

Conservation archaeogenomics: ancient DNA and biodiversity in the Anthropocene

Courtney A. Hofman^{1,2,3}, Torben C. Rick², Robert C. Fleischer³, and Jesús E. Maldonado^{3,4}

¹ Department of Anthropology, University of Maryland, College Park, MD 20742, USA

² Program in Human Ecology and Archaeobiology, Department of Anthropology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013-7012, USA

³ Center for Conservation and Evolutionary Genetics, Smithsonian Conservation Biology Institute, National Zoological Park, Washington, DC 20013-7012, USA

⁴ Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013-7012, USA

There is growing consensus that we have entered the Anthropocene, a geologic epoch characterized by human domination of the ecosystems of the Earth. With the future uncertain, we are faced with understanding how global biodiversity will respond to anthropogenic perturbations. The archaeological record provides perspective on human–environment relations through time and across space. Ancient DNA (aDNA) analyses of plant and animal remains from archaeological sites are particularly useful for understanding past human–environment interactions, which can help guide conservation decisions during the environmental changes of the Anthropocene. Here, we define the emerging field of conservation archaeogenomics, which integrates archaeological and genomic data to generate baselines or benchmarks for scientists, managers, and policy-makers by evaluating climatic and human impacts on past, present, and future biodiversity.

Ancient DNA, archaeology, and the Anthropocene

Throughout much of our history, humans have altered the biosphere, impacting plants, animals, and ecosystems through a variety of activities, and producing an archaeological record of human interactions with the natural world [1,2]. Although major anthropogenic impacts on biodiversity are linked to industrialization and the modern period, ancient peoples also interacted with, and influenced, the environment. Modern ecosystems are products of this deep history, and long-term perspectives on their evolution both with and without humans can provide important information on their capacity to withstand perturbations [3–5]. The pace and scale of modern anthropogenic environmental impacts and growing recognition of the importance of investigating ancient human–environmental interactions

have an important role in the Anthropocene debate (see [Glossary](#)), which centers around whether we have entered a new geologic epoch characterized by human domination of Earth's ecosystems [6–9]. While researchers debate if and when the Anthropocene began, one thing that is clear is that we need new data sets and approaches to help us understand and transcend the major environmental challenges of our time, including climate change, loss of biodiversity through extinction, emerging infectious diseases, and a host of other issues.

Here, we focus on one of these new approaches, which we call 'conservation archaeogenomics', or the genomic analysis of the archaeological remains of plants, animals, soils, and other materials to enhance present-day biological conservation and management. Archaeological sites contain evidence of important environmental and cultural changes that span millennia or more, and archaeological data sets can contribute much to conservation biology and management by allowing researchers to reconstruct past environments and the place of humans within those

Glossary

Ancient DNA (aDNA): DNA extracted from nonliving sources, including teeth, bones, toepads, desiccated tissue, seeds, plant remains, and paleofeces.

Anthropocene: the proposed recent geological epoch during which humans have dominated the earth's landscape.

Archaeogenomics: utilizing materials from archaeological sites to generate genomic information.

Archaeology: study of the human past using material remains.

Environmental DNA (eDNA): DNA obtained from environmental samples, including soil or water.

Historical ecology: the interdisciplinary study of ecosystem dynamics using historic and prehistoric data sets, often used to inform conservation.

Metagenomics: genomic analysis of DNA samples from mixed sources.

Midden: ancient trash deposits, often containing shells, bones, and plant materials.

Paleofeces: ancient feces from humans or animals. This differs from coprolites, which are fossilized feces.

Paleogenomics: the study of past genomes using aDNA methods.

Provenience: location of an object within a site and in relation to other artifacts and ecofacts.

Shifting baselines: the concept that what we view as natural changes through time.

Corresponding author: Hofman, C.A. (hofman@si.edu).

Keywords: ancient DNA; historical ecology; archaeology; conservation genetics.

0169-5347/

© 2015 Elsevier Ltd. All rights reserved. <http://dx.doi.org/10.1016/j.tree.2015.06.008>

ecosystems, assess historical ecological variability, and identify past and present cultural practices impacting biodiversity [1–5]. Building on recent syntheses of the value of aDNA studies for directly addressing a variety of fundamental questions in ecology and evolution [10–13], we focus specifically on the power of aDNA data from archaeological materials to improve biological conservation and chart a course for future research on the topic.

Genomic approaches have become a promising tool for conservation practice, because using genome-wide data can offer a dramatic increase in the number of genetic markers that can be used to improve the precision of estimating adaptive and neutral diversity, and demographic parameters of relevance. This, in turn, results in better wildlife management recommendations, including the preservation of genetic diversity, identification of populations with unique evolutionary history and potential, and the mitigation of the effects of small population sizes on viability [14,15]. While there are challenges in undertaking effective conservation genomics projects [15], genomic analysis of archaeological samples (archaeogenomics) can extend patterns deep into the past and, along with complementary paleogenomic data from fossil and subfossil samples [12,16,17], can provide key information on long-term ecosystem responses to disease, human activities, and climate change [10,11,13,18–20]. Here, we focus on the following question: how can genomic analysis of archaeological materials enhance the conservation, management, and restoration of present-day (and future) biodiversity? To evaluate this question, we focus on five interrelated issues of broad significance: population and distribution changes, translocations, extinction, disease ecology, and environmental reconstruction.

Conservation archaeogenomics: a transdisciplinary approach

While there is an abundance of new terminology associated with the ‘-omics’ era, we treat archaeogenomics and paleogenomics as complementary (but distinct) approaches and much of our synthesis highlights the interrelationship between the two. Paleogenomics was first described as the study of ancestral regions of the genome and ancestral-state genome reconstruction using comparative approaches in extant taxa [21,22], but the field now also encompasses the reconstruction of past genomes through aDNA methods [12,16]. Archaeogenomics differs from paleogenomics because of the general cultural context of the archaeological samples being studied, which often provides a direct linkage to human–environmental interactions in a broad sense and can provide samples that may be rare or nonexistent in paleontological sites (Figure 1). Both archaeogenomics and paleogenomics have been transformed by recent advances in aDNA methods and high-throughput DNA sequencing (HTS) technology, expanding the types of question that can be addressed (Box 1). The case studies presented here reflect the infancy of the field of conservation archaeogenomics because most studies published to-date have focused on short mitochondrial DNA fragments (mtDNA) or a few nuclear markers. However, genome-level analyses are quickly becoming standard and we seek to demonstrate the value and future

Box 1. Archaeogenomics methods: old and new

Similar to genomics, aDNA has changed rapidly with the advent of HTS technology. Due to the existence of relatively few samples and limitations on destructive analyses, early aDNA studies focused on evolutionary relationships and bottleneck detection, and utilized PCR to amplify short mitochondrial fragments or a few nuclear markers and Sanger sequencing methods [83]. However, with HTS technology, it is now possible to study ancient population dynamics and landscape genetics [11,19]. There are now many different ways of collecting genomic data from fresh tissues, including RAD, exome, intron and whole-genome sequencing, and SNP capture. However, when comparing modern and archaeogenomic data, genomic markers must be selected for not only their informativeness and resolution power, but also their successful applicability to degraded samples. While mtDNA has been the marker of choice in aDNA studies due to its ease of recovery in old and degraded samples, high variability, matrilineal inheritance, and haploidy [84,85], SNPs offer higher power to detect bottlenecks, especially those with fast recoveries [32]. However, there is also a greater potential for ascertainment bias, especially when SNP arrays are designed from subsets of modern genetic diversity [86]. The feasibility of a particular project will depend on the goals, scale (i.e., number of taxa and samples), and budget. Furthermore, these new genomic approaches are best used in concert with other data that can improve the context and chronology of a particular sample and be guided by specific procedures and analysis of morphology, proteomics, accelerator mass spectrometry (AMS) radiocarbon dating, isotopes, and other techniques (Figure 2, main text). Together, these data sets can be integrated to explore human impacts on biodiversity and to inform conservation and management for the future.

impact that archaeogenomic research will have on conservation practice and policy.

Conservation biologists and managers rely on baseline data when evaluating potential actions for species management and preservation, and conservation archaeogenomics has a unique role in these reconstructions (Box 2). Conservation archaeogenomics involves collaboration between archaeologists, with intimate knowledge of local and regional sites, cultural histories, and faunal data sets (and their limitations); genomicists, with the capacity to execute methodological and analytic techniques; managers, who make policy and management decisions; and other relevant scientists. These teams can address the multiplying threats facing biodiversity by integrating novel technologies with unique data sets, including archaeological data (Figure 2), to study the evolution of ecosystems through space and time and evaluate their capacity to withstand human perturbations.

Archaeological sites provide subsamples of past environments, as ancient peoples interacted with, and used, the resources that were available to them. Past peoples intentionally created a record of their activities (by building structures, writing histories, and burying human and animal remains and associated artifacts) and unintentionally deposited materials as waste (including shellfish, bones, broken tools, plant remains, stone, and pottery into middens). Although selecting sites and materials associated with human activities for genomic analysis may seem limiting because it does not allow the survey of an entire ecosystem, it has the ability to provide a powerful perspective for understanding the cultural context of human–ecosystem interactions. Archaeological contexts can provide materials from sites that are tens of thousands or more years old all the way up to the past 50 years or so.

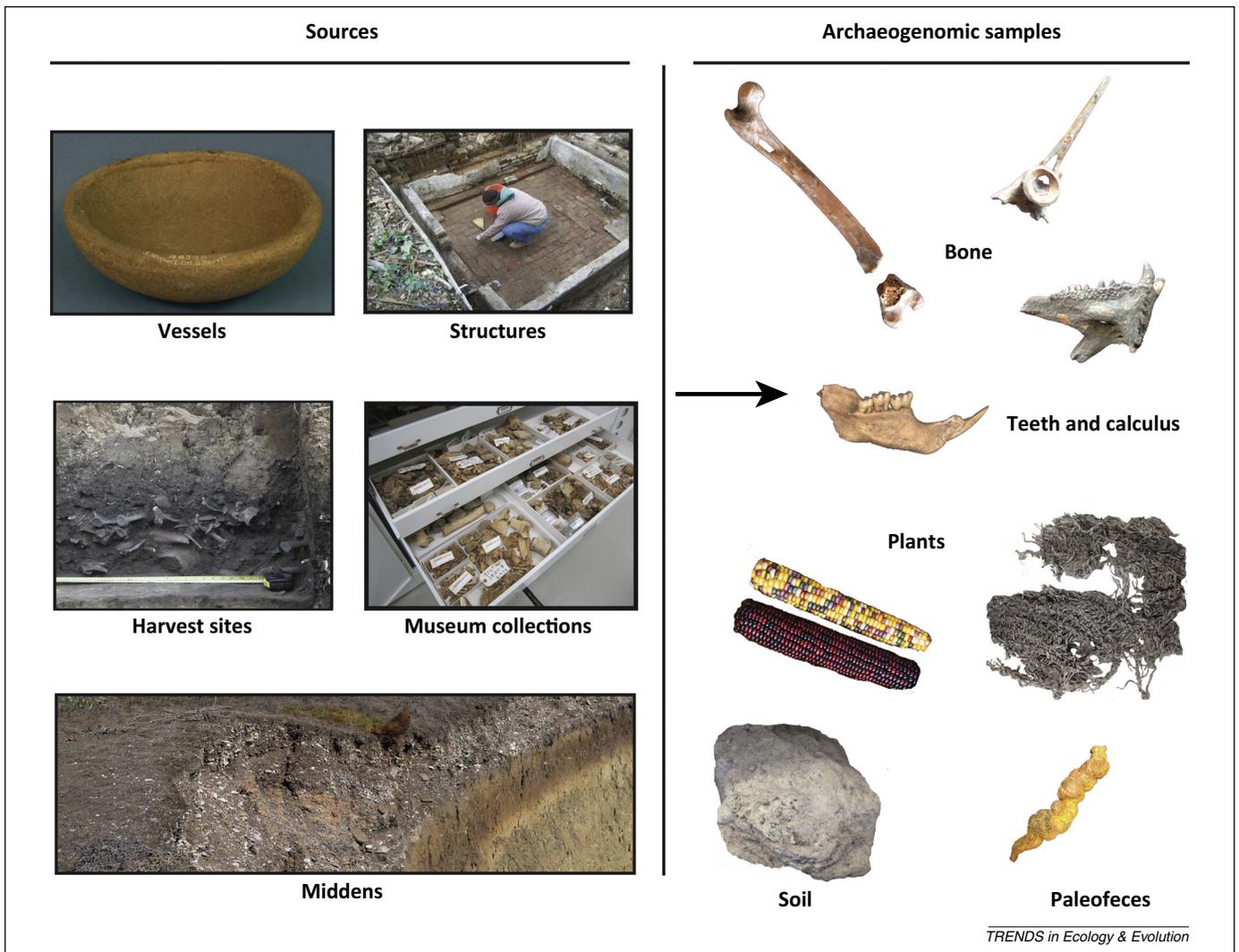


Figure 1. Archaeogenomic samples recovered from different contexts. Archaeogenomic samples can include bone, teeth, plant remains, soil, paleofeces, and other materials. These materials can be recovered from ancient structures, middens, storage vessels, harvest sites, caves, or existing museum collections.

They are particularly common during the Holocene, when there were major shifts in plant and animal distributions, but there is a limited fossil and subfossil record in some regions or for some organisms (e.g., pinnipeds; [Box 3](#)). Additionally, archaeological sites often include dense accumulations of a broad spectrum of local plant and animal materials that, to recover in a subfossil context, would require more intense and broader sampling. Archaeological sites can also contain plant and animal remains that were deposited naturally and/or incidentally (e.g., mice that lived in the same spot as humans) rather than through cultural practices, and complement the natural accumulations of plants and animals represented in paleontological sites. Thus, archaeological materials provide rigorous access to a baseline composition of modern-day flora and fauna under pre-industrial conditions for a critical long-term perspective on biodiversity trends throughout the Anthropocene.

Demographic and distributional shifts

With growing climatic uncertainty and human impacts, a major concern is the reduction or loss of appropriate habitat for many taxa, forcing changes in species distributions,

population bottlenecks, local extirpation, or extinction [23]. Although some species may be able to shift their ranges, many have specific resource requirements that might be impacted by climatic range shifts. For example, North American birds show considerable variability in the projected range shifts under three different climate forecasts [24]. While some species may expand their ranges, others will face considerable declines. Population declines could result in reduced genetic diversity and adaptive potential, and, therefore, are an important focus for conservation archaeogenomic research. Archaeologists have assessed range shifts by examining temporal and spatial relative abundances of animal bones from several archaeological sites. When genetic data are incorporated into these studies, they can disentangle the causes of range shifts and identify their impact on genetic diversity ([Box 3](#)), and these data sets can be compared to climate forecasts. Archaeogenomic studies also provide context for interpreting changes in behavior and range as these species recover [25].

Assessing historical genetic diversity and the timescale on which it is lost or gained is an important part of examining the effects of long-term environmental change

Box 2. What is natural?

Managers rely on baselines that serve as targets for restoring an ecosystem or organism, but a key question is: what is natural [101]? Ecological baselines change through time and the perception of 'what is natural' can be heavily influenced by past human activities and changing generational perceptions (aka 'shifting baselines' [88]). Historical ecology provides perspectives on ecological change through time that can help establish desired future conditions and forecast future ecosystem and organismal responses to climate change and human activities [5].

Genomics is poised to have a key role in historical ecology. With the ability to determine genetic patterns in the past and present, document bottlenecks, and make connections between genetic diversity and population structure, genetic analysis of archaeological and paleontological samples offers a framework for constructing baselines. These archaeogenomic data transcend simplistic notions of restoration to a 'natural state' and instead document change through time and ecological variability that can help explore the conservation challenges of the Anthropocene.

Differences between the prehistoric and modern abundance of Guadalupe fur seals (GFS, *Arctocephalus townsendi*) and northern elephant seals (NES, *Mirounga angustirostris*) on San Miguel Island, California, provide an example of how archaeological and genetic data can help understand shifting baselines. Both species were pushed to the brink of extinction during the 19th- and early 20th-century fur and oil trade, but have recovered since then. However, the abundance today does not match the prehistoric abundance documented in the archaeological record [4]. NES dominate today but were rare during the past 3000 years; conversely, GFS are rare to absent today but were common prehistorically (Figure 1). Genetic analyses of NES and GFS suggest that they were both more genetically diverse prehistorically than today [87,89,90] but future, more detailed, archaeogenomic analyses could provide greater insight into this discrepancy and how it might help us manage for global change in the Anthropocene.

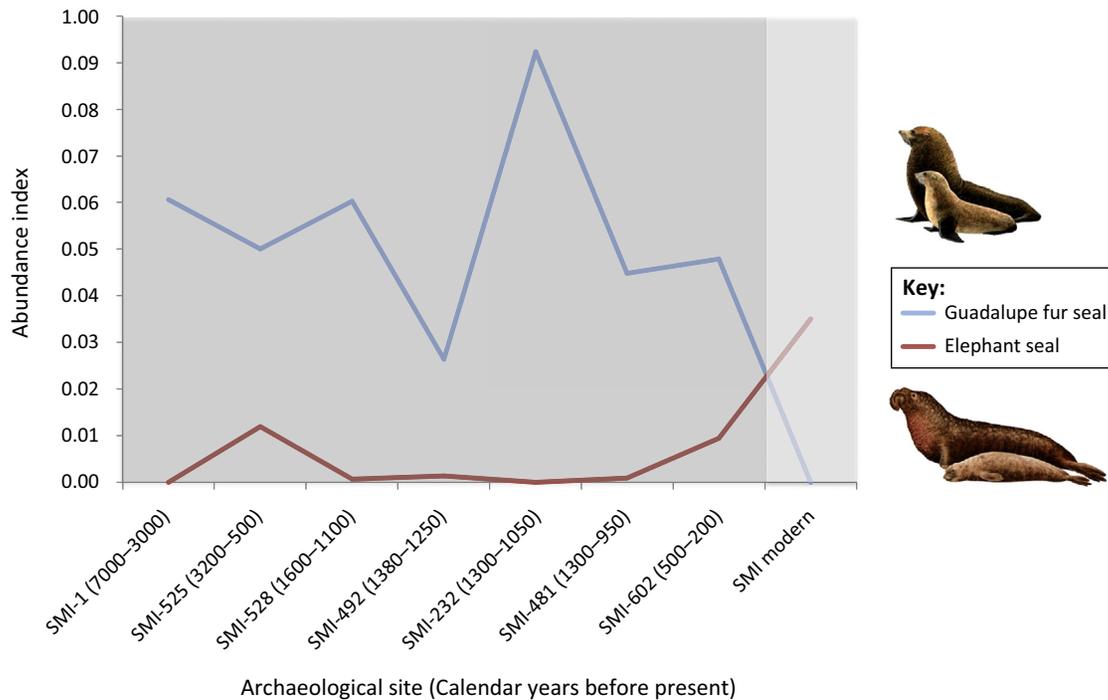


Figure 1. Archaeological and modern abundance of Guadalupe fur seal (GFS) and Northern elephant seal (NES). Data available in [4,25] and references cited therein. Note the greater prehistoric abundance of GFS and greater modern abundance of NES through time.

on biodiversity [11,26]. In the case of the sea otter (*Enhydra lutris*), genetic data from microsatellites show dramatic losses in heterozygosity and allelic diversity following the fur trade; however, otter population structure seems consistent through time [27]. Interestingly, mtDNA of archaeological sea otters from Oregon showed that they were more closely related to the least genetically diverse otter population from California, rather than Alaska, the source population for the unsuccessful Oregon otter reintroduction [28]. Studies such as these demonstrate the value of archaeological samples for identifying appropriate source populations for reintroductions. Archaeogenomic data can expand these studies by providing fine-scale resolution to changes in modern and ancient population genetic structure, including replacements that might not be detected in the archaeological record alone [29–31]. This

can help identify populations that have undergone dramatic loss of genetic variability and unveil cryptic species or evolutionarily significant units that might be in need of conservation efforts.

Identifying changes in population genetic diversity caused by anthropogenic or climate-related forces necessitates careful temporal and spatial sampling [10]. Our ability to confidently detect bottlenecks varies considerably depending on temporal sampling, bottleneck intensity, recovery speed, generation time, and the genetic marker used [32]. Rapid recovery and moderate bottlenecks are difficult to detect, but sampling just before and after the bottleneck increases the power of detection [32]. Therefore, well-dated archaeogenomic data are critical for detecting historical anthropogenic bottlenecks by anchoring estimates of genetic diversity loss within human

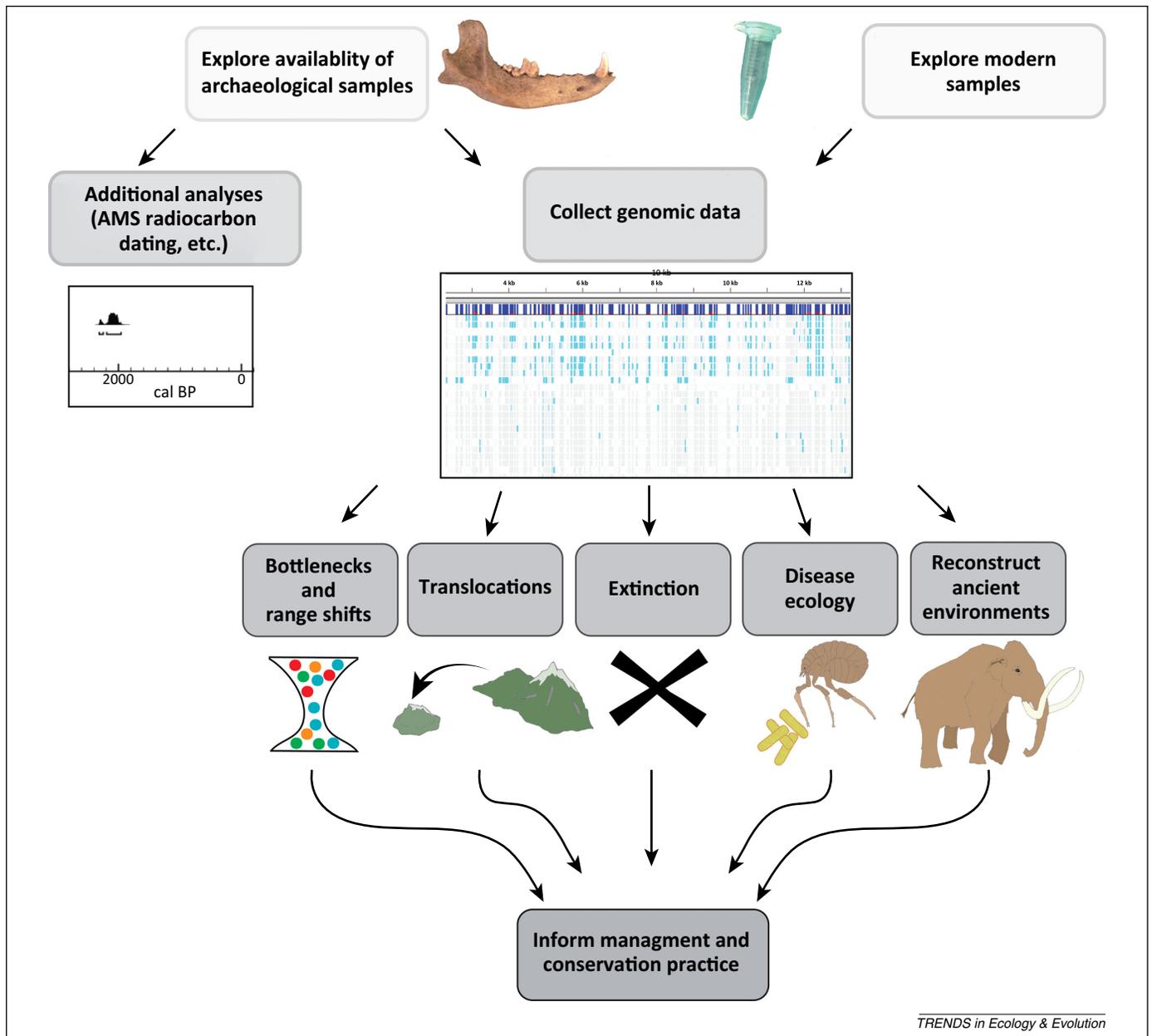


Figure 2. Workflow for an archaeogenomic approach to conservation. Abbreviation: AMS, accelerator mass spectrometry.

history. Data obtained from single nucleotide polymorphisms (SNPs) from archaeological herring (*Clupea pallasi*) bones have shown promise for elucidating historical population structure and anthropogenic impacts on this important fishery [33]. Sequence capture methods (including SNPs) and whole-genome sequencing of ancient samples have become more affordable and are useful tools to assess long-term population demographics, especially bottlenecks, in species of conservation or management concern.

Translocations

Translocation is the movement of plants, animals, or other organisms from one location to another by humans. Ancient translocations have been significant in establishing current species distributions of wild and domesticated plants and animals [1]. For example, humans have moved

bananas from Asia to Africa [34], domesticated dogs around the world [35,36], and brought several domestic and wild animals to the Pacific islands [37–41]. There are also numerous wild species that have been translocated since the Pleistocene. The grey cuscus (*Phalanger orientalis*), a small marsupial, was translocated to New Ireland approximately 10 000–19 000 years ago (possibly from New Britain), to the Solomon Islands by 9000 BP, and to Timor by 4500 BP [42,43]. Insects (beetles, lice, fleas, and flies) were introduced to Iceland and Greenland by the Norse; various species of snails followed human migration across the Pacific; several species of hutia were transported across the Caribbean; and shrews, mice, deer, foxes, and rats have been introduced to various islands in the Mediterranean, North America, and Oceania [1].

Many ancient translocation studies rely on the presence of animal bones or plant remains in assemblages, their age,

Box 3. Exemplar case studies

Case study A

In a large study of six different herbivores from around the world, 846 radiocarbon-dated mtDNA sequences, 1439 directly dated faunal remains, and 6291 radiocarbon dates associated with human occupation, all taxa showed dramatic range contractions from the terminal Pleistocene to the early Holocene [56]. Four species (horse, reindeer, bison, and musk ox) show a positive correlation between range size and genetic diversity through four time points. When demographic changes are compared with environmental history, archaeological abundance data, and radiocarbon dates, climate change rather than human hunting is suggested as the likely cause for the demographic changes in horse, reindeer, and musk ox. Data such as these show that climate change can have significant effects on the ranges and the demographics of plants and animals, and we should be concerned for how future fluctuations will impact wildlife populations, especially those with already limited ranges or low genetic diversity.

Case study B

One of the best-documented and most-dramatic anthropogenic extinctions is that of Pacific birds [91–93]. An estimated 2000 species went extinct following the human expansion across the Pacific islands [94]. Whether due to introduction of commensal and/or invasive

species, such as the rat, or to anthropogenic landscape change [91,92], the extinction of endemic island avifauna has transformed island ecosystems. In Hawaii, mtDNA from paleontological, archaeological, historic, and extant samples of the endangered nene (*Branta sandvicensis*) show considerable loss in mtDNA variation following human colonization [95]. While many other Hawaiian geese and other birds went extinct during this period [93,96], the nene survived, potentially as a result of intentional or unintentional cultural practices protecting the species [95]. However, ancient mtDNA revealed that the endangered Hawaiian petrel (*Pterodroma sandwichensis*), the most abundant seabird in the prehuman islands, and presumed extinct by the mid-20th century, retains significant levels of its historical genetic diversity in surviving present-day populations [97]. The long generation time of the species and its ability to ‘hide at sea’ may have allowed a larger effective population size and greater retention of genetic variability. The 20th-century-observed population decline correlated with a change in isotope values suggesting a trophic shift from large to small prey items, likely a result of fishery depletion in the Northeast Pacific [98]. Additionally, aDNA studies on endangered Laysan ducks (*Anas laysanensis*) and Millerbirds (*Acrocephalus familiaris*) were influential in the translocation of these species to other islands as insurance populations [99,100].

and association with or without humans, but a growing number of researchers are incorporating genetic information from modern samples [44] and a few include aDNA data. Archaeogenomic methods have been used to test a commensal model for the human settlement of the Pacific through radiocarbon dating and genetic analysis [39,45]. This commensal model asserts that certain animal species can be used to track the movement of humans because it is likely only through human transport that these species moved to new environments. For example, mtDNA sequences of extant Pacific rat (*Rattus exulans*) populations revealed genetic relationships between different Pacific islands that reflect human colonization patterns [46]. The addition of archaeological rat samples improved the chronology of human colonization of the Pacific islands and genetic analysis of additional species, including pigs and chickens, have generated interspecific patterns of human expansion across the Pacific [38–40,45,47]. Commensal models have now been applied in other areas of the world, including the North Atlantic translocations of house mice (*Mus musculus*) [48,49].

The introduction or translocation of plants and animals, either recent or ancient, can have considerable impacts on an ecosystem. The invasive species epidemic has demonstrated the significant impacts of introduction events: local extirpation, trophic cascades, and extinction. Some ancient translocations had similar impacts on new environments. However, the implications of ancient translocations for conservation and management are complicated and intertwined with cultural values and ideals. Should prehistoric human translocations be eradicated? How long is enough time to be considered native? Is the mechanism of arrival important? Some ancient translocated species are adored, while others are abhorred [50]. How do human values and culture impact this designation? These questions show that a nuanced discussion of ancient translocations is essential when making conservation and management decisions. Any management practice including eradication, establishing captive populations, reintroduction, genetic

rescue, and so on, should be carefully considered. Conservation archaeogenomics is an ideal tool for exploring baselines or restoration targets to evaluate how ancient translocations impacted ecosystem structure and function at specific time points and a starting point for discussion on how they should be managed in the future.

Extinction and de-extinction

The dramatic loss of biodiversity over the past 200 years has some researchers placing us in a sixth mass extinction event [51,52]. While extinction is a natural process, the rate of anthropogenic extinctions of certain taxa has increased dramatically during the Anthropocene [51,53,54]. Archaeological data can tell us when and where a species lived and potentially how it interacted with humans, allowing us to explore the timing and cause of extinctions. Archaeogenomics helps correlate changes in genetic diversity with cultural and environmental history to potentially identify cause and effect of extinction. Ancient and more recent extinctions have also had profound implications for the structure and function of future ecosystems. The extinction of birds on Pacific islands following the arrival of humans and their commensals has had a dramatic impact on island ecosystems (Box 3). The study of past extinctions presents an opportunity to understand the human activities and behaviors that may have caused the extinction. This will help us better evaluate the activities that need to be changed or minimized to reduce the risk of extinction in the future.

Researchers have long debated the cause of the extinction of the Pleistocene megafauna. Hypotheses range from overhunting to climate change, disease, an asteroid, or a combination thereof [6,55]. As Orlando and Cooper [10] noted, aDNA data have an important role in helping resolve the long-standing debate over megafauna extinction. These data have shown that there is not a general pattern for all megafauna extinctions; rather, there are species-specific responses to a variety of factors (Box 2), including climate change, range contraction, hunting and

encroachment by humans, and introduction of predators [56–58]. Archaeo- and paleogenomic samples and species distribution modeling suggest climate change as the most likely cause of the extinction of musk ox in Eurasia [5], while humans may have been involved in the demographic collapse of bison after 16 000 BP [56] and a combination of causes could have led to the extinction of woolly mammoths [56,59].

Understanding the cause, timing, and impact of these extinctions remains important because rewilding advocates have proposed introducing proxy animals to recover the ecosystem function lost following the extinction of megafauna [60]. Recent advances in cell and molecular biology have given scientists the technological tools to aspire to bring back species that went extinct as a result of recent anthropogenic actions [10]. This process is known as ‘de-extinction’ or ‘species revivalism’. Given short fragments of degraded DNA and missing data, the first challenge to de-extinction is sequencing a complete ancient genome. Additional biological challenges include genome editing and developing the reproductive biology necessary for producing living animals. De-extinction would also require considerable investments in reconstructing the behavior and landscape of the extinct species, preventing disease, and protecting animal welfare. This concept is being explored by conservation biologists, journalists, ethicists, and other scientists [61–63], but it is controversial and poses many challenges, both biological and ethical.

Ancient disease ecology

Emerging infectious diseases pose serious public health concerns and are a considerable threat to biodiversity through changing host–pathogen biology and biogeography [64]. During the past few decades, dramatic human population explosion, rapid global expansion of transportation networks, and accelerating climate fluctuations have acted together to increase the frequency of emerging diseases, but this phenomenon is not restricted to recent human history. A growing body of aDNA research examines ancient disease transmission and evolution. Archaeological and genetic research on ancient human disease has yielded considerable data on not only the impact of diseases such as tuberculosis on human populations [65,66], but also the evolution and movement of the disease agent to the New World, potentially by pinnipeds [67]. Zoonotic bacteria and other infectious bacteria have been detected in ancient human dental calculus microbiomes [68] and could also be studied in faunal calculus samples to examine transmission between humans and wildlife. Past and present disease outbreaks in wildlife and humans, pathogen evolution, and the human role in the emergence and movement of diseases can also be explored with archaeogenomic data.

The influence of disease on wildlife and domestic animals can be tested using archaeological materials. Infectious diseases can have significant impacts on populations, and species of conservation concern may be susceptible to disease outbreaks because small effective population sizes limit adaptability. For example, ancient Tasmanian devils show low major histocompatibility complex (MHC) diversity that might contribute to their susceptibility to a

contagious facial cancer [69]. Archaeological and genomic resources present the opportunity to evaluate whether taxa have been exposed to disease in the past, how they responded, and how they might respond in the future. New methods that utilize sequence capture for detecting particular diseases [70] have provided reliable tools for investigation of ancient disease dynamics. Bos *et al.* applied sequence capture and an archaeogenomic approach to examine the evolution of the zoonotic bacterium *Yersinia pestis*, which is transmitted to humans by fleas carried by rats and causes plague [71]. This strain appears ancestral to modern strains, suggesting that the transmission of the Black Death across Europe contributed to the distribution of all *Y. pestis* strains pathogenic to humans that have been identified on a genomic basis thus far. Depending on DNA preservation and disease biology (e.g., transmission, progression, symptomatology, host specificity, etc.), animal hosts or commensal animals might be additional sources of information on pathogen transmission and evolution.

Museum samples fill important time gaps between archaeological collections and the present when examining long-term patterns, including pathogen evolution and transmission. Museum genomics has confirmed the presence or absence of particular pathogens, allowing us to trace the spread and understand the demographic impacts of disease. Koala (*Phascolarctos cinereus*) museum skins have been used to reconstruct 130 years of rapid evolution in koala retrovirus, which is in the process of invading the koala genome and may be tied to declines in some parts of Australia [72,73]. In humans, archived human medical specimens have been used to reconstruct the genome of the cholera strain responsible for an 1849 Philadelphia outbreak [74]. These studies are valuable because museum collections, their field records, and historical demographic data can test theory and develop methodology that can be applied to older, more-degraded archaeological samples. When utilizing both museum and archaeological collections, care must be taken to ensure that samples are properly identified and labeled [75,76], but ancient DNA from the host, in addition to a pathogen, can be useful in detecting cryptic species and misidentifications.

Reconstruction of ancient environments

Understanding how paleoecosystems functioned during periods of climatic instability or in response to environmental conditions similar to predicted future environments will be useful for making decisions about the future. Historical ecologists, including archaeologists and paleoecologists, have approached environmental reconstruction by integrating faunal abundances with climatic data from geological cores. Our ability to reconstruct paleovegetation was historically limited to identifiable botanicals recovered in archaeological sites, and pollen cores of lakes or ponds, which are geographically confined. Ecological niche modeling of paleoecosystems has filled in some of these gaps, but archaeogenomic approaches have great potential for reconstructing vegetation and ecosystem history.

New developments in metagenomics and environmental DNA (eDNA) technologies have provided the tools to detect

traces of ancient animals and plants from stratified soil samples (i.e., 'dirt DNA') to reconstruct these paleoecosystems [10,20,77–81]. These methods help address questions of population continuity, migration, or ecosystem structure and evolution. Using both archaeological and eDNA data sets, 50 000 years of arctic vegetation history shows that plant communities may have changed dramatically in response to climate change and potentially due to the loss of large herbivores [20]. In another study, ancient eDNA from high-altitude tropical cores reflect the local vegetation, while traditional methods examining pollen may represent a broader geographic region [80]. While there are challenges to an eDNA approach [81], advancements in eDNA technologies have led to positive developments for reconstructing vegetation and landscape histories by facilitating the recovery of highly degraded DNA from archaeological plant remains that are often found fragmented or burnt [82].

Archaeogenomics provides vast potential to investigate reintroduction locations for endangered or threatened taxa with limited ranges. Considerable environmental change between locations within a historic range and the current range can decrease the success of species reintroductions. Environmental DNA sampling of soils and archaeological sites can tell us how different the current environment is from the past and help predict reintroduction success. When integrated with archaeogenomic data on local extinctions and historic ranges, especially if historical ranges are unknown, we can determine the timing and the potential reasons for the disappearance of the species from the landscape. Reconstructing paleoecosystems provides a synthesis of ancient plant and animal interactions, from historic ranges to human-mediated translocations and ancient pathogens, that together can generate a more complete picture of how ecosystems have changed during considerable climatic and anthropogenic variation.

Conservation archaeogenomics and the Anthropocene

We have described how the nascent field of conservation archaeogenomics can complement conservation genomics and paleogenomics to generate data with direct implications for management decisions today and in the future. Genomic analysis of archaeological materials improves our understanding of historic ranges and bottlenecks, and can suggest appropriate source populations for reintroduction of locally extirpated populations.

Inferences derived from archaeogenomic data can also help detect ancient translocations, their impact on ecosystems, and generate baseline information on ecosystem change. Through the study of climate-induced, anthropogenic, recent, and ancient extinctions, we can better understand the risks, causes, and effects of extinctions to change human behavior and mitigate human impacts. Archaeogenomics of disease can identify ancient vectors and hosts, and explore susceptibility to diseases in ancient wildlife and human populations. These investigations allow us to reconstruct ancient ecosystems and evaluate how different past, present, and future ecosystems are from each other as we plan for the conservation, management, and restoration of local and global ecosystems.

The question is where do we go from here? Ongoing and impending changes during the Anthropocene situate archaeologists, paleobiologists, and other researchers to help address the rapidly changing environmental crisis by adding a historical perspective to debates on appropriate baselines, human impacts, and desired future conditions. Archaeogenomics can fill the gaps in our knowledge of historic and prehistoric environments and document ranges of ecological variability. In the past, aDNA studies of archaeological materials suffered from limitations associated with PCR methods and were greatly limited by issues of scale (sample sizes, data recovery, etc.); however, advances in genomic technologies have transformed the types of questions that can now be addressed. These developments have made archaeological samples an invaluable source of information on the changes in spatial and temporal distributions of plants, animals, disease, and ecosystems.

Conservation archaeogenomics provides a useful framework for researchers and managers alike in their efforts to protect and preserve biodiversity as we prepare to face an uncertain future. However, Shafer *et al.* [15] described several challenges in translating genomic data into conservation practice, including an increasing gap between academia and policy-makers due to rapid technological change and differences in funding priorities. These challenges hold true for conservation archaeogenomics and an additional challenge remains in the limited overlap in publication and conference venues between biologists, archaeologists, managers, and decision-makers. Therefore, we advocate close interaction with managers and policy decision-makers from the outset of a conservation archaeogenomics project to ensure the utility of the research, the appropriate interpretation of the biology of the organism and of the genomic data, and the development of feasible action steps. We are optimistic that archaeogenomics will contribute to future management and conservation decisions that can lead to positive policy changes as we face the increasing challenges of the Anthropocene.

Acknowledgments

We would like to thank the CCEG writing group for their helpful comments that improved the quality of this manuscript, Melissa T.R. Hawkins for help with figure artwork, Pieter Folkens for permission to use the pinniped illustrations in Figure 1, and the participants of the 2013 TedX: DeExtinction conference at the National Geographic Museum for their discussion of extinction and de-extinction. We also acknowledge Todd Braje, Christina Boser, Paul Collins, Tim Coonan, Jon Erlandson, Kate Faulkner, Chris Funk, Julie King, Klaus-Peter Koepfli, Scott Morrison, Seth Newsome, Kathy Ralls, and Scott Sillett for thoughtful discussions about island conservation and management. This manuscript also benefited greatly from comments from three anonymous reviewers.

References

- Grayson, D.K. (2001) The archaeological record of human impacts on animal populations. *J. World Prehistory* 15, 1–68
- Redman, C.L. (2004) *The Archaeology of Global Change: The Impact of Humans on their Environment*, Smithsonian Books
- Wolverton, S. and Lyman, R.L. (2012) *Conservation Biology and Applied Zooarchaeology*, University of Arizona Press
- Erlandson, J.M. and Rick, T.C. (2010) Archaeology meets marine ecology: the antiquity of maritime cultures and human impacts on marine fisheries and ecosystems. *Annu. Rev. Mar. Sci.* 2, 231–251

- 5 Rick, T.C. and Lockwood, R. (2013) Integrating paleobiology, archeology, and history to inform biological conservation. *Conserv. Biol.* 27, 45–54
- 6 Braje, T.J. and Erlandson, J.M. (2013) Human acceleration of animal and plant extinctions: a late Pleistocene, Holocene, and Anthropocene continuum. *Anthropocene* 4, 14–23
- 7 Crutzen, P.J. and Stoermer, E.F. (2000) The ‘Anthropocene’. *Global Change Newsl.* 41, 17–18
- 8 Smith, B.D. and Zeder, M.A. (2013) The onset of the Anthropocene. *Anthropocene* 4, 8–13
- 9 Corlett, R.T. (2015) The Anthropocene concept in ecology and conservation. *Trends Ecol. Evol.* 30, 36–41
- 10 Orlando, L. and Cooper, A. (2014) Using ancient DNA to understand evolutionary and ecological processes. *Annu. Rev. Ecol. Syst.* 45, 573–598
- 11 De Bruyn, M. *et al.* (2011) Faunal histories from Holocene ancient DNA. *Trends Ecol. Evol.* 26, 405–413
- 12 Shapiro, B. and Hofreiter, M. (2014) A paleogenomic perspective on evolution and gene function: new insights from ancient DNA. *Science* 343, 1236573
- 13 Leonard, J.A. (2008) Ancient DNA applications for wildlife conservation. *Mol. Ecol.* 17, 4186–4196
- 14 Funk, W.C. *et al.* (2012) Harnessing genomics for delineating conservation units. *Trends Ecol. Evol.* 27, 489–496
- 15 Shafer, A.B.A. *et al.* (2015) Genomics and the challenging translation into conservation practice. *Trends Ecol. Evol.* 30, 78–87
- 16 Poinar, H.N. *et al.* (2006) Metagenomics to paleogenomics: large-scale sequencing of mammoth DNA. *Science* 311, 392–394
- 17 Orlando, L. *et al.* (2013) Recalibrating *Equus* evolution using the genome sequence of an early Middle Pleistocene horse. *Nature* 499, 74–78
- 18 Allaby, R.G. *et al.* (2015) Using archaeogenomic and computational approaches to unravel the history of local adaptation in crops. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 370, 20130377
- 19 Parks, M. *et al.* (2015) Ancient population genomics and the study of evolution. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 370, 20130381
- 20 Willerslev, E. *et al.* (2014) Fifty thousand years of Arctic vegetation and megafaunal diet. *Nature* 506, 47–51
- 21 Jurka, J. (1994) Paleogenomics: investigation of an ancient family of repetitive sequences present in great numbers in human genome. *Am. J. Hum. Genet.* 55 (Suppl. 3), 44
- 22 Birnbaum, D. *et al.* (2000) ‘Paleogenomics’: looking in the past to the future. *J. Exp. Zool.* 288, 21–22
- 23 McGill, B.J. *et al.* (2015) Fifteen forms of biodiversity trend in the Anthropocene. *Trends Ecol. Evol.* 30, 104–113
- 24 National Audubon Society (2014) *Audubon’s Birds and Climate Change Report: A Primer for Practitioners*, National Audubon Society
- 25 Braje, T.J. and Rick, T.C. (2011) *Human Impacts on Seals, Sea Lions, and Sea Otters: Integrating Archaeology and Ecology in the Northeast Pacific*, University of California Press
- 26 Beadell, J. *et al.* (2009) The role of ancient DNA in conservation biology. In *Population Genetics for Animal Conservation* (Bertorelle, G. *et al.*, eds), pp. 198–220, University of Cambridge Press
- 27 Larson, S. *et al.* (2012) Genetic diversity and population parameters of sea otters, *Enhydra lutris*, before fur trade extirpation from 1741–1911. *PLoS ONE* 7, e32205
- 28 Valentine, K. *et al.* (2007) Ancient DNA reveals genotypic relationships among Oregon populations of the sea otter (*Enhydra lutris*). *Conserv. Genet.* 9, 933–938
- 29 Krause, J. *et al.* (2010) The complete mitochondrial DNA genome of an unknown hominin from southern Siberia. *Nature* 464, 894–897
- 30 Lazaridis, I. *et al.* (2014) Ancient human genomes suggest three ancestral populations for present-day Europeans. *Nature* 513, 409–413
- 31 Rawlence, N.J. *et al.* (2015) Radiocarbon-dating and ancient DNA reveal rapid replacement of extinct prehistoric penguins. *Quat. Sci. Rev.* 112, 59–65
- 32 Mourier, T. *et al.* (2012) Statistical guidelines for detecting past population shifts using ancient DNA. *Mol. Biol. Evol.* 29, 2241–2251
- 33 Speller, C.F. *et al.* (2012) High potential for using DNA from ancient herring bones to inform modern fisheries management and conservation. *PLoS ONE* 7, e51122
- 34 Lejju, B.J. *et al.* (2006) Africa’s earliest bananas? *J. Archaeol. Sci.* 33, 102–113
- 35 Freedman, A.H. *et al.* (2014) Genome sequencing highlights the dynamic early history of dogs. *PLoS Genet.* 10, e1004016
- 36 Thalman, O. *et al.* (2013) Complete mitochondrial genomes of ancient canids suggest a European origin of domestic dogs. *Science* 342, 871–874
- 37 Anderson, A. (2008) The rat and the octopus: initial human colonization and the prehistoric introduction of domestic animals to remote Oceania. *Biol. Invasions* 11, 1503–1519
- 38 Larson, G. *et al.* (2007) Phylogeny and ancient DNA of *Sus* provides insights into neolithic expansion in island Southeast Asia and Oceania. *Proc. Natl. Acad. Sci. U.S.A.* 104, 4834–4839
- 39 Matisoo-Smith, E. (2009) Commensal model for human settlement of the Pacific 10 years on: what can we say and where to now? *J. Isl. Coast. Archaeol.* 4, 151–163
- 40 Storey, A.A. *et al.* (2010) Mitochondrial DNA from 3000-year old chickens at the Teouma site, Vanuatu. *J. Archaeol. Sci.* 37, 2459–2468
- 41 Heinsohn, T. (2003) Animal translocation: long-term human influences on the vertebrate zoogeography of Australasia (natural dispersal versus ethnophoresy). *Aust. Zool.* 32, 51–76
- 42 Flannery, T.F. and White, J.P. (1991) Animal translocations. *Natl. Geogr. Res. Explor.* 7, 96–113
- 43 White, J.P. (2004) Where the wild things are: prehistoric animal translocation in the circum New Guinea archipelago. In *Voyages of Discovery: The Archaeology of Islands* (Fitzpatrick, S.M., ed.), Greenwood Publishing Group
- 44 González-Porter, G.P. *et al.* (2011) Patterns of genetic diversity in the critically endangered Central American river turtle: human influence since the Mayan age? *Conserv. Genet.* 12, 1229–1242
- 45 Storey, A.A. *et al.* (2013) DNA and Pacific commensal models: applications, construction, limitations, and future prospects. *J. Isl. Coast. Archaeol.* 8, 37–65
- 46 Matisoo-Smith, E. *et al.* (1998) Patterns of prehistoric human mobility in Polynesia indicated by mtDNA from the Pacific rat. *Proc. Natl. Acad. Sci. U.S.A.* 95, 15145–15150
- 47 Matisoo-Smith, E. and Allen, J.S. (2001) Name that rat: molecular and morphological identification of Pacific rodent remains. *Int. J. Osteoarchaeol.* 11, 34–42
- 48 Jones, E.P. *et al.* (2012) Fellow travellers: a concordance of colonization patterns between mice and men in the North Atlantic region. *BMC Evol. Biol.* 12, 35
- 49 Jones, E.P. *et al.* (2013) Genetic tracking of mice and other bioproxies to infer human history. *Trends Genet.* 29, 298–308
- 50 Macdonald, D.W. *et al.* (2006) Introduced species and the line between biodiversity conservation and naturalistic eugenics. In *Key Topics in Conservation Biology* (Macdonald, D.W. and Service, K., eds), pp. 187–206, Wiley
- 51 Barnosky, A.D. *et al.* (2011) Has the Earth’s sixth mass extinction already arrived? *Nature* 471, 51–57
- 52 Wake, D.B. and Vredenburg, V.T. (2008) Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proc. Natl. Acad. Sci. U.S.A.* 105, 11466–11473
- 53 Harnik, P.G. *et al.* (2012) Extinctions in ancient and modern seas. *Trends Ecol. Evol.* 27, 608–617
- 54 Urban, M.C. (2015) Accelerating extinction risk from climate change. *Science* 348, 571–573
- 55 Stuart, A.J. (2015) Late Quaternary megafaunal extinctions on the continents: a short review. *Geol. J.* 50, 338–363
- 56 Lorenzen, E.D. *et al.* (2011) Species-specific responses of Late Quaternary megafauna to climate and humans. *Nature* 479, 359–364
- 57 Campos, P.F. *et al.* (2010) Ancient DNA analyses exclude humans as the driving force behind late Pleistocene musk ox (*Ovibos moschatus*) population dynamics. *Proc. Natl. Acad. Sci. U.S.A.* 107, 5675–5680
- 58 Campos, P.F. *et al.* (2010) Ancient DNA sequences point to a large loss of mitochondrial genetic diversity in the saiga antelope (*Saiga tatarica*) since the Pleistocene. *Mol. Ecol.* 19, 4863–4875
- 59 MacDonald, G.M. *et al.* (2012) Pattern of extinction of the woolly mammoth in Beringia. *Nat. Commun.* 3, 893
- 60 Donlan, J.C. *et al.* (2006) Pleistocene rewilding: an optimistic agenda for twenty-first century conservation. *Am. Nat.* 168, 660–681
- 61 Jørgensen, D. (2013) Reintroduction and de-extinction. *Bioscience* 63, 719–720

- 62 Sherkow, J.S. and Greely, H.T. (2013) What if extinction is not forever? *Science* 340, 32–33
- 63 Zimmer, C. (2013) Bringing extinct species back to life. *Nat. Geogr. Soc.* 223, 28–43
- 64 Daszak, P. *et al.* (2000) Emerging infectious diseases of wildlife: threats to biodiversity and human health. *Science* 287, 443–449
- 65 Wilbur, A.K. *et al.* (2009) Deficiencies and challenges in the study of ancient tuberculosis DNA. *J. Archaeol. Sci.* 36, 1990–1997
- 66 Harkins, K.M. *et al.* (2015) Screening ancient tuberculosis with qPCR: challenges and opportunities. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 370, 20130622
- 67 Bos, K.I. *et al.* (2014) Pre-Columbian mycobacterial genomes reveal seals as a source of New World human tuberculosis. *Nature* 514, 494–497
- 68 Warinner, C. *et al.* (2014) Pathogens and host immunity in the ancient human oral cavity. *Nat. Genet.* 46, 336–344
- 69 Morris, K. *et al.* (2013) Low major histocompatibility complex diversity in the Tasmanian devil predates European settlement and may explain susceptibility to disease epidemics. *Biol. Lett.* 9, 20120900
- 70 Bos, K.I. *et al.* (2015) Parallel detection of ancient pathogens via array-based DNA capture. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 370, 20130375
- 71 Bos, K.I. *et al.* (2011) A draft genome of *Yersinia pestis* from victims of the Black Death. *Nature* 478, 506–510
- 72 Tsangaras, K. *et al.* (2014) Hybridization capture reveals evolution and conservation across the entire Koala retrovirus genome. *PLoS ONE* 9, e95633
- 73 Ávila-Arcos, M.C. *et al.* (2013) One hundred twenty years of koala retrovirus evolution determined from museum skins. *Mol. Biol. Evol.* 30, 299–304
- 74 Devault, A.M. *et al.* (2014) Second-pandemic strain of *Vibrio cholerae* from the Philadelphia cholera outbreak of 1849. *N. Engl. J. Med.* 370, 334–340
- 75 Boessenkool, S. *et al.* (2010) Lost in translation or deliberate falsification? Genetic analyses reveal erroneous museum data for historic penguin specimens. *Proc. Biol. Sci.* 277, 1057–1064
- 76 Rawlence, N.J. *et al.* (2014) Morphological and ancient DNA analyses reveal inaccurate labels on two of Buller's bird specimens. *J. R. Soc. N. Z.* 44, 163–169
- 77 Andersen, K. *et al.* (2012) Meta-barcoding of 'dirt' DNA from soil reflects vertebrate biodiversity. *Mol. Ecol.* 21, 1966–1979
- 78 Hebsgaard, M.B. *et al.* (2009) The farm beneath the sand: an archaeological case study on ancient 'dirt' DNA. *Antiquity* 83, 430–444
- 79 Giguet-Covex, C. *et al.* (2014) Long livestock farming history and human landscape shaping revealed by lake sediment DNA. *Nat. Commun.* 5, 3211
- 80 Boessenkool, S. *et al.* (2014) Use of ancient sedimentary DNA as a novel conservation tool for high-altitude tropical biodiversity. *Conserv. Biol.* 28, 446–455
- 81 Rawlence, N.J. *et al.* (2014) Using palaeoenvironmental DNA to reconstruct past environments: progress and prospects. *J. Quat. Sci.* 29, 610–626
- 82 Brown, T.A. *et al.* (2015) Recent advances in ancient DNA research and their implications for archaeobotany. *Veg. Hist. Archaeobotany* 24, 207–214
- 83 Rizzi, E. *et al.* (2012) Ancient DNA studies: new perspectives on old samples. *Genet. Sel. Evol.* 44, 21
- 84 Ho, S.Y.W. and Gilbert, M.T.P. (2010) Ancient mitogenomics. *Mitochondrion* 10, 1–11
- 85 Ramakrishnan, U. and Hadly, E.A. (2009) Using phylochronology to reveal cryptic population histories: review and synthesis of 29 ancient DNA studies. *Mol. Ecol.* 18, 1310–1330
- 86 Stoneking, M. and Krause, J. (2011) Learning about human population history from ancient and modern genomes. *Nat. Rev. Genet.* 12, 603–614
- 87 Hoelzel, A.R. *et al.* (2002) Impact of a population bottleneck on symmetry and genetic diversity in the northern elephant seal. *J. Evol. Biol.* 15, 567–575
- 88 Pauly, D. (1995) Anecdotes and the shifting baseline syndrome of fisheries. *Trends Ecol. Evol.* 10, 430
- 89 Weber, D. *et al.* (2000) An empirical genetic assessment of the severity of the northern elephant seal population bottleneck. *Curr. Biol.* 10, 1287–1290
- 90 Weber, D.S. *et al.* (2004) Genetic consequences of a severe population bottleneck in the Guadalupe fur seal (*Arctocephalus townsendi*). *J. Hered.* 95, 144–153
- 91 Szabo, J.K. *et al.* (2012) Global patterns and drivers of avian extinctions at the species and subspecies level. *PLoS ONE* 7, e47080
- 92 Steadman, D.W. (2006) *Extinction and Biogeography of Tropical Pacific Birds*, University of Chicago Press
- 93 Olson, S.L. and James, H.F. (1982) Fossil birds from the Hawaiian Islands: evidence for wholesale extinction by man before western contact. *Science* 217, 633–635
- 94 Steadman, D.W. (1995) Prehistoric extinctions of Pacific island birds: biodiversity meets zooarchaeology. *Science* 267, 1123–1131
- 95 Paxinos, E.E. *et al.* (2002) Prehistoric decline of genetic diversity in the nee. *Science* 296, 1827
- 96 Paxinos, E.E. *et al.* (2002) mtDNA from fossils reveals a radiation of Hawaiian geese recently derived from the Canada goose (*Branta canadensis*). *Proc. Natl. Acad. Sci. U.S.A.* 99, 1399–1404
- 97 Welch, A.J. *et al.* (2012) Ancient DNA reveals genetic stability despite demographic decline: three thousand years of population history in the endemic Hawaiian petrel. *Mol. Biol. Evol.* 29, 3729–3740
- 98 Wiley, A.E. *et al.* (2013) Millennial-scale isotope records from a wide-ranging predator show evidence of recent human impact to oceanic food webs. *Proc. Natl. Acad. Sci. U.S.A.* 110, 8972–8977
- 99 Fleischer, R.C. *et al.* (2007) Genetic variability and taxonomic status of the Nihoa and Laysan millerbirds. *Condor* 109, 954–962
- 100 Cooper, A. *et al.* (1996) Ancient DNA and island endemics. *Nature* 381, 484
- 101 Willis, K.J. and Birks, H.J.B. (2006) What is natural? The need for a long-term perspective in biodiversity conservation. *Science* 314, 1261–1265