in overlying unit RRI broadly match the historic community (Klein 1983). Roan antelope are absent from the uppermost unit at Nelson Bay Cave; considering the proximity of the cave to Gordon's historic sighting, this likely represents sampling error or a temporary extirpation from the vicinity of the site.

12.3.4 Oakhurst

The Oakhurst shelter, located ~85 km west of Nelson Bay Cave, was excavated by Goodwin from 1932 to 1935 (Goodwin et al. 1938). Klein (1974) reported a mixture of blue and roan antelope from the site and this is consistent with my observations in the lab. The artifact industries from the site (Oakhurst and Wilton) suggest an age range of between 12,000 and 4,000 years ago (Deacon and Deacon 1999). Unfortunately, the stratigraphic context of the fossils is unclear, limiting biogeographic interpretations. Nevertheless, the probable temporal overlap with specimens from Byneskranskop 1 and Nelson Bay Cave supports a broad Holocene distribution for the taxon.

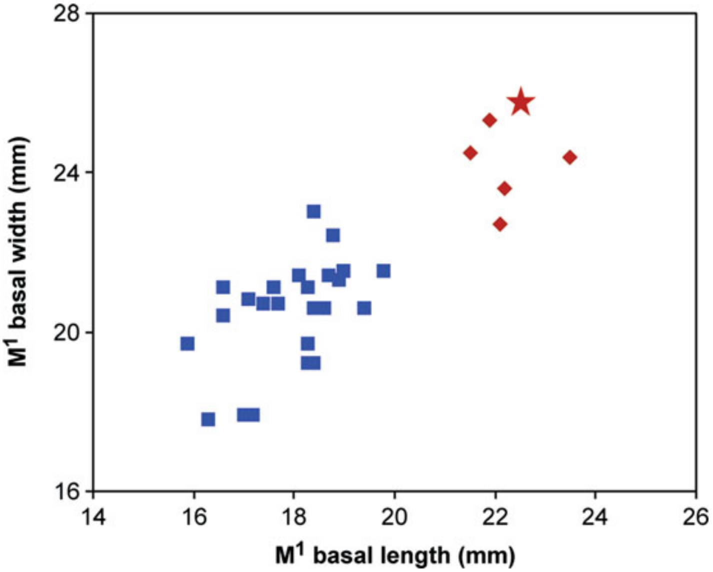

Fig. 12.4 The relationship between basal length and basal width of the maxillary M^1 for blue antelope (*squares*) and roan antelope (*diamonds*). The roan antelope indicated with a star corresponds to unit IC at Nelson Bay Cave (see Table 12.3)

12.4 Conservation Implications

Gordon's probable 1778 sighting of a roan antelope – which now appears increasingly likely in light of the fossil evidence – provides good reason to believe that a population of roan antelope historically inhabited the CFR in the vicinity of Plettenberg Bay. The fossil record is consistent with this observation, showing that roan antelope inhabited the southern coast of the CFR for at least the past ~20,000 years. Evidence of roan antelope at two CFR sites within the last 5,000 ^{14}C years BP implies that the contemporary climate regime is capable of supporting viable populations of the species. Overall, the combination of historic and fossil evidence clearly demonstrates that roan antelope are native to the CFR.

Roan antelope were likely extirpated from the CFR shortly after Gordon's sighting in 1778, roughly coinciding with the extinction of the blue antelope ~1800 (Klein 1974) and the near-extinction of the bontebok during the early 1800s (van Rensburg 1975; Skinner and Chimimba 2005). Nearly 150 years later, the Cape mountain zebra almost succumbed to extinction as well (Novellie et al. 2002). The roughly synchronous decline of large grazers following European colonization of the CFR is not surprising in light of the fossil history of the region. Fossil evidence shows that environmental change – in particular, the loss of grassland habitats – at the onset of the Holocene resulted in diminished grazer diversity and abundances (Klein 1983; Faith 2011c). Limited access to grassy forage is a central challenge to the conservation of grazing ungulates in the CFR today (Watson et al. 2005; Smith et al. 2007; Watson and Chadwick 2007; Kraaij and Novellie 2010; Smith et al. 2011; Faith in press), and it comes as little surprise that hunting pressure and especially habitat loss in historic times devastated an already diminished grazing community.

If the conservation goal for the CFR mammals is to establish viable populations of all extant species that are native to the region (see discussion in Kerley et al. 2003), then roan antelope should be considered a target for conservation action. Like many of the large mammals that formerly inhabited the CFR, establishing a viable roan antelope population will require the reintroduction of animals to suitable reserves. Doing so will not only enhance the richness of the CFR ungulate community, but also dramatically increase the geographic range of a taxon that experienced a massive decline in historic times.

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Chapter 13
Paleoecology and Conservation Paleobiology: Future Directions

Julien Louys

Abstract The preceding chapters have demonstrated several ways that paleontological data has been used in ecological and conservation studies, and has indicated some fruitful directions that paleoecology could go in the future. In this chapter, I expand on some of these ideas, focusing particularly on the interaction between the taxonomic, temporal and spatial scales and proactive conservation strategies. I refer to both paleoecology sensu stricto, that is, the examination of ecological theory in deep time as well as the development of ecological theories from the paleontological record; and paleoecology sensu lato, that is, all ecological studies in deep time, conservation paleobiology and reconstructive paleoecology inclusive.

Keywords Holocene • Rewilding • Spatial scale • Taxon-free • Taxonomic scale • Temporal scale

13.1 Introduction

The preceding chapters in this book have provided practical examples and reviews of the many ways that paleontological data can inform on ecology and conservation science. Many of the chapters suggested some future directions that research in paleoecology and conservation paleobiology might take. In this last chapter, I explore a few of these in more detail, and from a largely theoretical point of view. To reflect the title of this book, this chapter is divided into two sections: one examining paleontology in ecology (Sect. 13.2) and the other paleontology in conservation science (Sect. 13.3). However, as should be clear from the many interdisciplinary studies espoused and highlighted in this book, such divisions of study into separate scientific disciplines are purely artificial. Specifically, I examine

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the links between the spatial, temporal and taxonomic scales, and proactive conservation strategies.

13.2 The Links Between the Spatial, Temporal and Taxonomic Scales

Both Bennington and Aronson (2012) and Louys et al. (2012) specify the three dimensions (taxonomic, spatial and temporal) over which paleontological and neontological data differ. Studying the interactions or links between these three dimensions will lead to the development of novel ecological theories and hypotheses.

The links between the spatial and the temporal dimensions are already known in modern biogeographical and ecological studies. In essence, the spatial dimension can be considered a proxy for the temporal dimension (e.g., Eronen 2007; Emerson and Gillespie 2008; Beaudrot and Marshall 2011). Any divergence between two communities will result from their division or differential construction from a common source or metacommunity. In such cases, the spatial distance between two communities might be considered a proxy to the amount of time since this happened. The fossil record could be used to specifically (and quantitatively) test to what extent the correlation between time and space holds, and at which scales.

Alternatively, examining the amount of time since divergence can provide the explanation as to why communities are different. For example, Louys et al. (2011) examined the interactions between historical contingency (i.e. the random events which impact on a given region) and ecological convergence on the structure of diverse mammal communities in three separate continents: South and Central America, Asia and Africa. They found that once ecological factors were accounted for, Asian and African communities were structurally convergent. They suggested that the amount of time of separation between these two biotas was not enough for their communities to diverge in structure. American communities, on the other hand, have been separated from those of Africa and Asia for between 120 and 90 million years, apparently sufficient time to cause divergence of structure.

Interestingly, the means of comparing between these disparate continents represents a form of taxon-free analysis, where each species in the community is assigned to a specific functional group (see Louys et al. 2011 for a detailed methodology), and this is the same method that paleoecologists can use to compare between temporally disparate faunas. Hence the spatial relationships between communities can simultaneously be compared temporally. So, for modern communities in specific regions across geographical space, their properties (e.g., ecometrics (Polly et al. 2011), community structure (Louys et al. 2011), etc.) could be to quantified; this would represent the end point in the temporal dimension. Should paleontological records exist for fossil communities in those regions, then the temporal dimension could be expanded. In this way, the spatial properties of communities could be examined through time, or alternatively, the temporal properties of communities could be examined through space. In fact, this latter type of analysis is already well established in the paleontological literature, largely examining changing species distributions through time (e.g., FAUNMAP Working Group 1996; Alroy 1999; Barnosky et al. 2003). Such analyses are increasingly relying on paleontological databases, many of which are available online. These databases are one of the most important resources in modern paleoecological research, an importance that will certainly increase in the future. Databases such as the Paleobiology Database (http://paleodb.org), Neotoma (http://www.neotomadb.org), FAUNMAP/MIOMAP (http://www.ucmp.berkeley.edu/neomap), NOW (http://www.helsinki.fi/science/now), and NOAA (http://www.ncdc.noaa.gov/palaeo/palaeo.html) provide the large scale, spatiotemporal data necessary to conduct macroecological studies spanning more than the last few decades. The integration of several different types of fossils and associated data in the databases (e.g., vertebrates, pollen, sedimentology data), along with more sophisticated and precise dating methods means that large scale patterns in environmental change through time can be examined in addition to inherent ecological properties of the ecosystems under examination.

In a sense, the examination of spatiotemporal patterns through taxon-free analysis, or alternatively examining single taxonomic groups through time, has the effect of holding the taxonomic scale constant while the other two dimensions are examined. In a similar way, holding the spatial scale constant while examining the interaction or properties of the temporotaxonomic dimensions can lead to interesting biological and ecological hypotheses not detectable from neontological observations. For example, Roopnarine and Angielczyk (2011) discuss the levels of organisation of biological systems interacting through time. They suggest that the development of selfish characteristics by individual agents in a larger interactive system will be detrimental to that system. In a biological sense then, species within an ecological network that develop traits which are self-serving, but are at the detriment of the network as a whole, affect the robustness of their community, and hence the very network they are reliant on. Roopnarine and Angielczyk detected such a ‘tragedy of the commons’-effect from a trophic network (i.e. food web) model of Permian-Triassic terrestrial communities through time. Such an effect would be unobservable from data gathered in a modern ecological study, however it is clearly an important ecological concept.

Thus future advances in palaeoecology sensu stricto will benefit from analyses holding either the taxonomic scale constant (or mitigated) and studying spatiotemporal patterns, or alternatively holding the spatial scale constant or mitigated and examining temporotaxonomic patterns within an environmental context. (Of course, holding the temporal scale constant is the purview of modern biology when examining the recent, or paleontology within a specific geological time period.) Studying the relationships and patterns between different levels of resolution within and between the dimensions will potentially reveal new patterns not discernable from neontological studies (e.g., Finarelli and Flynn 2009). Spatiotemporal patterns can be examined at decadal, centennial and millennial time scales, and over biogeographic regions, biomes and continents. Comparing spatial patterns at the biome level at centennial and millennial time scales with spatial patterns at the continental level over the same temporal dimensions, to take one example, may lead to novel ecological observations. Similarly, the taxonomic scale can be incorporated into such analyses, with organisms classified into species, genera or families, and examined at the individual, population, community, and metacommunity levels. In such a way all three dimensions might theoretically be examined simultaneously, and the emergent properties of ecosystems at only one scale compared across and between the different dimensions. This will provide paleoecologists and ecologists novel insights into how ecosystems function not discernable from examining phenomena at single scales.

13.3 Proactive Conservation Strategies

Just as conservation biology can be considered a sub-discipline of ecology, conservation paleobiology falls under the remit of paleoecology sensu lato. And just like paleoecological advances, future contributions to conservation science from paleontology will stem from the evidence-based retrodictive models developed from the fossil record, which can then be forecast to determine how extant ecosystems, habitats and species will respond to future changes, be they climate-related or otherwise. Thus, conservation paleobiology's strength will be in informing proactive strategies for conservation, for both in situ and trans situ conservation approaches.

As already well summarised by the contributions in this volume as well as other authors, the core objective of conservation biology is to preserve the Earth's biodiversity at 'normal' levels, for a given value of normal. This amounts to saving species, saving ecosystem functions, and preserving wild places as perceived by humans (Meine et al. 2006). Unfortunately these goals cannot be achieved by simply fencing off protected areas (Barnosky 2009; Heller and Zavaleta 2009; Hodgson et al. 2009; Thomas 2011). Hadly and Barnosky (2009) summarise the problems with this approach:

1. The boundaries of nature reserves are often strictly delineated, such that species found within those reserves cannot successfully track changes in climate.
2. The current rate of global warming is faster than any that extant species have experienced in their past.
3. The Earth is entering a new climate state with respect to the climatic states that current species and ecosystems evolved in, with some projections indicating temperatures reaching levels higher than any since many modern species evolved.

Rather, and in concert with maintaining large areas of high quality habitats (Hodgson et al. 2009), means of connecting these habitats via suitable corridors or stepping-stones will increasingly be developed (Heller and Zavaleta 2009), and

Fig. 13.1 Ascension Island's artificially created botanical community forms a cloud forest, very unlike the species poor fern-dominated ecosystem present before active human manipulation. All of the plants shown in this photo are introduced (Wilkinson pers. comm.) (Photo courtesy of DM Wilkinson)

translocations seriously considered (Donlan et al. 2006; Thomas 2011; Zimov et al. 2012). For such strategies, palaeoecology can provide the necessary evidence-based projections of:

1. How species and communities in current nature reserves will react to predicted levels of climate change in terms of migrations, range shifts, extirpations and extinctions (in situ conservation)
2. Which species might be expected to naturally migrate along the corridors or stepping-stones in light of climate change, and the effects of such migrations (natural trans situ conservation)
3. What combination of species may be suitable for translocations beyond their historical ranges to completely new regions (artificial trans situ conservation)
4. How ecosystems might be expected to react to trans situ conservation efforts in the longer term
5. How ecosystems could be artificially built from scratch (*terraforming*)

This last strategy is as yet hypothetical, but logically follows on from the rewilding strategies suggested by those who advocate a return of Pleistocene ecosystems through the reintroduction of large-bodied grazers and their predators to grasslands (e.g., Donlan et al. 2006; Zimov 2005; Zimov et al. 2012). Complete ecosystem rewilding and other less extreme forms of artificial trans situ conservation strategies have inevitably attracted much criticism (e.g., Ricciardi and Simberloff 2009; Vilà and Hulme 2011; Webber et al. 2011), and in light of these artificially creating ecosystems from scratch might sound like science fiction. However, a brief review of history of Ascension Island (Fig. 13.1) is informative in this regard.

When originally sighted by Darwin in 1836, Ascension Island was an ecologically impoverished place, sporting only 25–30 vascular plant species, only around 10 of which were endemic (Cronk 1980; Ashmole and Ashmole 2000). However an active translocation program was initiated under the suggestion of Joseph Hooker, which radically changed the island from a species-poor fern-dominated ecosystem to a species-rich cloud forest (Wilkinson 2004). While even Hooker had second thoughts about the conservation implications of this program, it does demonstrate that creating an artificial, translocated, yet fully functioning ecosystem is theoretically possible.

Needless to say, such a conservation strategy is extreme, and if considered at all should only be done so as a last resort, with target areas chosen such that they do not harbour endemic species and are suitably fenced off from surrounding regions. Such areas might include abandoned industrial complexes or war-ravaged provinces. Whether such extreme conservation strategies will ever need to be implemented remains to be seen.

Nevertheless, should such a strategy be considered necessary in the future, the paleontological record could inform us which combinations of species might be viably put together in such a reserve (‘ecological fitting’ sensu Janzen 1985). For example, taxon-free synecological analyses could determine which combination of functional groups in a community might be suitable for the given abiotic and biotic conditions of the reserve. By being taxon-free, such analyses would not be restricted by geographical and temporal boundaries; and furthermore, would also allow the consideration of species combinations that have never existed. In the less extreme case of inter-regional translocations, understanding of function of ecosystems through time from a taxon-free perspective will allow ecologists to predict how translocated species might impact their new ecosystems, particularly for translocations of species well outside their range as indicated by their historical or fossil record.

Understanding the impact and speed of global warming on ecosystems requires finding analogous warming events in the geological past. Vegas-Vilarrúbia et al. (2011) identify several geological periods that might be informative in this regard. They include the rapid warming event that occurred at the transition between the Younger Dryas cold event and the Holocene, around 11.5 kyr BP; and the Paleocene-Eocene Thermal Maximum, around 55 Ma. Paleoecological analyses of ecosystems transitioning through these warming events are providing critical data that should directly inform conservation policies. Examples of such analyses include studies of North American small mammal faunas that span the Younger Dryas and the beginning of the Holocene (Blois et al. 2010; Lyman 2012; Pardi and Smith 2012), where it was found that these communities experienced a loss of biodiversity in response to the warming event. Such findings have obvious implications for small mammal communities experiencing extreme levels of warming today.

Unfortunately the Holocene fossil record has a somewhat unfashionable reputation amongst some paleontologists. This is probably because almost all species studied by Holocene paleontologists are extant; but also because the time-depth represented by this Epoch is (geologically) tiny and extends into the present. However this is in fact this Epoch's strength; and because the Holocene represents the transition between geological time and ecological time it is in this Epoch that investigations should be prioritized if the aims of paleontologists are to advance the field of conservation paleobiology. Studies of 'subfossils' and, as discussed by Behrensmeyer and Miller (2012), the recently dead can provide unique conservation insights not easily discernable from either deep time paleontology or modern ecology.

Returning to the core objective of conservation biology, if it is to preserve the Earth's biodiversity at 'normal' levels, for a given value of normal, then achieving this objective requires an understanding of what normal means. One major finding of paleoecologists over the last 20–30 years has been the recognition that species tend to have individualistic, or Gleasonian, responses to long-term environmental changes (Davis 1981; Graham and Grimm 1990; FAUNMAP Working Group 1996; Bennett 1997; Pardi and Smith 2012). These responses explain the extensive presence of non-analogous, or 'disharmonious' assemblages in the Quaternary record: that is the co-occurrence of species in space that today are allopatric. Understanding these 'disharmonious' communities, how they function, and how they respond to change is essential if we are to manage the non-analogous communities that are predicted to result from climate change (Williams and Jackson 2007; Williams et al. 2007). The individuality of species' characteristics implied by these results also means that, in order for paleoecologists to develop an understanding of past ecosystem dynamics, they must understand the paleobiology of each species within a paleoecosystem. Such an undertaking will be lengthy, and autecological analyses of fossil taxa across all invertebrates, vertebrates and plants in a community are rare. Nevertheless this should be seen as a priority in paleoecologists' efforts to understand paleoecosystems.

Contrary to these Gleasonian observations, communities exhibiting resistance (the ability of community structure to withstand perturbations) and resilience (the ability of community structure to return to a stable state after perturbations) provide support for the existence of community continuity and stasis through time. The fossil record provides many examples of stasis in several groups of plants, insects and mammals (DiMichele et al. 2004), and structural continuity – the persistence of the same community structure independent of species composition – has been proposed for Pleistocene mammal communities in Spain (Rodríguez 2004) and Southeast Asia (Louys 2011). While these communities exhibit resistance or resilience, there comes a point when they are subjected to perturbations or disturbances severe enough, or alternatively conditions may gradually reach certain critical thresholds. In such cases, the structure of the community switches to an alternative stable state (Rodríguez 2006). This response system, as observed in the fossil record, corresponds to the concept of non-equilibrium ecology, where non-linear and complex dynamics are invoked to explain sudden and unexpected ecosystem reactions to change (Holling 1973; May 1977). Given the stochastic nature of these reactions, predicting their occurrences, understanding their causes and preventing their consequences will only be possible through an examination of the fossil record (Vegas-Villarrúbia et al. 2011). It should be noted that these perturbations or threshold-crossing events might be independent of any global warming predictions, and we need to understand ecosystem reactions to such events in addition to responses to climate change.

13.4 Summary

The paleontological record can provide many new and important insights and novel data to the fields of ecology and conservation biology. Future directions for paleoecology sensu stricto could include more analyses across and between the taxonomic, spatial and temporal scales at different hierarchical levels. Future directions for conservation paleobiology should focus on greater taxon-free understanding of ecosystems, renewed efforts to increase the autecological knowledge of individual fossil species, and greater analyses of communities and ecosystems spanning the Holocene. The examples provided by the chapters in this book are testament to the successful collaboration possible between paleontology, ecology and conservation science.

However, the successful integration between these multidisciplinary fields will never be completely realised without a greater level of discourse between its practitioners (Flessa et al. 2005; Dietl and Flessa 2009; Louys et al. 2009; Behrensmeyer and Miller 2012). Paleoecologists should increasingly seek to present their findings and theories at ecological conferences and in ecological journals, and actively participate in ecology discussion forums, societies and workshops. Ecologists should incorporate detailed paleontological data and discussions into their textbooks and undergraduate and postgraduate courses, and actively seek to employ paleoecologists in their faculties and schools.

Arguably the most important ecological and conservation insights provided by the fossil record is that change is typical, fluctuations and variability in ecosystems are normal, and that life is not static. The fossil record emphasises that the unusual and the unexpected can, and often do happen. It is only by understanding this natural variability – how and where it originates and what its consequences to organisms, populations, communities and ecosystems are – that we can truly begin to develop the holistic research programs necessary to understand and protect the unique biodiversity that still exists today.

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Appendix A
Modern Bone Survey Sheet Example and Instructions

Anna K. Behrensmeyer and Joshua H. Miller

A.1 Goals

1. Obtain statistically viable samples of the surface (modern) bone assemblage (macro- and micro-vertebrates) in order to characterize the species present and their relative abundances.
2. Compare the results with other types of censuses (live animal counts, trapping samples, etc.) in order to contribute to ecological monitoring programs.
3. Establish baseline data for different habitats and ecosystems so that ecological change can be documented in future standardized surveys.
4. Record damage on the bones and the survival of different skeletal parts as evidence for the impact of different types of predators (e.g., lions vs. hyenas) on prey populations.
5. Calibrate rates of weathering in different habitats and climates to establish time-since-death (postmortem duration) for skeletal remains.

A.2 Methods

Key to successful bone surveying is having one or more team members who is/are able to identify species and body parts in the field from fragmentary skeletal remains. This is a skill that can be acquired through study of museum osteology collections. Sketching or photographing the most common bones that survive in

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surface assemblages (e.g., skulls, jaws, teeth, ends of major limb bones) from different aspects (distal, proximal, lateral, medial views) plus practice in the field is the best way to learn bone identification. Even experienced workers take reference skeletons with them in the field, as well as reference books and photographic catalogues that aid in identification. If ID is uncertain, it is very important to mark the bones or skeletons with "??" on the data sheets, photograph or collect them and identify them using comparative collections before finalizing the data.

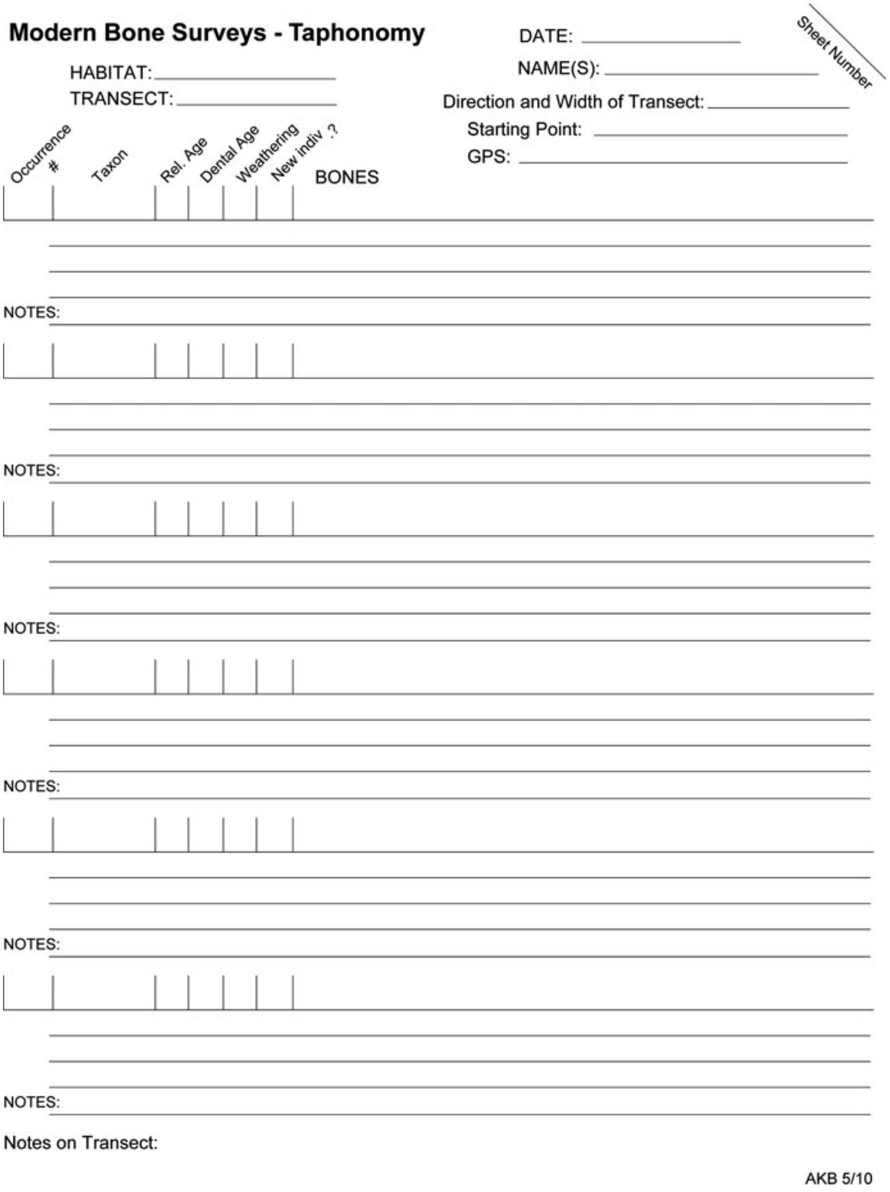
A.2.1 Bone Sample Plots

Using airphotos, satellite imagery and/or maps, areas for sampling and general locations for plots are chosen; the exact locations can be chosen using randomized or evenly spaced protocols. On the ground, the end points (and any points where the plot or linear transect is broken or changes direction) must be documented using GPS to provide coordinates that can be entered into a GIS. Plots can be oriented North–south or East–west to make it easier to maintain a straight line using a compass or GPS. Accurate GIS coordinates will allow calibration of the area searched and also permit future surveys of the same area. Photographs of distinctive features (e.g., trees, topography, etc.) and markers such as small cairns at sample plot endpoints are also helpful for relocation.

Surface bone sampling works best in areas of limited grass or other ground cover; in Amboseli we sample during the dry season, when vegetation cover is low and bones are more likely to be visible. Plot width is determined by visibility; in dense vegetation, 10–30 m either side of the midline (often where a vehicle is driven); in open vegetation 30–50 m on either side. Bones that are outside this area should be excluded from the sample. Usually two to four individuals walk over plots, covering as much of the ground as possible. Data on all observed bone occurrences are recorded on standardized data sheets. For examples of bone survey datasheets see: Figs. A.1 and A.2 or http://www.mnh.si.edu/ete/ETE_People_Behrensmeyer.html. Bones that cannot be identified in the field, or those of special taphonomic interest, are collected for later examination.

An OCCURRENCE is one to many bones in close spatial proximity (belonging to one individual animal). Body parts likely belonging to the same individual but dispersed more than 15–20 m away from each other generally are given separate occurrence numbers. When two different animals occur at the same place, they are given separate occurrence numbers. One person should be responsible for making final decisions about identification and for collecting all required information on the data sheets; this is important to assure that differences between transects are not due to differences in observer methods or ability.

Data recorded include: taxon, ontogenetic age (adult, sub-adult, yearling, neonate, state of tooth eruption), skeletal parts present, habitat, weathering stage, breakage and other damage features such as tooth marks and degree of burial. In Amboseli, we continued the transect until we had 20 individuals ("MNI" =



Modern Bone Surveys - Taphonomy

DATE: ____________

NAME(S): ____________

Sheet Number

HABITAT: ____________

TRANSECT: ____________

Direction and Width of Transect: ____________

Starting Point: ____________

GPS: ____________

Occurrence #	Taxon	Rel. Age	Dental Age	Weathering	New indiv ?	BONES

NOTES:

NOTES:

NOTES:

NOTES:

NOTES:

NOTES:

Notes on Transect:

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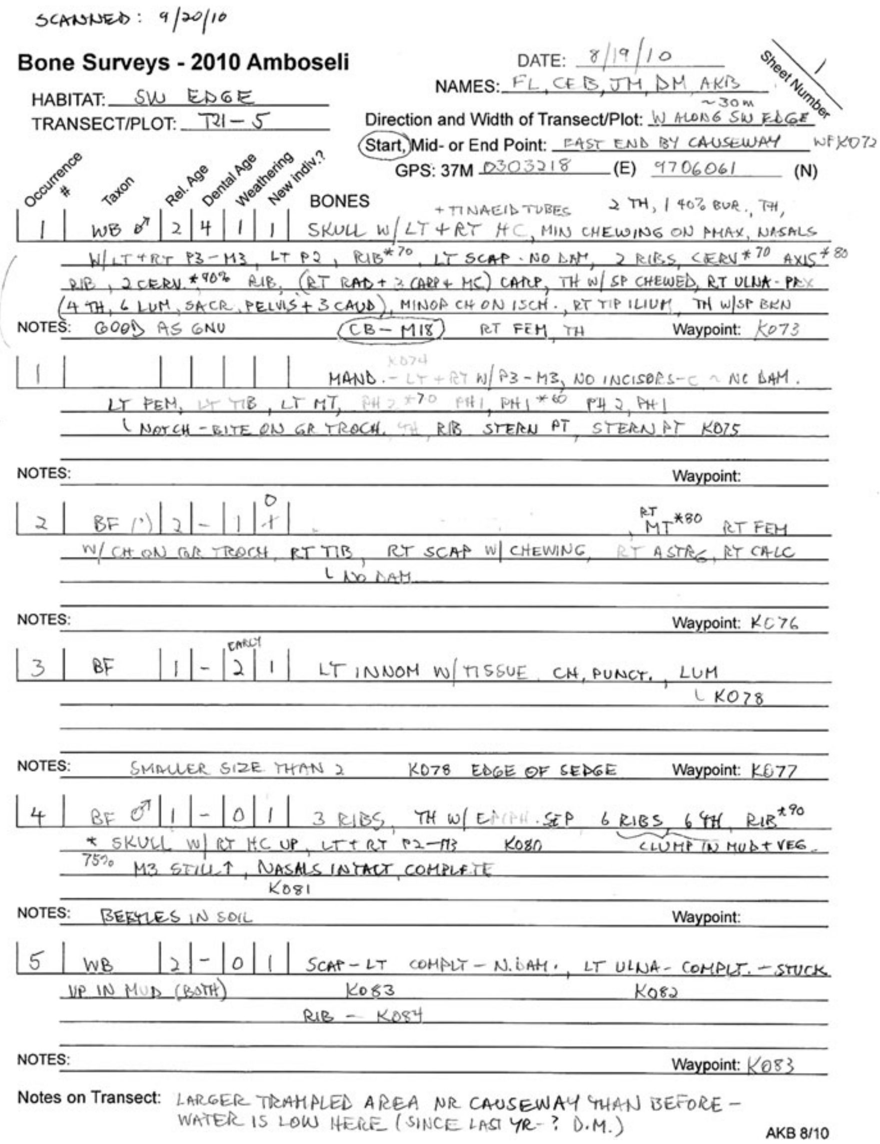
Fig. A.1 Bone survey datasheet



SCANNED: 9/20/10

Bone Surveys - 2010 Amboseli

HABITAT: SW EDGE

TRANSECT/PLOT: TRI – 5

DATE: 8/19/10

Sheet Number 1

NAMES: FL, CEB, JM, DM, AKB

Direction and Width of Transect/Plot: W ALONG SW EDGE ~30 m

(Start,) Mid- or End Point: EAST END BY CAUSEWAY WP K072

GPS: 37M 0303218 (E) 9706061 (N)

Occurrence #	Taxon	Rel. Age	Dental Age	Weathering	New indiv.?	BONES	NOTES	Waypoint
1	WB ♂	2	4	1	1	+ TINAEID TUBES 2 TH, 1 40% BUR., TH, SKULL W/ LT + RT HC, MIN CHEWING ON PMAX, NASALS W/ LT + RT P3 – M3, LT P2, RIB^{*70}, LT SCAP - NO DAM, 2 RIBS, CERV^{*70} AXIS^{*80} RIB, 2 CERV.$^{*90\%}$ RIB, (RT RAD + 3 CARP + MC) CARP, TH W/ SP CHEWED, RT ULNA - PRX (4 TH, 6 LUM, SACR, PELVIS + 3 CAUD), MINOR CH ON ISCH., RT TIP ILIUM, TH W/SP BRN	GOOD AS GNU (CB – M18) RT FEM, TH	K073
1						K074 MAND. – LT + RT W/ P3 – M3, NO INCISORS – C ^ NO DAM. LT FEM, LT TIB, LT MT, PH 2^{*70} PH 1, PH 1^{*60} PH 2, PH 1 NOTCH - BITE ON GR TROCH, TH, RIB, STERN PT, STERN PT K075		
2	BF (?)	2	–	1	0 +	RT MT^{*80} RT FEM W/ CH ON GR TROCH, RT TIB, RT SCAP W/ CHEWING, RT ASTRG, RT CALC NO DAM		K076
3	BF	1	–	EARLY 2	1	LT INNOM W/ TISSUE, CH, PUNCT., LUM K078	SMALLER SIZE THAN 2 K078 EDGE OF SEDGE	K077
4	BF ♂	1	–	0	1	3 RIBS, TH W/ EPIPH. SEP 6 RIBS, 6 TH, RIB^{*90} CLUMP IN MUD + VEG. * SKULL W/ RT HC UP, LT + RT P2 – M3 K080 75% M3 STILL ↑, NASALS INTACT, COMPLETE K081	BEETLES IN SOIL	
5	WB	2	–	0	1	SCAP – LT COMPLT – N. DAM., LT ULNA – COMPLT. – STUCK UP IN MUD (BOTH) K083 K082 RIB – K084		K083

Notes on Transect: LARGER TRAMPLED AREA NR CAUSEWAY THAN BEFORE – WATER IS LOW HERE (SINCE LAST YR – ? D.M.)

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Fig. A.2 Example of completed bone survey datasheet

mininum number of individuals). MNI is based on the number of different individual animals that can account for the documented bones; decisions are made in the field, based on body size, species ID, growth stage (juvenile vs. adult), weathering stage, etc. The general approach is to assume that an unknown bone is not a separate individual unless demonstrated otherwise. This provides a conservative estimate that works against inflation of the MNI count.

For more information on the prototype sampling methods in Amboseli Park, Kenya, see Behrensmeyer and Dechant (1980) and Behrensmeyer (1993). Generally, a sample of at least 100 MNI is necessary to characterize the common species in a particular habitat (i.e., 5–6 transects), though more may be required to capture the rare species. In Amboseli, 2–3 plots per day are possible, thus one can obtain an adequate sample of several different habitats in a week of bone surveying. This depends, of course, on the density of bones on the ground and the time required by the team to locate and identify these bones.

A.2.2 Targeted Samples

Additional sampling can be used to document the effects of the dispersal and destruction of carcasses around predator dens or areas of particular concentration ("predation arenas"), including human habitation sites. For example, this can involve radial plots around known hyena denning areas and investigation of other places where hyenas or other predators are known to "lie up" during the day (e.g., dense clumps of grass, palm woodlands) as well as direct observations of predators at kills, when possible.

A.2.3 Small Mammal Bone Concentrations

These occur around predator roosts and marking areas (latrines) and provide information that can supplement the survey plots, where small animal bones can be missed. It is best to collect bulk samples of these concentrations, including carnivore scat piles and owl pellets, for later processing and identification in the laboratory. Such concentrations and their context (e.g., under a tree, on a rocky outcrop) should be photographed and described PRIOR to collection, and a GPS and/or map record must be made of their location.

A.2.3 Bone and Carcass Mapping

With modern GPS technology, it is possible to map every bone or carcass on a plot by recording GPS coordinates for the center of the occurrence. This can be done in selected areas to provide detailed maps of the landscape distribution of the skeletal remains and the species they represent. This will allow researchers to develop a picture of where different species are dying and how this has changed through time. If one has a handheld computer with GPS data logging capability, the time devoted to recording the position of each bone occurrence is minimal. However each additonal data-type takes time to log and each sample plot may include hundreds to thousands of bones. Thus, the team leader must decide how to balance the benefits of more detailed spatial data and the need for large bone samples, based on the goals of the project.

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J. Louys (ed.), *Paleontology in Ecology and Conservation*,
Springer Earth System Sciences, DOI 10.1007/978-3-642-25038-5,