



CONSERVATION PALEOBIOLOGY

Opportunities for the Earth Sciences



ON THE COVER

Top: Modern oyster bed in Hewlett's Creek, Wilmington, North Carolina; image by Gregory Dietl.

Bottom: Pleistocene oyster shell layer, Intracoastal Waterway, North Myrtle Beach, South Carolina; image by Stephen Durham.

Conservation Paleobiology

Opportunities for the Earth Sciences

Report of an NSF-Funded Workshop
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Modern death assemblage, Sea of Galilee, by Chmee2

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EXECUTIVE SUMMARY

Humans are now a major force in altering the Earth and its biota—we live in the Anthropocene. Current challenges include finding ways to mitigate human impacts on biodiversity, and developing means to sustain and restore the ecosystem services on which we depend. The past two million years provide valuable perspectives on natural environmental variability of modern systems as well as interactions between humans and ecosystems; fossil records of all ages provide insights into how species and ecosystems respond to environmental change. Paleobiological data and analyses thus open the door for a broad-based science of biological vulnerability and resilience that speaks directly to societal concerns about, for instance, altered biogeochemical cycles, design of biological reserves, effects of biological change on ecosystem services, and consequences of biological invasions and extinctions. Such insights are vital to managing for the future.

Conservation Paleobiology, the application of geohistorical records to the conservation and restoration of biodiversity and ecosystem services, can lead this effort. This emerging discipline uses geohistorical data to develop and test models of how biotas respond to climate and other natural and anthropogenic environmental change. Basic research and applications that emerge from *Conservation Paleobiology* will benefit society by evaluating environmental impacts of the recent past and providing guidelines for mitigation and restoration. *Conservation Paleobiology* also has the potential to leverage funding from private foundations and deliver new approaches to government agencies, non-governmental organizations, and commercial organizations involved with environmental management.

We seek NSF's help to:

- Develop the basic theory, research tools, and infrastructure of *Conservation Paleobiology*. We need to expand our understanding of the fossilization process, improve analyses of past genetic diversity, develop new proxies for environmental and biotic conditions, improve methods of correlation and strengthen capabilities for high-precision age calibration of data, and promote collection, curation, and data management for natural archives of past environmental and biotic change.
- Train a new generation of conservation paleobiologists through cross-disciplinary workshops, internships, postdoctoral fellowships, and scientist-in-residence programs. Few scientific fields are as attractive to students as the environmental sciences and few fields other than *Conservation Paleobiology* require the breadth and depth of individual training necessary to address national needs. Cross-disciplinary training will break down the boundaries between the traditional fields of geology and biology.
- Foster research approaches and partnerships that can deliver results relevant to conservation by improving communication and collaboration between scientists and resource managers to identify basic research needs. We seek to develop the best science to address a pressing national need.

We seek a funding allocation for a decade-long initiative to (1) support basic geohistorical research and training aimed at conservation of biodiversity and ecosystem services, and (2) promote innovative partnerships that will cut across disciplinary boundaries and leverage funding with other agencies and organizations.



1. INTRODUCTION

“An integrated and interdisciplinary approach in the geosciences will lead to new paradigms for human interactions with the Earth and guide us to solution-oriented applications.” (Geo Vision, 2009)

Humans are now a major force in altering the Earth and its biota—we live in the Anthropocene. Future scientific challenges include finding ways to ameliorate human impacts on biodiversity, and ways to sustain and restore the ecosystem services on which we depend. The past two million years provide valuable insights into human-ecosystem interactions and fossil records of all ages reveal how species and ecosystems respond to environmental change. Fundamental paleontological findings can thus speak directly to societal concerns regarding topics such as altered biogeochemical cycles, design of biological reserves, effects of biological changes on ecosystem services, and consequences of biological invasions and differential extinction. Such insights are vital to planning for the future.

The National Science Foundation’s (NSF’s) Geosciences Directorate can play a critical role in developing the theory, methods, and human capital to use the past to manage for the future. *Conservation Paleobiology*—the application of geohistorical records to the conservation and restoration of biodiversity and ecosystem services—can lead this effort. It can also deliver useful information to government agencies, non-governmental organizations (NGOs), and commercial enterprises involved with protecting or restoring environments for the future. Basic research in *Conservation Paleobiology* benefits society by evaluating environmental impacts of the recent past and developing theories about biotic responses to environmental change using the entire geologic record, which serves as an archive of “natural experiments.”

At present, NSF provides *ad hoc* support for *Conservation Paleobiology*. Proposals submitted to existing programs must not appear too applied. Principal investigators face the additional challenge of having to describe geological techniques to biologists in such a way that they do not appear too simplistic to geologists, and *vice versa*. Critical tool development, such as research on biomarkers and their intercalibration, or on the taphonomic underpinnings of paleontologic data, can appear too geological or method-focused to biologists, whereas the ultimate proposal objectives of understanding biological vulnerability and resilience can seem too biological for geologists.

Integrating research across disciplines that span NSF directorates is thus a challenge. Opportunities exist for collaborative research on some large efforts, often in response to special initiatives. For example, *Conservation Paleobiology* has been a component of awards from cross-cutting programs such as Research Coordination Networks (RCN), Dynamics of Coupled Natural and Human Systems (CNH), and MacroSystems Biology, and it should be possible to incorporate it into such initiatives as Frontiers in Earth System Dynamics (FESD) and Science, Engineering and Education for Sustainability (SEES). Inclusion of a *Conservation Paleobiology* component, however, rarely provides educational opportunities or includes development of new techniques. Although such efforts as Long-Term Ecological Research (LTER) Network and National Ecological Observatory Network (NEON) generate valuable information on environmental and biotic variability, the time scales addressed are relatively short (decades), and data typically come from particular experimental sites not chosen with paleontological analysis in mind. Furthermore, the start date for such projects (20 years ago, or now) is late with respect to unfolding anthropogenic effects.

*“NSF is the agency
best equipped to
develop the emerging
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Paleobiology.”*

NSF is the agency best equipped to develop the emerging field of *Conservation Paleobiology*. Whereas the Environmental Protection Agency (EPA) supports graduate students (EPA-STAR) and undergraduates (EPA-GRO), its programs are largely driven by regulatory needs and rarely support basic research. The National Aeronautics and Space Administration’s (NASA’s) Graduate Fellowships in Earth Systems Science discourage participation by students working in Earth system history. And although the National Oceanic and

Atmospheric Administration’s (NOAA’s) support of paleoclimate research has yielded enormous benefits to climate science, and its National Estuarine Research Reserve (NERR) fellowships support graduate training, the agency’s disciplinary and geographic foci limit its role in *Conservation Paleobiology*.

We propose that the NSF portfolio expand to:

- develop the basic research tools and infrastructure of *Conservation Paleobiology*;
 - train a new generation of cross-disciplinary conservation paleobiologists; and
 - establish programs that foster delivery and implementation of basic science to benefit government agencies, NGOs, and commercial enterprises.
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The Geosciences Directorate supports basic research and education. Support for translation of research results into applications has been largely limited to partnerships with industry (e.g., Grant Opportunities for Academic Liaison with Industry; GOALI) rather than with government agencies, NGOs, or environmental consulting firms. Clearly, nonindustrial applications that emerge from *Conservation Paleobiology* can benefit society by assessing past environmental impacts and providing guidelines for management and restoration. *Conservation Paleobiology* holds special promise for leveraging private funding and delivering new approaches for protecting and restoring habitats.

We call on NSF to help develop the emerging discipline of *Conservation Paleobiology* from a community now scattered across diverse academic departments. The Geosciences Directorate's Earth System History (ESH) program is an excellent example of how a discipline was developed successfully. Focused funding over 15 years nurtured paleoclimatology, transforming it from a traditional discipline-based Earth science into a lively interdisciplinary culture. Teams now routinely cross boundaries and use models, data, statistical analyses, and site-specific studies in broad regional or global contexts to infer past environments and climate dynamics. A similar effort could enable *Conservation Paleobiology* to address an array of basic science questions motivated by societal issues.

NSF support for *Conservation Paleobiology* will promote development of the basic science needed to address emerging environmental issues, strengthen instrumental capabilities, provide opportunities for interdisciplinary training of students, and enable engagement with a broad community of

stakeholders. Few disciplines can promise such rapid translation of basic scientific research into knowledge and approaches that directly address environmental problems. Moreover, few scientific fields are as attractive to students as the environmental sciences. Furthermore, few fields other than *Conservation Paleobiology* require the breadth and depth of training necessary to effectively address national needs. Cross-disciplinary training will break down the traditional boundaries between geology and biology. Engagement with practitioners in government agencies, NGOs, and commercial firms will guarantee that basic science is used to address environmental problems and will ensure abundant career opportunities for students.

This report is the product of the NSF-funded workshop on "*Conservation Paleobiology in the Coming Decades*" convened at the Paleontological Research Institution in Ithaca, New York, June 3-5, 2011. Eighteen scientists with diverse backgrounds in the geological and biological sciences attended (see Workshop Participant List). It also reflects discussions at a series of earlier workshops, most notably those resulting in the 2005 NRC Report "*The Geological Record of Ecological Dynamics*," and complements the NSF reports: "*DETELON: Science Plan*" (2011) and "*TRANSITIONS: The Changing Earth-Life System—Critical Information for Society from the Deep Past*" (2012).



2. MAJOR SCIENCE THEMES IN CONSERVATION PALEOBIOLOGY

Conservation Paleobiology has emerged over the last decade as a powerful tool, using geohistorical records to acquire long-term perspectives on species, communities and ecosystems, beyond the limited timeframe of direct human observation (Flessa, 2002; Kowalewski, 2004; NRC, 2005; Willis & Birks, 2006; Dietl & Flessa, 2009, 2011). The overarching goal of *Conservation Paleobiology* research is to provide principles and tools for conserving biodiversity and ecosystem services. Basic research in *Conservation Paleobiology* generally takes one of two approaches.

The “near-time” approach uses the Recent fossil record to provide a context for present-day conditions, focusing largely on extant species. Geohistorical records, at nested time scales within the last two million years, are used to compare conditions “before” and “after” disturbance or to develop a narrative of biotic variability. For instance, fish scales from marine sediment cores record population variation over the last 1,700 years, establishing that two key commercial species are strongly cyclic,

but out of phase (Baumgartner *et al.*, 1992): 20th century crashes in one and concomitant rises in the other, observed under conditions of commercial fishing, are thus likely entirely natural, tracking climate oscillations or regime changes such as the Pacific Decadal Oscillation, which is a long-lived, El Niño-like pattern of Pacific climate variability. In this case, the fossil record exonerates human activity as the primary driver of recent changes in species abundances (see also lake records of mixed climate and fishing impacts on salmon abundance; Finney *et al.*, 2000, 2002).

The “deep-time” approach uses the longer geologic record as an archive of repeated “natural experiments.” It can be utilized to investigate biological responses to system perturbations of diverse kinds and magnitudes, some of which are similar to present-day disturbances or to those expected to occur in the near future, such as continued climate warming, accelerated introduction of invasive species, and decline in cultural eutrophication. This approach permits the testing of ecological theory concerning biological responses to ecosystem perturbations under an array



Quarry in upstate New York exposing Middle Devonian limestones

of conditions broader than are available in the modern world. Repeated responses can provide insights sufficiently general to apply to novel anthropogenic stresses and can provide a foundation for general theories of biotic response to stress. For instance, the common pattern evident in the fossil record of asymmetry in large-scale biotic interchanges—the spread of many species from one geographic area to another—could help identify the likely direction of interoceanic invasion as Earth’s climate warms over the next century (Vermeij & Roopnarine, 2008), providing predictive power relevant to systematic conservation planning.

Uniting both approaches is the motivation to understand biological vulnerability and resilience to major environmental stressors (Fig. 1). The most important direct drivers of current biodiversity loss and change in ecosystem services are (MEA, 2005): habitat change, climate change, exploitation (loss) of wild species, biological invasions, and biogeochemical disturbance. *Conservation Paleobiology* studies can address the responses of biota to these stressors on time scales that are appropriate to the biological and

environmental phenomena of concern (e.g., the long life spans of forest or reef-forming species, and the processes of ecological succession, community assembly, and establishment of diversity gradients), which are commonly beyond the reach of direct observation by biologists.

HABITAT CHANGE

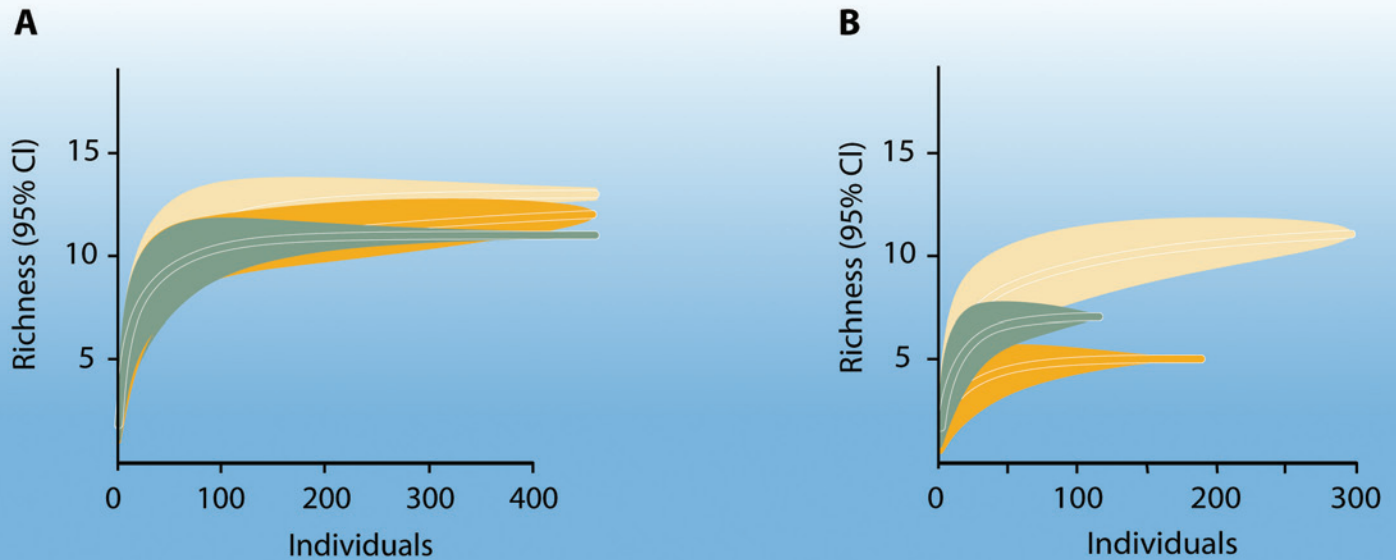
Anthropogenic alteration, conversion, and fragmentation of terrestrial habitats began with early land clearance for agriculture and mining, accelerated through antiquity, and surged with the Industrial Revolution. More than 50% of the land area in four of the world’s 14 large biomes was converted to human use (agriculture, urban) in the 20th century (MEA, 2005). In coastal and open seas, “dead zones” have spread rapidly since the 1960s and are now reported from 400 systems (Diaz & Rosenberg, 2008). By the last decade, if the effects of fishing and by-catch are included, every square kilometer of ocean was affected by an anthropogenic driver of ecological change, and 41% was affected by multiple drivers, with continental shelf and slope areas incurring both land- and ocean-source stresses (Halpern *et al.*, 2008). Predicting biotic responses to these habitat alterations using only direct observations has proven difficult, with especially large uncertainties attached to the time and extent of biodiversity losses owing to habitat transformation.

The fossil record provides innumerable examples of biotic responses to habitat change. For example, using the Quaternary fossil record from islands in the Gulf of California, Wilcox (1978) found that lizard species richness was determined largely by the duration of island isolation rather than island area. Islands became isolated as sea level rose in response to warming climate, but lizard species richness did not decline to theoretically expected values for at least 10,000 years (and see similar estimates of such “extinction debt” among alpine small mammals, and century- to millennial-scale lags detected or inferred in systems ranging from birds to conifer forests; Ewers & Didham, 2006). Readily cored sedimentary records of lakes, estuaries, and

Fig. 1. Direct drivers of biodiversity loss and change in ecosystem services. Arrows indicate that any given system (single species, community, or ecosystem) can experience multiple stresses or stress releases simultaneously or in succession. See Photo Credits at the end of this report for image sources.



Fig. 2. Species richness of small mammal communities from two Great Basin cave localities with differing magnitudes of anthropogenic influence. (A) Rarefaction analyses of data from an undisturbed locality indicate that modern live (orange), and decadal (green) and centennial (yellow) scale time-averaged death assemblages of skeletal remains concentrated by raptor predators are similar to one another in terms of species richness. (B) In contrast, at a locality characterized by significant anthropogenic impact over the last century, modern live and decadal scale time-averaged death assemblage samples were species poor relative to samples of the centennial scale time-averaged death assemblage. Modified from Terry (2010); reprinted with permission from The Royal Society.



caves are also rich archives of the ecological impacts of habitat change, not just on shifts in species richness, but also on the fates of individual species, community structure, and ecosystem services. For instance, raptor-concentrated assemblages of small mammal bones from two taphonomically similar cave localities in the Great Basin of the western U.S. document biotic response to diverging anthropogenic land-use practices. Over the last century, structure of the small mammal community, in terms of species abundance and evenness, remained relatively unchanged at an undisturbed site in Nevada, but was rapidly restructured at a recently disturbed locality in Utah, which has served as a military test and training range since the mid-1960s (Fig. 2; Terry, 2010). Studies summarized by Calderon-Aguilera & Flessa (2009) also document the response of the Colorado River's estuarine ecosystem in the Gulf of California to habitat change driven by upstream dams and the diversion of water to cities and farms in the U.S. and Mexico. Biotic responses ranged from individual-level (*e.g.*, reduced growth rate of a once commercially important but now endangered fish species) to ecosystem-level changes in the estuary's food web.

Records of biotic responses to past habitat changes are thus a valuable resource to help constrain predictions and yield general insights into species and ecosystem behavior, providing long-term perspectives when ecological theory is insufficient, direct observations are unavailable, or experimentation is difficult or unethical.

CLIMATE CHANGE

Climate change is altering modern biodiversity and is a concern for conservation. Direct observations show that climate-induced

range shifts, changes in population sizes, the timing of reproduction or migration events, and increases in frequency of disease outbreaks, are underway for many species (Walther *et al.*, 2002; MEA, 2005; Parmesan, 2006; Chen *et al.*, 2011). Greenhouse gas accumulation has initiated climate change (Solomon *et al.*, 2009) and projections of future climate changes indicate major geographic displacements and population shifts for most species within the 21st century (IPCC, 2007). Biotic responses to recent and future climate changes have been studied largely using observational data that span the limited range of climate variability over the past few decades, and with limited empirical and theoretical models that are difficult to validate.

Geohistorical records can provide unique information on the biological consequences of climate changes of different types, rates, magnitudes, and durations (Willis *et al.*, 2010). Independent lines of evidence for these climate changes (*e.g.*, geochemical, sedimentological, paleobiological) are increasingly being linked with records of biological responses, in other words, changes in fossil assemblages and in morphology, anatomy, and organic and isotope geochemistry of fossil remains. Such records expand our understanding of Earth's climate changes and their consequences for life.

Radiocarbon-dated records of pollen, charcoal, and macrofossils (*e.g.*, plants, insects, mollusks, corals, and vertebrates) indicate a range of biotic responses to climate changes over the past 10,000 years, both fast and slow. In many cases, species have maintained local populations despite major climate changes, whereas other species have shifted along local elevational, topographic, and microhabitat gradients (Fig. 3; see also Dawson *et al.*, 2011). Some species ranges have shifted at regional to subcontinental scales,

with range displacement from early to late Holocene spanning 10^1 – 10^3 km. Populations expanded and contracted and biotic communities assembled and disassembled.

The geohistorical record that extends to the limits of ^{14}C dating, *i.e.* the last 50,000 years, reveals biotic responses of the deglacial, which commenced *ca.* 20,000 years ago and included episodes of gradual and rapid warming and cooling (*e.g.*, the Younger Dryas). This period was characterized by plant and animal communities different from any that exist today (“no-analog” assemblages; Jackson & Williams, 2004) and widespread megafaunal extinctions (Barnosky *et al.*, 2004). Ecological dynamics of the deglacial are important for conservation because the period includes abrupt climate changes, complex trophic interactions, and “no-analog” climates and ecosystems, all of which are likely to occur again and pose conservation challenges in the coming decades.

Although geohistorical records extending back more than 50,000 years cannot be dated by ^{14}C , they are characterized by a broad range of climate scenarios, some of which can be temporally correlated using event-horizons such as regional volcanic-ash layers, or global isotopic signatures (*e.g.*, the Paleocene-Eocene Thermal Maximum). The range of rates and magnitudes of climate change, during greenhouse and icehouse conditions, provide “natural experiments” for which biotic responses can be inferred.

The geological record thus contains a wealth of information on how ecological systems have responded to a wide array of climate changes in the past. Paleoecological study has revealed biotic responses to past climate changes that could not have been predicted solely from modern ecological data and theory.

EXPLOITATION (LOSS) OF WILD SPECIES

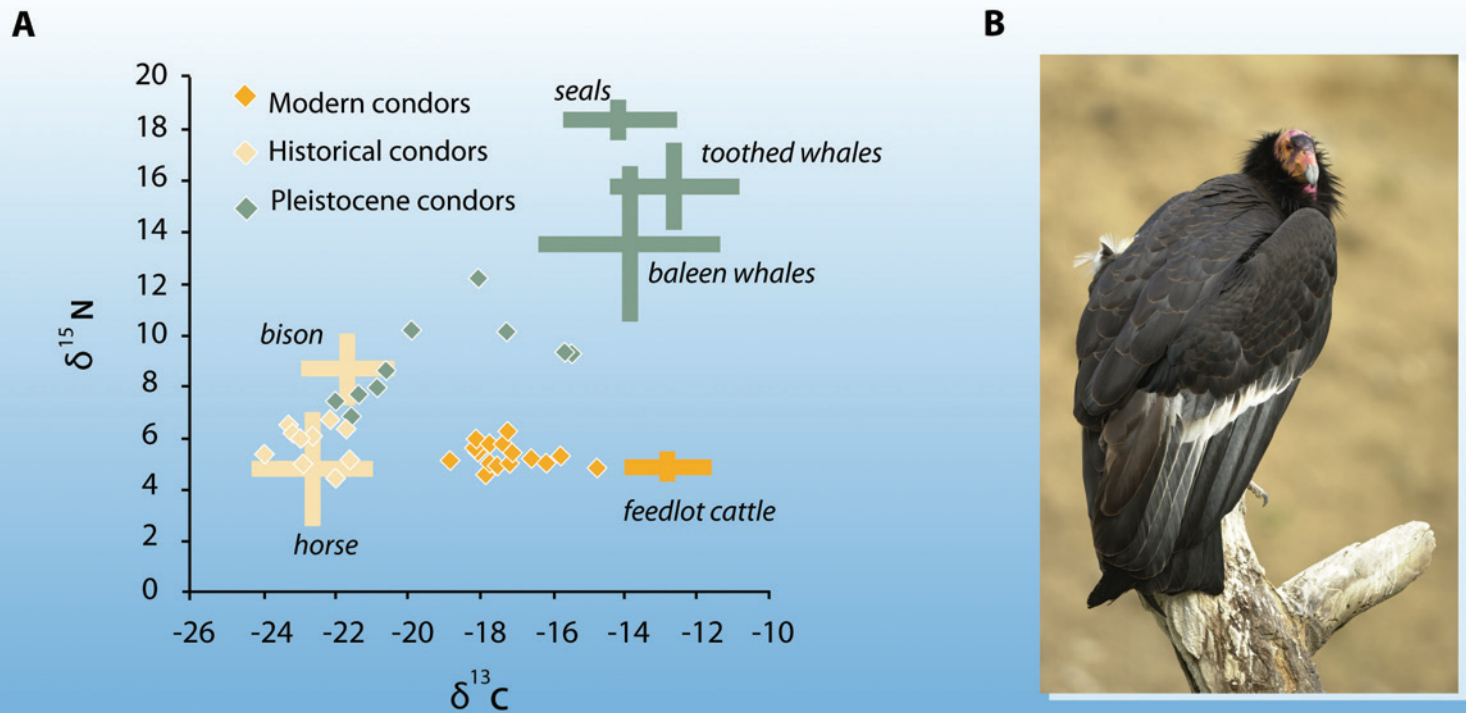
Human exploitation of wild plants and animals for food, construction, fuel, luxury or status items, and other commodities has led to the extinction of many species and reduction in the ranges, population sizes, and ecological roles of others. Humans, unlike “natural” consumers, often continue to exploit target species even as they become rare, focusing on the largest, healthiest individuals. Human exploitation can induce rapid changes in morphology, behavior, and life history in species and populations (Darimont *et al.*, 2009). At the community level, growing experimental and observational data show that human-induced declines in species richness can reduce community stability (Tilman *et al.*, 2006; Stachowicz *et al.*, 2007). At the ecosystem level, long-term commercial data suggest that species loss can have negative impacts on ecosystem services (Hooper *et al.*, 2005; Worm *et al.*, 2006). Species removal can also generate trophic cascades, reduce ecosystem connectivity, and push systems into alternative states (Estes *et al.*, 2011). The lack of well-documented, time series information has posed a significant barrier in assessing the impact of human exploitation for many species and ecosystems.

Paleobiological study of species that declined and recovered can reveal the behavioral or ecological attributes that enabled them to bounce back from exploitation. For example, the northern fur seal was extirpated from much of its breeding range by *ca.* 1800 CE, but attained high abundance following protection in the early 20th century. Ancient DNA revealed that high dispersal rates and Arctic refugia prevented loss of genetic diversity in this marine mammal (Pinsky *et al.*, 2010), making it resilient to environmental changes and perhaps amenable to assisted reintroduction. Geohistorical records also offer insights into the tempo of

Fig. 3. Geographic distribution of acroporid corals off the coast of Florida. (A) Present-day northern limit of acroporid corals (green), the distribution of relict Holocene acroporid-dominated coral reefs (orange), and the location of recently discovered colonies of acroporid corals (black dot). (B) Fossil colony of elkhorn coral (*Acropora palmata*) from a Holocene-age relict reef. (C) Northernmost known colony of elkhorn coral in the western Atlantic. Modified from Precht & Aronson (2004); images by William F. Precht.



Fig. 4. Isotopic tracking of the diets of California condors (*Gymnogyps californianus*), demonstrating that the diets of Pleistocene animals included marine resources (represented here by whales and seals). From historical contact into the 1960s, free-ranging birds on the California coast consumed mostly terrestrial foods from a C3-dominated foodweb (represented here by bison and horse from La Brea). For modern birds (1993–2001), which were released from captive breeding programs, there is a large dietary supplementation from feedlot cattle, which consume corn, a C4 plant with high carbon isotope values. All data are from bone collagen; condor data have been corrected for trophic fractionation so that they are directly comparable to diet values. Modified from Chamberlain *et al.* (2005).



population or species recovery, which can be slow relative to the scale of observational studies.

Species composition in past communities can provide a target for restoration. The success of reintroductions can be evaluated by comparison to species compositions, ecological interactions, or ecosystem processes present in ancient systems. For example, reintroduced California condors have recently “rediscovered” marine carrion, a food source that they exploited in the Pleistocene (Fig. 4; Chamberlain *et al.*, 2005). Conspecifics, congeners, or distantly related ecological analogs might be introduced to restore lost ecosystem function. For example, introduced herbivores might reduce fire loads, restore nutrient cycling, increase open space, and perhaps induce state changes in ecosystems (*e.g.*, tundra to steppe tundra in Siberia), increasing biodiversity and ecosystem stability (Johnson, 2009; Wardle *et al.*, 2011). Finally, the stability of restoration targets can be explored by modeling paleobiological communities as complex dynamic systems, using differential equations, generalized linear modeling, and other approaches (Yeakel *et al.*, 2010). Fossil communities offer essential baselines against which to compare model outcomes about community dynamics.

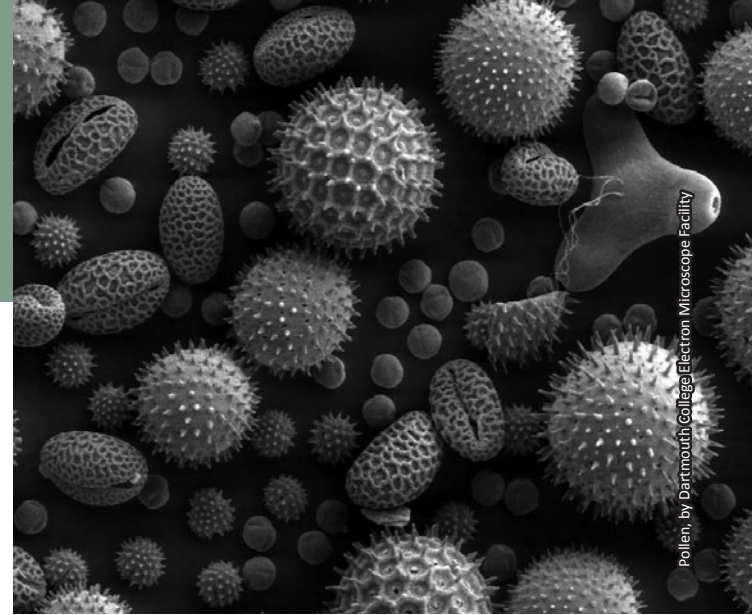
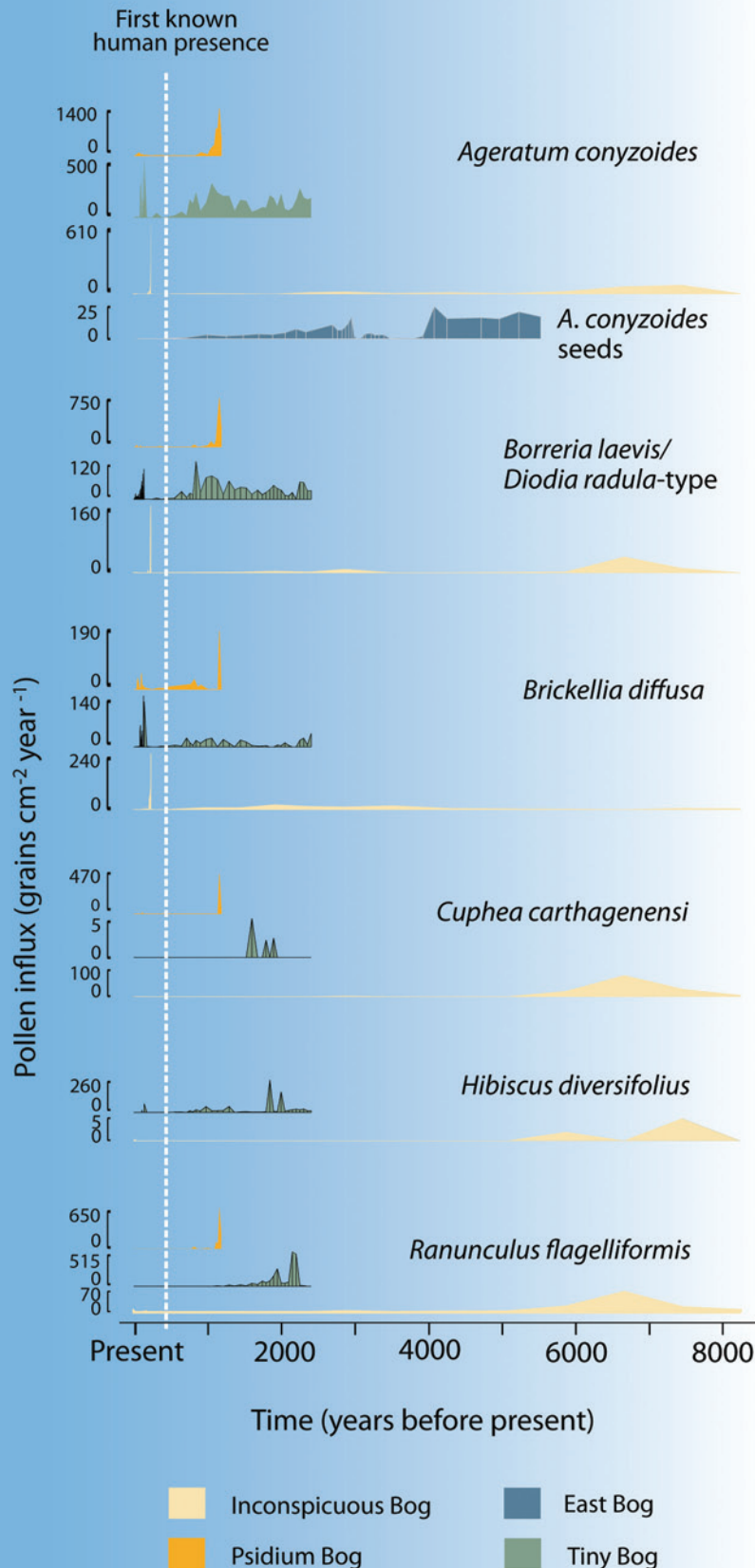
The fossil record is thus a valuable source of information on how “resource depression” by humans has affected the body size, age structure, and species composition of communities, on land (Grayson, 2001) and in the sea (Jackson *et al.*, 2001). Such information will be essential for determining realistic and appropriate management goals, ensuring the long-term sustainable use of wild species for food and other products.

BIOLOGICAL INVASIONS

The conservation community is currently debating how much effort should be devoted to eradicating non-native species (Davis *et al.*, 2011; Simberloff *et al.*, 2011). Non-native species have become established in some areas, often altering ecosystem function and the course of evolution. The Hawaiian Islands, for instance, host > 1,000 non-native plant species that became naturalized (locally breeding) within the last century, matching the number of indigenous species, of which *ca.* 50% are at risk of imminent extinction (Wagner *et al.*, 1999). Approximately one third of freshwater species are “high-profile” invaders, and non-native taxa constitute > 30% of fish species in a majority of North American lakes (Strayer, 2010).

The fossil record enables researchers to evaluate the conditions that lead to success or failure when biotas are united or exotics are introduced. For instance, the fossil record shows that many successful invasions go from larger to smaller areas (*e.g.*, Beard, 1998; Vermeij, 2005). This observation has bearing on a major issue in conservation, that is, whether invasion asymmetry is related to the relative sizes of the donor and recipient landmasses, or whether prior asymmetry in extinction promotes asymmetry in subsequent biotic interchanges. Paleontological evidence also suggests that prior or ongoing disturbance in a region can be more important than its diversity or area in setting invasion intensity (Jablonski & Sepkoski, 1996; Valentine *et al.*, 2008), which has important implications for anticipating present-day invasions and prioritizing efforts toward reducing introduction and impact of invasive species.

Fig. 5. Distribution of fossil pollen and seed (grains/fragments cm^{-2} of sediment year^{-1}) remains preserved in sedimentary deposits from four sites in the Santa Cruz highlands, Galápagos, Ecuador, over the last *ca.* 8,200 years showing that at least six presumed non-native or doubtfully native species (*Ageratum conyzoides*, *Borreria laevis*/*Diodia radula*-type, *Brickellia diffusa*, *Cuphea carthagenensis*, *Hibiscus diversifolius*, and *Ranunculus flagelliformis*) are in fact native to the Galápagos archipelago. Modified from van Leeuwen *et al.* (2008); reprinted with permission from AAAS.



Late Quaternary and particularly late Holocene records from remote islands reveal that rates of invasion accelerated after human arrival. The number of species that invaded large landmasses like Australia and the Americas along with pre-historic humans is relatively low. On the other hand, extinctions of native species on remote islands have been numerous and driven primarily by human-assisted invasion, rather than direct human exploitation (Burney & Flannery, 2005; Cheke & Hume, 2010). Geohistorical data also have helped refine the concept of what is actually native versus non-native. A pollen study in the Galápagos Islands, for example, showed that several presumed non-native plant species that grow aggressively and were being unsuccessfully controlled were in fact native (Fig. 5; van Leeuwen *et al.*, 2008).

Fossil evidence also indicates that some large herbivores, considered deleterious invasives by management agencies, might be “returning natives.” Paleoeological studies showed that horse grazing on eastern U.S. salt marshes can contribute to higher bird diversity, crab density, and other positive outcomes. Horses were members of the community until the late Pleistocene (Levin *et al.*, 2002). Such “empty niches” can stem from relatively recent, perhaps human-driven extinctions, and this has led to the idea of “Pleistocene Rewilding” (Donlan *et al.*, 2005), which has sparked heated debate in North America. On some remote islands, where late Holocene, human-driven extinction is well documented, rewilding using the fossil record as a guide is less controversial. For instance, paleoecological records from Makauwahi Cave, Hawaiian Islands, on the pre-human presence of rails (*Gallirallus* spp.) and other birds, spearheaded a successful program of avian rewilding (Burney & Burney, 2007).

Geohistorical records thus have contributed to our understanding of the seriousness and complexity of biological invasions. The long time perspective provided by the fossil record was essential to our fully appreciating the multiple responses to biological invasions. Such information will be essential for developing strategies to address the impacts of invasive biota.

BIOGEOCHEMICAL DISTURBANCE

Human activities have transformed the global cycling of elements and water. Agriculture and grazing lands now cover over 70% of the Earth's landscape (Foley *et al.*, 2011), and land-use changes have accelerated soil erosion and water withdrawal well beyond natural regeneration rates. Fertilizers and fuel combustion have perturbed nitrogen cycles in soils, lakes and rivers, and in the marine realm, where excess nutrients are causing expanded "dead zones" within coastal oceans (Diaz & Rosenberg, 2008). Soil loss, acid deposition, and industrial activities are mobilizing metals well beyond natural rates, impacting both ecosystems and human health (AMAP/UNEP, 2008). Fossil fuel combustion has lifted atmospheric carbon dioxide to levels not experienced by the Earth for the last 35 million years (Pagani *et al.*, 2005). Carbon release is accelerating due to agriculture and land use changes (Gibbs *et al.*, 2010).

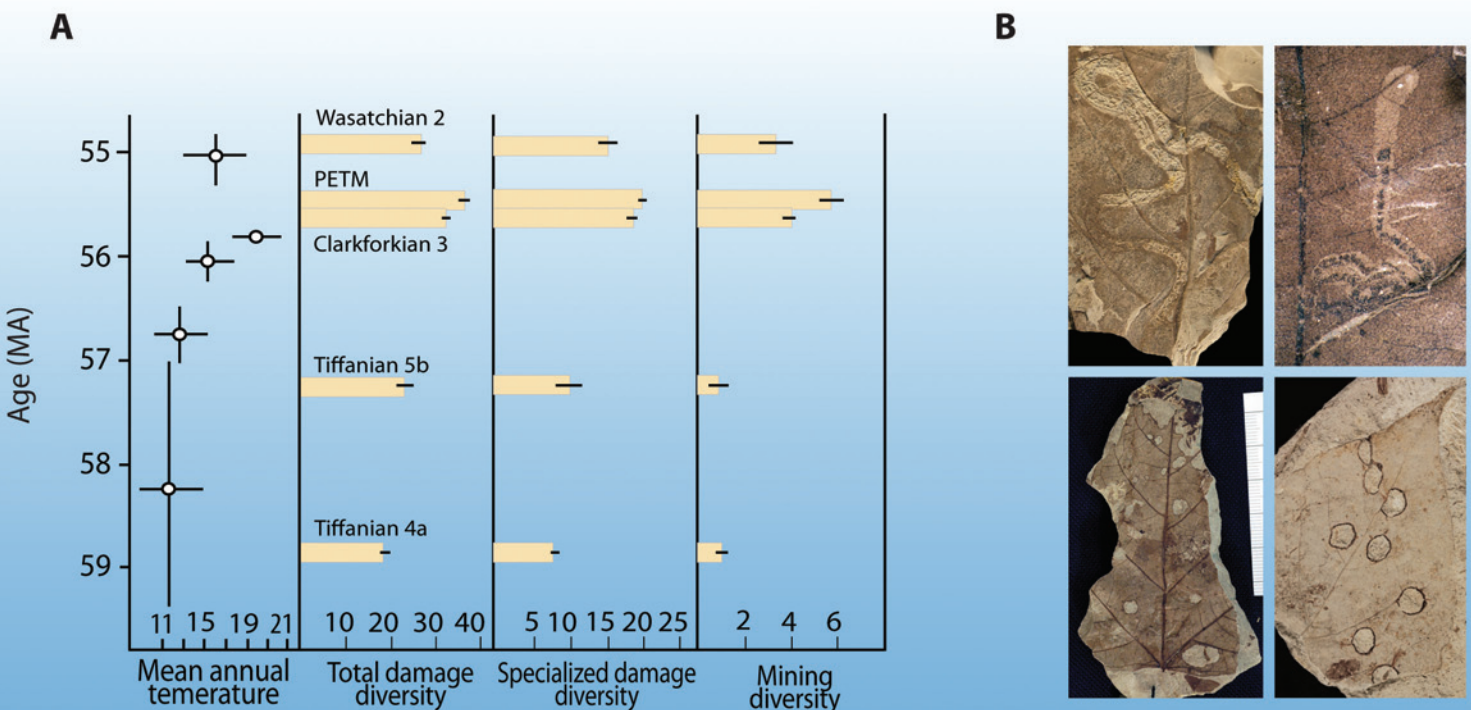
Geochemical records from ancient soils and other sedimentary archives provide a measurable context from which to understand the scope and biological consequences of human-catalyzed changes in element and water cycles. Geochemical, isotopic, and biomarker proxies document rates and extent of past biogeochemical changes, such as deoxygenation of marine waters and ocean acidity and circulation (Freeman & Goldhaber, 2011). Biotic responses to these changes have revealed fundamental aspects of ecological dynamics. For example, the massive release of carbon during the Paleocene-Eocene Thermal Maximum, *ca.* 56 million years ago, led to sharp increases in frequency and diversity of insect damage to North American plants (Fig. 6; Currano *et al.*, 2008). This finding suggests that herbivorous insects

can expand their ranges, and perhaps population densities, in response to elevated $p\text{CO}_2$ at rates that exceed the capacity of their natural enemies to control them. Additionally, Hannisdal *et al.* (in press) used fossil coccolithophores to predict the biotic response of calcifying phytoplankton in the oceans to rising $p\text{CO}_2$ and ocean acidification. Their data show that coccolithophores were more abundant, widespread, larger, and more heavily calcified in the world's oceans during the greenhouse conditions of the Eocene than they are today. These results have implications for understanding how projected anthropogenic changes in ocean chemistry over the next century will impact marine ecosystems.

Geochemical archives also provide baseline data for assessing biotic response to elements released from the landscape, and cycled within the biosphere. For example, nitrogen isotope archives, such as algal tests, minerals, pigment biomarkers, and in bulk organic matter, define changes in nutrient cycling (Canfield *et al.*, 2010). The fossil record provides numerous examples of biotic response to changes in the availability or access to nutrients. For example, at the individual level, Kirby & Miller (2005) used paleoecological data derived from archeological sites and sediment cores to determine the growth response of a suspension feeder (the eastern oyster, *Crassostrea virginica*) to almost three centuries of anthropogenic eutrophication in Chesapeake Bay.

Although the vast differences are difficult to comprehend, much less quantify, linking biogeochemical conditions and ecologic patterns prior to human impacts will enable holistic decisions about the conservation, restoration, and stewardship of land, water, and ecosystems.

Fig. 6. Traces of insect damage on plant leaves from before, during, and after the Paleocene-Eocene Thermal Maximum (PETM; 59-55.2 million years ago) in the Bighorn Basin of Wyoming. (A) Temporal patterns of mean annual temperature and damage diversity (total, specialized, and mining) on each flora indicate that the intensity of insect herbivory peaked during the PETM. Modified from Currano *et al.* (2008), © National Academy of Sciences, USA. (B) Examples of insect damage diversity on Eocene leaves from the Bighorn Basin; images courtesy of Ellen Currano.





Long sediment cores from Lake Peten-Itza, Guatemala, by Mark Brenner

3. FRONTIERS IN CONSERVATION PALEOBIOLOGY

Few *Conservation Paleobiology* studies have considered the combined effects of multiple stressors on natural systems (e.g., Smol, 2010; Desellars *et al.*, 2011; Guilizzoni *et al.*, 2012). Most ecosystems are subject to multiple human and natural stresses today, and reflect a history of different stresses and stress release (Fig. 1). Without knowing how stressors interact with each other, across scales linked through space and time, we will not be able to develop “predictive” modeling tools to anticipate responses of ecosystems to environmental changes. Interactions among ecological stressors can generate nonadditive effects with unexpected and complex interactions (Christensen *et al.*, 2006; Crain *et al.*, 2008; Darling & Cote, 2008; Brook *et al.*, 2008). A critical step in the advancement of *Conservation Paleobiology* will be to quantify the effects of multiple stressors and their interactions on biodiversity and the delivery of ecosystem services.

Key research frontiers include enhancing the ability to:

- recognize interactive effects among multiple stressors, which can amplify or dampen impacts;
- rank the relative importance of factors that account for stress;
- identify tipping points and thresholds in system histories that presage collapse or interfere with recovery;
- understand feedbacks that stabilized systems in the past;
- assess duration of lag effects in ecosystem responses to environmental changes;
- evaluate interactions between “fast” and “slow” processes in ecosystems; and
- quantify frequency of rare events in ecosystems, and the time needed to recover from them.

Developing these capabilities requires basic research. We need nothing less than a broad-based science of biological vulnerability and resilience.

The following examples illustrate how conservation paleobiologists can address these research frontiers in unique ways:

Non-linear behavior in ecosystems—for example, sudden changes after prolonged stability, despite continued or intensifying stress, indicating the operation of some critical threshold—is a rapidly developing concern in environmental manage-

ment (Scheffer & Carpenter, 2003). Passing a threshold marks a sudden change in feedback mechanisms, with potential effects on ecosystem services (Carpenter *et al.*, 2009). However, the dynamics of threshold behavior are extremely difficult to study empirically, except after the fact. Geohistorical time series offer a rich potential for identifying nonlinear behavior in ecosystems, the feedbacks involved, and evaluating the relative importance of factors. For instance, Ireland & Booth (2012) used paleoecological data derived from peat cores to show that deforestation by European settlers triggered an ecosystem state-shift in a kettle peatland in Pennsylvania. Macrofossil data document more decomposition within post-settlement vascular plant communities relative to pre-settlement communities. High rates of decomposition and rapid nutrient cycling sustained by the post-settlement plant communities provided a feedback mechanism to maintain the new ecosystem state.

*“We need nothing less
than a broad-based
science of biological
vulnerability
and resilience.”*

Geohistorical data also hold promise in teasing apart the stressors involved in abrupt ecosystem changes. For example, Caribbean reef corals have suffered a dramatic decline since the 1980s, which has been attributed to the onset and intensification of coral bleaching and disease events due to anthropogenic climate change. Cramer *et al.* (2012), however, used fossil assemblages of corals and mollusks from Panama to show that Caribbean reef collapse due to local, anthropogenic stressors, such as habitat change (e.g., deforestation) and overfishing, was already occurring before coral bleaching and disease outbreaks began.

The controls on “slow” processes (Carpenter & Turner, 2001) and the long-term effects of rare events in ecological systems can be understood only by using geohistorical records. For instance, Seddon *et al.* (2011) used paleoecological methods to investigate the ecological resilience of coastal mangrove communities in the Galápagos Islands over the last 2,700 years. They found that a combination of fast and slow processes, such as increased aridity stress due to precipitation changes and falling sea level, helped erode resilience, driving a threshold response to an alternative stable state, in which the mangrove community transitioned to a microbial mat.

Conservation Paleobiology research in these frontier areas stands at the forefront of developing a more complete understanding of how biological systems respond to environmental stress.



4. EMERGING OPPORTUNITIES FOR THE EARTH SCIENCES

Support for the discipline of *Conservation Paleobiology* will allow Earth scientists to develop the basic science needed to address pressing issues in the environmental sciences.

Earth scientists will develop process models central to prediction of coming environmental change and evaluate the skill of these models via comparison to the empirical record of past global change. To do this work, they will strengthen the methodologies and instrumental capacities needed for this and associated disciplines.

MODEL DEVELOPMENT AND VALIDATION

Sophisticated models of Earth systems (e.g., atmosphere, oceans, solid Earth, and biota) and their feedbacks are needed to predict impending anthropogenic change. Critical feedbacks in the Anthropocene include:

- impact of vegetation change on high latitude albedo;
- release of methane and other biogenic greenhouse gases from melting permafrost and clathrates;
- greenhouse gas uptake and/or release by floras and faunas;
- faunal/vegetation/fire relations;
- marine and freshwater eutrophication and anoxia from fertilizer run-off and enhanced erosion; and
- impact of ocean acidification on carbon cycling by calcareous and noncalcareous organisms.

The near-time geohistorical record is ideally suited for examining the perturbations and feedbacks associated with human actions. For example, Doughty *et al.* (2010) modeled the impact on climate (via change in albedo) of the rapid, late Pleistocene expansion of beech (*Betula*) across Alaska and the Yukon, a response to collapse of the regional megafaunal community, apparently extirpated by humans. The deep-time geohistorical record offers a view of these feedbacks in other worlds, most importantly in a warmer, greenhouse world. For example, the Paleocene-Eocene Thermal Maximum (ca. 56 million years ago) was characterized by a series of transient hyperthermal events related to greenhouse gas release, which abated as global climate cooled in the late Eocene (McInerney & Wing, 2011).

Models used to assess system feedbacks must be robust at the regional scale to be useful for conservation and other societal needs. Computational limits present a challenge for global-scale models, so regional results are produced by downscaling from global models or by embedding a dynamic regional model within a global model. Both approaches yield spatially resolved simulations of regional dynamics, but they have been sharply criticized

(Kerr, 2011). Also, although different statistical results sometimes converge, this does not guarantee accuracy. The only strong test is to simulate Earth system history and compare results to the long-term instrumental or geohistorical record. Instrumental records are data rich and can be high resolution, but their relatively short duration and limited time frame provide a small sample of Earth system variation and therefore cannot test model skill under conditions of environmental change outside recent experience or beyond an array of mostly physical and chemical attributes. Although less detailed geohistorical records (paleoecological, sedimentologic, geochemical) are typically longer, they are available for a range of time frames in Earth's history, and include information on biotic presence/absence and abundance, proxy indicators of fire, redox, pH, $p\text{CO}_2$, productivity, erosion and deposition, and ocean circulation. Regional geohistorical records should be used to document the skill of regional Earth system models before the latter can be relied upon to assess the vulnerability of species or human populations to future change.

ANALYSIS AND MODELING OF THE NEAR-TIME FOSSIL RECORD

Recent taphonomic work on modern death assemblages using pollen, marine mollusks, mammals, and corals has generated a wealth of insights into the temporal and spatial resolution of biotic remains and their generally high fidelity to the living communities that produced them (e.g., Pandolfi & Greenstein, 1997; Kidwell, 2007; Western & Behrensmeier, 2009). The data helped to generate protocols for sampling and biological interpretation of very young, not-yet-buried fossil records, and to permit modeling of the dynamics of fossilization. Other key groups and habitats need to be evaluated, most notably finfish, freshwater fauna, and high-latitude sites, which are all under elevated stress from human exploitation and/or climate change. The temporal resolution and fossilization of planktic and benthic meiofauna are also under-investigated, given the critical role they play in paleoenvironmental models and evaluating ecosystem response to stressors. Finally, there remain many questions about the resolution and fidelity of fully buried fossil assemblages. For instance, does burial below the upper mixing zone of the sedimentary column simply freeze in the qualities of death assemblages? Or does temporal resolution coarsen and does bias from differential preservation increase, under the combined influences of diminished input of newly dead individuals and continued diagenesis? Comparisons among living, recently dead, and young fossil assemblages are scarce and yield conflicting results (e.g., Greenstein, 2007). Systematic analyses and modeling are needed to evaluate this critical formation process in fossil records.

SCALING AND OTHER ISSUES FOR MERGING NEO- AND PALEOBIOLOGICAL DATA

In contrast to the fine, snapshot-like temporal resolution of data based on census of exclusively living individuals, organic remains that have accumulated naturally on landscapes and seafloors—death assemblages—are typically time-averaged and/or spatially averaged to some degree. That is, they sum input from multiple generations at a site, owing to low net rates of sediment accumulation or other factors that delay burial, and usually sum input from multiple patches or habitats in a region, owing to short-term fluctuations in environmental conditions at the site, habitat migration, and random variability in living communities during the window of time-averaging; post-mortem transport of remains is also important for some groups. Such time-averaged assemblages dominate the fossil record, providing most paleobiological data and specimens for geochemical analysis. This spatial and temporal resolution does not make paleontological data inherently poorer in quality than neontological data, only coarser in scale, much as regional or annual accountings of living species represent coarser-scale information than the point inventories that they sum (the well-known species-area and species-time relationships of ecology). Enough comparative data now exist for modeling efforts to quantify the relatively predictable effects of scaling on paleobiological data (Tomasovych & Kidwell, 2009a, b, 2010a, b) and disentangle these from the potentially complex effects of post-mortem bias (Tomasovych & Kidwell, 2011). However, building a mechanistic understanding of postmortem preservation will be critical to devising reliable protocols for paleontologic sampling and data integration. What determines levels of resolution and fidelity and their variation among settings, groups, and geologic age?

PROXY DEVELOPMENT FOR ENVIRONMENTAL AND BIOTIC CONDITIONS

New and refined proxies for environmental conditions have revolutionized paleoecological analysis over the last several decades—increasingly paleoenvironmental conditions can be inferred from independent sedimentary, geochemical, and molecular evidence, liberating fossil material to be used to evaluate biotic responses to environmental change (NRC, 2005). Proxy records, however, are only rarely calibrated to give the accuracy and precision of instrumental data. For instance, transfer functions (or “calibration functions”; Birks *et al.*, 2010) based on the relationship between a proxy and an environmental variable in a modern setting—a standard tool in paleoecology—are open to considerable error in prediction because of the effects of strongly correlating variables on the response function (Birks & Birks, 2006; Saros, 2009; Sayer *et al.*, 2010; Dearing *et al.*, 2012). The difficulty of separating effects due to multiple stressors across an irregularly sampled time series also hampers our ability to determine the key driver or drivers of change (Anderson *et al.*, 2006). Overcoming these limitations will require the development of innovative numerical methods (Birks *et al.*, 2010), but also a sound knowledge of the ecology of organisms, particularly how species (and their interactions) are influenced by and modify their environment (Sayer *et al.*, 2010).

IMPROVING METHODS OF INTERCORRELATION AND AGE CALIBRATION OF DATA

Our ability to precisely and accurately quantify geological time has improved dramatically in the last decade due in large part to community-driven efforts, such as the EARTHTIME¹ Initiative. A variety of geochronological tools now exist (*e.g.*, tree rings, accretionary growth bands in corals, radiocarbon, amino acid racemization, U-Th series, Pb-210, Ar-Ar, U-Pb; see NRC, 2005), which enable accurate correlation of events in the geologic record with temporal resolutions that closely approach modern measurements. Precise and accurate ages are needed for measuring and documenting rates of change and disentangling biotic responses to multiple drivers. As precision and accuracy of the methods have increased, however, an appreciation that small but significant errors between geochronological clocks (*e.g.*, Ar-Ar and U-Pb methods) has emerged, hindering our ability to assess geologically short-lived events. A more systematic and coordinated approach to provide intercalibration of clocks, understand error propagation, and characterize material standards that are used for these methods (Palike & Hilgen, 2008) will be critical to meeting increasing demand in the broader geological community for high-precision geochronology.



Tree rings. by Serdell

5. SCIENCE DELIVERABLES AND THEIR TRANSLATION FOR HUMAN WELL-BEING

Conservation Paleobiology has already yielded valuable insights about biotic responses to the most important stressors acting today. Such research, despite only *ad hoc* support, has also already demonstrated its utility to conservation biologists and resource managers. Indeed, paleobiological studies increasingly influence decisions regarding priorities and challenges in conservation and restoration. The following examples serve to illustrate how research in *Conservation Paleobiology* has already resonated with conservation biologists and other environmental scientists. We focus on cases for which direct observation of living biota and modern environmental conditions alone would lead to erroneous conclusions about the nature and magnitude of biotic change, vulnerability, and resilience.

IDENTIFYING INVASIVE SPECIES

Distinguishing native and non-native taxa is a first-order challenge for any conservation or restoration effort. However, the flora and fauna that characterized many areas prior to human colonization are typically poorly known (Jackson, 1997). Paleoecology can document precolonization biota and has revealed many surprises, including the fact that some species assumed to be exotic are in fact native. For instance, although the screwpine (*Pandanus tectorius*) and the flowering tree *Cordia subcordata* were thought to have been introduced into the Hawaiian Islands by colonizing Polynesians, pollen and seed evidence from excavations in a large sinkhole and cave system on the south coast of Kauai showed that both were present in the islands for thousands of years before human arrival (Burney *et al.*, 2001). These trees are now used in coastal and dry forest restoration efforts in the Hawaiian Islands.

MEASURING HISTORICAL VARIABILITY

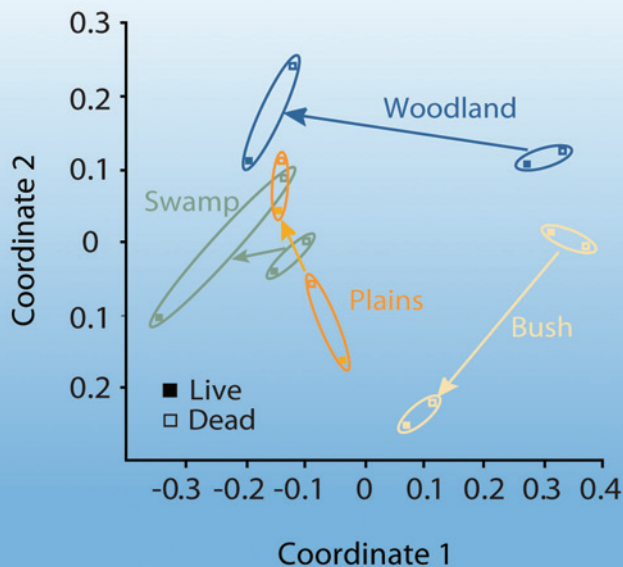
Resource managers on federal lands in the U.S. and other countries use the historical range of variability (HRV) as a dynamic management target (Keane *et al.*, 2009). Paleoecological records can be used to identify the HRV in specific settings (Landres *et al.*, 1999) and enable managers to discriminate variability around a stationary mean from variability associated with a long-term, usually anthropogenic, trend (Willard & Cronin, 2007; Smol, 2010). For example, Wolfe *et al.* (2001) used sediment cores from two alpine lakes in the Colorado Front Range to show a shift to higher abundances of mesotrophic diatoms and increasingly depleted nitrogen isotope values as a response to excess nitrogen

derived from agriculture and industrial sources since the 1950s. The rate and magnitude of these shifts far exceed the HRV over the 14,000-year postglacial history of the lakes. Paleoecology is also playing a key role in reassessing the scope and sustainability of HRV targets, in light of past environmental nonstationarity (Milly *et al.*, 2008) and anticipated rapid future changes (Wiens *et al.*, 2011).



Aerial view of the Makauwahi Cave Reserve, Kauai, Hawaii, by Ellen Coulombe, Wings over Kauai

Fig. 7. Nonmetric multidimensional scaling analysis of abundance data for living populations and modern bone assemblages of 15 herbivorous species from the Amboseli ecosystem in southern Kenya over a 40-year timespan (1964–2004). Results show a similar shift through time in both the live and dead samples for four different habitats reflecting decadal-scale ecological change. Live/dead pairs are connected by ovals; habitat samples are connected by arrows to show shifts through time. Modified from Western & Berensmyer (2009); reprinted with permission from AAAS.



QUANTIFYING PAST AND PRESENT BIODIVERSITY

Paleontological studies indicate that estimates of species richness and diversity using only live organisms can be deceiving, because modern ecosystems are often so disturbed that biodiversity estimates are likely compromised by the presence of exotic species and by unappreciated disappearance of endemic taxa. For example, accumulated bones in a Madagascar cave showed that the community of the semiarid spiny bushlands was much more diverse only a few millennia ago; many key guilds are now missing as a consequence of human-caused extinction or range contraction (Burney *et al.*, 2008). In addition, without evidence provided by the plant fossil record, the extinction of the aquatic fern *Azolla nilotica* in Egyptian Nile delta lakes would not have been recorded and the likely causes (changes from year-round inflow of fresh irrigation water and rise in the freshwater table due to inadequate drainage) would have remained obscure (Birks, 2002).

DETECTING RECENT SHIFTS IN SPECIES ABUNDANCE

Species population declines that fall short of local extinction can be difficult to detect in the absence of dedicated, continuous monitoring; most knowledge of temporal trends is limited to presence-absence or semiquantitative estimates of abundance. Fossil records and modern death assemblages can provide

valuable retrospective data about species and areas of critical concern. For example, Burney *et al.* (2001) used plant fossil data from a cave excavation on the island of Kauai in Hawaii to show that plant species that are now rare and restricted to remote montane habitats on the island were once, before human colonization, widespread in the coastal lowlands. Discordances in the proportional abundances of species between time-averaged death assemblages and living communities have also been able to detect known decadal-scale changes in community structure, driven by climate change, predator reintroductions, and exploitation (Fig. 7; Western & Behrensmyer, 2009; Miller, 2011).

PREDICTING SHIFTS IN SPECIES GEOGRAPHIC RANGES

Predicting changes in species distributions under different scenarios of global climate change is a major agenda in conservation biology. Paleocological data can be used to detect recent shifts in geographic distribution of species in response to current climate change. For example, Emslie *et al.* (1998) used paleoecological records to show that gentoo (*Pygoscelis papua*) and chinstrap (*Pygoscelis antarctica*) penguins that are now breeding on Anvers Island, Antarctic Peninsula, have only recently (within the last 50 years) expanded their ranges to this region in response to climate warming. In addition, only data from the fossil record can indicate where species occurred in the past outside their present-day geographic ranges. For instance, Greenstein & Pandolfi (2008) used paleoecological data to document how reef-building coral species from Western Australia responded to climate change since the Late Pleistocene. This understanding enabled them to forecast the response of the modern system to elevated temperatures predicted for the future in the region.

ASSESSING CHANGES IN GENETIC DIVERSITY AND IDENTITY

Ancient DNA (aDNA) technology is opening new opportunities for assessment of genetic impacts of human activities, population bottlenecks, and environmental change (Ramakrishnan *et al.*, 2005; Leonard, 2008). For instance, Heupink *et al.* (2012) used aDNA data from fossil bones of the king penguin (*Aptenodytes patagonicus*) from Macquarie Island, which was nearly driven extinct by historical human exploitation in the 1800s, to show that recent conservation efforts have resulted in a recovery of past genetic diversity. Specific conservation issues related to a particular population can also be informed by the genetic analysis of past populations. For example, Vila *et al.* (2003) used aDNA analysis to confirm that a population of Scandinavian wolf (*Canis lupus*) was not founded by illegally reintroduced zoo animals, and hence should be protected, not eradicated as advocated by some groups opposed to their existence.

DOCUMENTING SHIFTING BASELINES

The “shifting baseline” phenomenon (Pauly, 1995) has become all too common. Successive generations of scientists and non-scientists alike have diminished expectations of biodiversity and ecosystem services because their perspective is restricted to direct observations of their scientific generation, rather than incorporating long-term historical information. Paleobiological

studies have helped reconstruct the deep historical roots and globally accelerating rates of shifting baselines under the pressure of exploitation (Jackson *et al.*, 2001). The approach has sometimes led to controversial findings, such as the federal review elicited by reported historic declines in the number and body size of commercial finfish (NRC, 1995). Impacts of Colorado River damming on the productivity of coastal Gulf of California, revealed by paleontological evidence of the functional extinction of a key bivalve species, have also fueled discussions of water rights across the U.S.-Mexico border (Zamora-Arroyo & Flessa, 2009).

DISENTANGLING HUMAN IMPACTS FROM NATURAL PROCESSES

Many environmental issues are fraught with controversy over the extent to which human activities have contributed to present conditions, especially in cases when change is detected within a single (human) generation. For example, in the 1970s and 1980s, lake acidification in the northeastern U.S. was documented by direct pH measurements, but the magnitude and trajectory of change, and the extent to which industrial emissions were responsible, was controversial. Diatoms from short cores of lake sediments were used to infer past lakewater pH and showed that acidification coincided with an increase in sulfate and nitrate emission, not with other watershed factors (Charles & Smol, 1990).

DEVELOPING RESTORATION TARGETS

Conservation Paleobiology provides information on ecological conditions before human disturbance, thereby providing valid targets for mitigation and restoration efforts and a means to evaluate success (Brenner *et al.*, 1993; Jackson & Hobbs, 2009). Paleoecological studies are consequently playing a greater role in ecological restoration efforts (*e.g.*, Steadman, 1995; Burney & Burney, 2007; Willard & Cronin, 2007), and contribute to discussions regarding feasible restoration targets in a changing environment (Jackson & Hobbs, 2009). For example, Voltey *et al.* (2009) used geohistorical baseline data from Holocene oyster (*Crassostrea virginica*) reefs in the Everglades of southern Florida (which have diminished due in large part to reduction and redirection of freshwater Everglades discharge) to characterize the nature of estuarine conditions under which historical oyster reefs grew. These data are now used by resource managers to target areas suitable for oyster reef development under different Everglades flow restoration conditions.

INFERRING EXTINCTION RISK

Understanding why some species are more vulnerable to extinction than others is a central goal of conservation. *Conservation Paleobiology* can help to disentangle the relative importance of intrinsic (*e.g.*, ecological) versus extrinsic (abiotic) factors in determining extinction risk. For instance, Boyer (2009) used classification trees that integrated fossil and modern bird occurrence data to demonstrate that ecological traits (*e.g.*, endemism, body size, diet) were better predictors of extinction risk than abiotic factors for bird species from islands across the Pacific. Boyer's (2009) analysis of past extinctions also identified a number of



Eastern Oyster Bed, South Carolina, by Kirk Mantay



Tortoise rewilding at Makauwahi Cave Reserve, Kauai, Hawaii, by Lida Pigott Burney

misclassifications—species that share the traits of extinct species but are currently classified as unthreatened. This kind of information is proving helpful in identifying species potentially in need of conservation attention.

INFORMING SPECIES REWILDING DECISIONS

Conservation biologists now realize that restoration projects—such as recent proposals to restore lost ecosystem functions of extinct species by substituting them with extant species, related or ecologically similar—stand to gain from detailed information about extinct species and their ecosystems. Uses of paleoecology include identifying recently extinct species and reconstructing aspects of an extinct species' ecology (Burney & Burney, 2007; Hansen, 2010). This kind of information is central to selecting suitable candidates for rewilding projects. For instance, paleoecological analysis has shown that giant tortoises, which are strong interactors in island food webs, were much more widely distributed in the recent past than they are today. Since the Late Pleistocene, at least 36 tortoise species have become extinct, with the majority of extinctions occurring on islands (Hansen *et*

al., 2010). This knowledge of past extinctions has led to controversial proposals of rewilding extant tortoises in island restoration efforts to replace extinct species interactions and restore ecosystem functioning (Hansen *et al.*, 2010; Burney, 2011).

DESIGNING RESERVE-SELECTION STRATEGIES

Systematic conservation planning to establish biological reserves in which biodiversity can persist continues to grow as a discipline (Margules & Pressey, 2000; Hannah *et al.*, 2007; Langford *et al.*, 2011). *Conservation Paleobiology* can improve the utility and reliability of these methods. For example, Williams *et al.* (2012) used climate changes of the last glacial period [21,000-15,000 years ago] and the shifting distributions of fossil plant species across North America as a way of testing the predictive ability of various reserve-selection strategies. They compared results from an analysis of fossil data with an independent set of rankings based on actual present-day species distributions. They found that the predictive ability of the tested strategies was limited, as shown by moderate to low correlations between predicted and

actual reserve rankings, which has implications for their reliability in guiding conservation planning decisions.

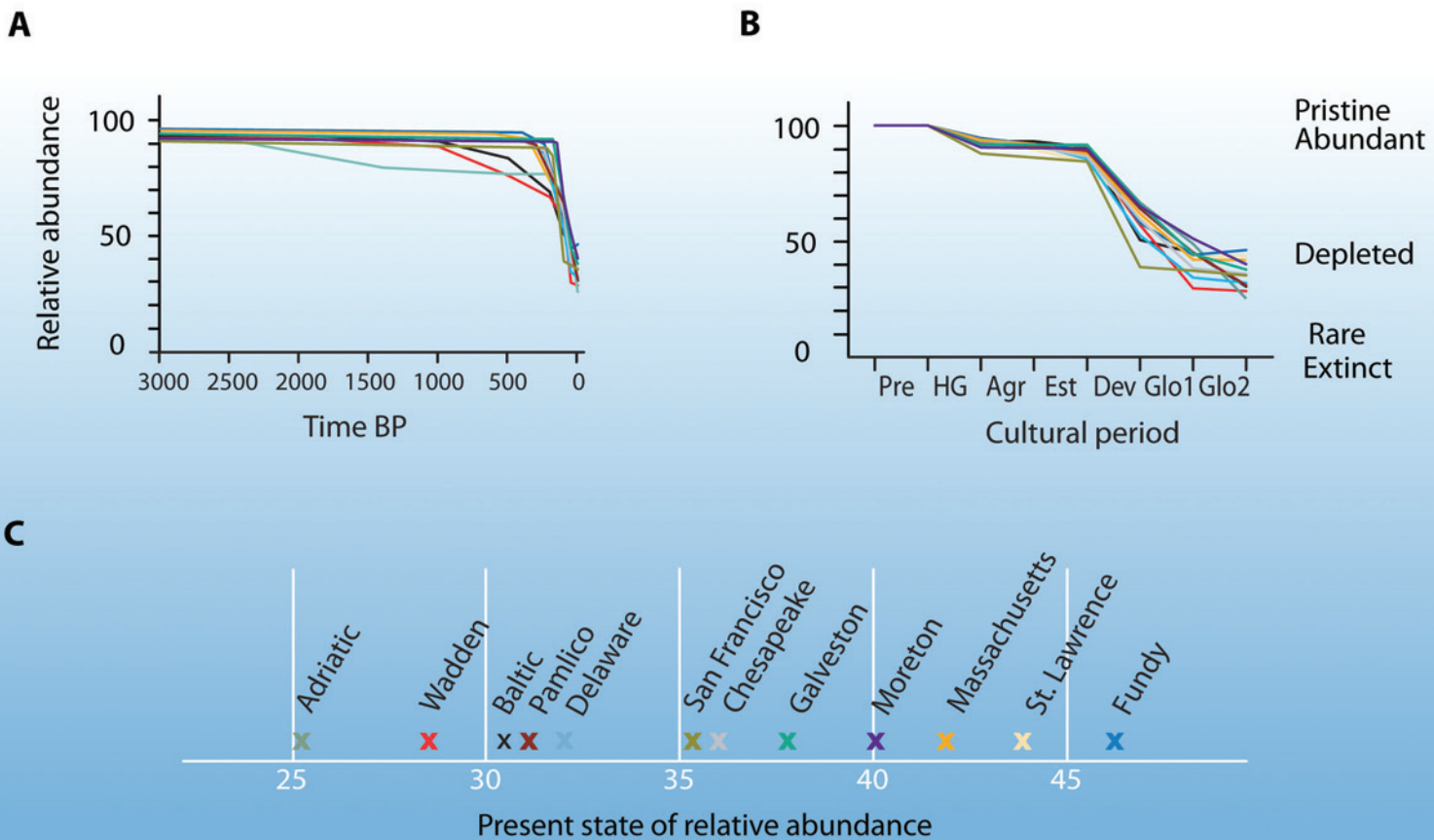
ESTABLISHING CONSERVATION PRIORITIES

The conservation community recognizes that resources are insufficient to save all threatened populations and species, and is debating what factors should be considered in setting conservation priorities. Although “conservation triage” remains controversial (Jachowski & Kesler, 2009; Parr *et al.*, 2009), it is increasingly accepted in light of ongoing changes to natural systems, finite funds, and lack of political will (Bottrill *et al.*, 2008; 2009). *Conservation Paleobiology* can inform prioritization discussions. For example, a global meta-analysis of paleontological and other historical data on key plant and animal groups (guilds) permitted 12 estuaries to be ranked according to their state of degradation and, inversely, their potential for remediation (Fig. 8; Lötze *et al.*, 2006). Paleoeological studies also indicate that some currently dominant, widespread tree species were rare during the last glacial maximum, *ca.* 23,000-19,000 years ago, and many abundant tree species of the glacial and late glacial are widely scattered today (Williams *et al.*, 2004). These findings suggest that species that seem unimportant today could prosper under a future climate scenario and provide critical ecosystem services (*e.g.*, land cover, carbon sequestration, and soil stabilization).



Chesapeake Bay, National Aeronautics & Space Administration

Fig. 8. History and present state of 12 estuarine and coastal ecosystems in North America, Europe, and Australia. Relative abundance trends calculated as arithmetic means of six ecologically important taxonomic groups (mammals, birds, reptiles, fish, invertebrates, and vegetation) plotted against (A) years before present and (B) cultural period (Pre, prehuman; HG, hunter gatherer; Agr, agricultural; Est, market-colonial establishment; Dev, market-colonial development; Glo1, global market 1900-1950; and Glo2, global market 1950-2000). (C) Present state of relative abundance, as indicated by the endpoints of historical trajectories in (A). Color codes in (A) and (B) refer to the 12 estuarine and coastal ecosystems as shown in (C). Modified from Lötze *et al.* (2006); reprinted with permission from AAAS.





TP 1-2
BAP V. 2(6), PL 1
BAP V. 2(9), PL 4-14
BAP V. 3(11), PL 1-2

TP 1-3
BAP V. 3(11), PL 3-12, Unfig.
BAP V. 3(13), PL 1
BAP V. 3(13), PL 15-16

BAP V. 4(21)
Plate 5

BAP V. 4(21)
Plate 7

BAP V. 5(27)
Plate 1

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6. INFRASTRUCTURE

Future progress in *Conservation Paleobiology* research is heavily dependent on maintenance and improvement of existing, and development of new, infrastructure. Funding for research, education, and outreach activities has not kept pace with the increased interest in *Conservation Paleobiology*, which has emerged from a growing sense of shared responsibility in the paleontological community to help conserve biodiversity for the advance of human society. To build on this interest, and to maintain the momentum needed for translation into conservation outcomes, we make several recommendations, which collect the ideas that came out of discussions at the “Conservation Paleobiology in the Coming Decades” workshop in Ithaca, New York, June 3-5, 2011. These recommendations are only a first step toward realizing the full potential of the *Conservation Paleobiology* approach.

COLLECTIONS AND PALEOECOINFORMATICS

Natural history collections are critical infrastructure for the geoscience and *Conservation Paleobiology* communities today and certainly will be into the future (NRC, 2002, 2005; NSTC, 2009). These collections provide vital and at times irreplaceable information and research opportunities. As the conservation application of these collections is more widely appreciated, it will become increasingly important to coordinate efforts to ensure that the wealth of information stored in them is fully utilized—often in unanticipated ways—by conservation paleobiologists and other stakeholders. To overcome barriers to effective use of these resources by the *Conservation Paleobiology* community, we recommend that NSF should:

- Support a series of workshops to discuss the challenges and concerns involved with establishing community standards for prioritizing the archiving of samples and collections of untraditional materials produced by *Conservation Paleobiology* studies (e.g., modern death assemblages). Many of these collections are currently in peril, often being discarded because they do not fit into traditional systematic and stratigraphic paleontological collections or systematic biological collections. These collections, which are often voluminous and of considerable redundancy, have special impediments and requirements for storage, specimen handling, and data capture. Guidelines that the collections management community can use for prioritizing which collections to save or rescue are needed.
- Promote collection of natural archives that are quickly disappearing due to ongoing environmental changes, such as those trapped in melting glaciers, permafrost, old-growth forests, drowning estuaries, and peatlands. These biological records are irreplaceable research and

development for our societies. Each time one of them is lost, we lose a benchmark for understanding how biological systems responded (or are likely to respond) to stressors acting on today’s biota in particular environments. The scale and time-sensitive nature of this problem requires a triage-based approach to “salvage” what we can before it is lost.

- Create an online clearinghouse of information about *Conservation Paleobiology* collections. This clearinghouse would enable conservation paleobiologists, as well as other stakeholders, including NGOs, resource managers, and governmental agencies, to locate scientific collections with potential value for their research. The clearinghouse would also provide a useful management tool for locating an appropriate repository for new or “orphaned” collections with scientific value.
- Sustain and enhance community-wide paleoecoinformatic efforts (i.e., the development and use of paleoecological databases and tools; Brewer *et al.*, 2012; NRC, 2012) to develop an online hub for data management (such as the Neotoma Paleoecology Database² and iDigBio³) to facilitate effective archiving and sharing of *Conservation Paleobiology* data. Currently, much of the data associated with *Conservation Paleobiology* research is accessible only in a distributed and uncoordinated way, often through individual initiatives. A dedicated infrastructure would provide transparent access to discipline-specific information critical to understanding biological response to environmental change.

LAB FACILITIES AND TOOLS

The research efforts proposed here require additional support for facilities and tools for high-precision geochronology and the analysis of ancient genetic diversity.

The community needs continued and increased support for dating facilities, including preparation and analyses for age determination using AMS-radiocarbon, Pb210 and associated short-lived isotopes, U-series, and amino acid racemization. The costs and in some instances the lag time presently associated with dating materials are prohibitive at most funding levels. Following NRC (2012: 82), we recommend that NSF “explore new mechanisms for geochronology laboratories that will service the geochronology requirements of the broad suite of research opportunities while sustaining technical advances in methodologies. The approaches may involve coordination of multiple facilities and investment in service facilities and may differ for distinct geochronology systems.”

Many workers in the paleontological community need increased support for next-generation DNA sequencing facilities. Currently, U.S.-funded science is very poorly represented in the paleogenetics research community, with only a couple of labs devoted to this objective. European labs are particularly strong where they are able to extend ancient DNA technology through infrastructure developed for human genetic analyses, in part due to the fortuitous presence of Neanderthal fossils on the continent, and in part because these labs can more easily devote funds to paleogenetic analyses. Their funding is orders of magnitude higher for ancient DNA extraction, amplification, analyses, and computation.

EDUCATION

Cross-disciplinary training in *Conservation Paleobiology* requires that the walls between traditional academic silos be broken down. However, depth as well as breadth is required; students need to be at the cutting edge of theory and instrumentation in at least one discipline. Although cross-departmental undergraduate programs in environmental science provide the rigorous basic science needed at the B.S. level, we need to take a fresh look at graduate and postdoctoral training. Again, grounding in a single discipline is necessary, but it is not sufficient. Academic training might not provide the real-world experience vital to the translation of basic science to ensure a broader impact in society.

We propose support for both undergraduate and graduate students to participate in summer or semester-long internships with agencies, commercial firms, and mainstream environmental NGOs (e.g., The Nature Conservancy, Conservation International, World Wildlife Fund). Provision of matching funds would greatly facilitate such internships. The students' experiences will enhance their formal training and strengthen their prospects for employment both within and outside of academic and research institutions.

The nature of research on *Conservation Paleobiology* should also be structured to encourage and support the collaboration of professional biologists, geologists, and other scientists, as well as the training of a highly flexible next generation of scientists who take such interactions for granted. To foster this, we recommend establishing a postdoctoral program by the NSF whereby new Ph.D.s would collaborate and have as their mentors PIs from other directorates—such matches have the advantage of engaging scientists very early in their careers, with potential for a longer period of positive downstream effects.

KNOWLEDGE EXCHANGE WITH STAKEHOLDERS

Scientists frequently perceive the translation of basic research into the practice of conservation, management, and restoration as a one-way flow of information from scientists to managers or other stakeholders. However, interactions must be truly collaborative, with scientists actively seeking advice and comments from managers and others (Cabin, 2011). Such “reverse communication” is starting to occur, with conservation needs influencing and even driving some paleobiological research. A workforce that can achieve this translation must be developed, along with the projects that involve genuine collaborations among diverse researchers and stakeholders. Scientists and managers can find common ground in acquiring sound scientific information for application to conservation issues of concern. Such projects will permit training of a workforce in which communication between realms is the norm.

Individuals and organizations who can utilize and benefit from *Conservation Paleobiology* include members of the public and private sectors, such as policy makers, land managers, landowners, NGOs, businesses, federal, state and local agencies, and educational institutions, from K-12 through university. Stakeholders will also inform conservation paleobiologists on those needs that can be addressed by basic research. A true exchange



Live-dead sampling on tidal flats in North Carolina, courtesy of Patricia Kelley

of knowledge and needs is essential. Scientists cannot presume to tell stakeholders what they need to know: stakeholders should also tell scientists what they need to know. This is not a call for applied science but a call for basic science that informs decision-making. We propose that NSF foster the development of initiatives that will encourage partnering among research scientists and policy makers/managers, and that will elucidate the application of *Conservation Paleobiology* to modern conservation efforts through public programs. These efforts should:

- Encourage partnerships between research scientists and industries and NGOs (e.g., consulting firms such as Weston Solutions and BioHabitats, The Nature Conservancy, Wildlife Conservation Society, Conservation International) through “visiting scientist” and postdoctoral programs.
- Enhance cooperation between research scientists and government agencies at federal, state, and local levels (e.g., water management districts, the Environmental Protection Agency, the U.S. Fish and Wildlife Service, the National Marine Fisheries Service, the U.S. Congress), by developing “scientist-in-residence” programs and providing opportunities for agency employees to pursue graduate degrees with emphasis in conservation biology.
- Leverage innovative funding partnerships among multiple agencies to address complex problems in conservation biology. A past example of such a program at NSF was the EPA-NSF Water and Watersheds program.

INTEGRATION WITH THE SOCIAL SCIENCES

It is increasingly recognized that the dynamics of ecological and social systems are inextricably linked (Carpenter *et al.*, 2009), with changes in ecosystem dynamics triggering societal responses. Opportunities thus exist for the development of new conservation research partnerships to understand how socio-ecological systems have evolved. To take full advantage of these opportunities in the *Conservation Paleobiology* and social science communities, organizational and data-related infrastructure issues and barriers will need to be addressed. We propose that NSF convene a workshop to bring together the broader community of “near-time” conservation paleobiologists and social scientists to identify a set of research objectives and infrastructure needs to ensure that the social sciences are a sustained and fully integrated component of ongoing *Conservation Paleobiology* research and practice. The current early stages of *Conservation Paleobiology* research formulation and agenda setting offer an unprecedented window of opportunity for making the changes needed to support effective integration in the long run.

OUTREACH

Conservation Paleobiology has immediate societal relevance, perhaps more so than any other paleontological discipline, and so it is critical that research results reach the public directly. The topic is a natural for fostering scientific literacy, and also supports informed decision making by citizens. To ensure that public outreach activities within the emerging *Conservation Paleobiology* community are not disconnected from each other, we propose the development of a community-guided knowledge management system to support coordinated outreach activities.

Models on which such an initiative could be based include (but are not limited to): EarthCube⁴, and the Geoscience Education and Public Outreach Network (GEPON⁵; Scotchmoor *et al.*, 2005). For *Conservation Paleobiology*, the integrated management system could be used to align the major communication goals (two or three central messages that everyone should know) among outreach providers. The management system will do this both through annual meetings of outreach providers and team scientists, allowing them to share ideas, and through the creation of a central repository of *Conservation Paleobiology* content that users could then repurpose for different media and audiences. That content will include ongoing research results of conservation paleobiologists.

To advance the integration of *Conservation Paleobiology* research and public outreach, we also recommend that NSF establish fellowship opportunities for professional development and cross-disciplinary learning, so that conservation paleobiologists and outreach professionals gain a greater appreciation of and confidence in each other’s respective discipline. NSF should also support meetings, workshops, and partnership opportunities between conservation paleobiologists, science education researchers, and education practitioners to promote dialog and a culture of these communities working together. Such interactions will ensure that outreach activities developed through *Conservation Paleobiology* research reflect current scientific understanding, teaching approaches, and the best strategies to disseminate results to the public, including educators, students, managers, and policymakers.



Learning about Devonian Seas



Obtaining a sediment core from Cupola Pond, Missouri Ozarks, by Stephen Jackson

7. CALL TO ACTION

Conservation Paleobiology has emerged over the past decade as a powerful intellectual approach and effective tool to acquire long-term perspectives on species, communities, and ecosystems beyond the time scales of direct human observation. The selected studies highlighted here illustrate how the discipline can help advance basic ecological and environmental theory and contribute to biodiversity and ecosystem services conservation and restoration.

We seek NSF's help to develop *Conservation Paleobiology* over the next decade and advance a broad-based science of biological vulnerability and resilience. *Conservation Paleobiology* needs investments in infrastructure to further develop analytical techniques and theory. Translation of *Conservation Paleobiology* into applications that benefit society also requires new cross-disciplinary educational and research opportunities for early-career research scientists and practitioners.

Our collective experience in research, education, outreach, and application in *Conservation Paleobiology* led us to the following approach, which we conclude will be most effective. We seek a funding allocation for a decade-long initiative to:

- support basic paleontological research and training aimed at conservation of biodiversity and ecosystem services; and
- promote innovative partnerships that will cut across disciplinary boundaries and leverage funding from other agencies and organizations.

This initiative will:

- strengthen the basic science in *Conservation Paleobiology*;
- identify research needs by improving communication and collaboration between scientists and resource managers;
- stimulate cross-disciplinary education and training for undergraduates, graduate students, postdocs, and managers through workshops, internships, fellowships, and scientist-in-residence programs;
- promote collection, curation, data management, and digital access to information on the natural archives of past environmental and biotic change; and
- enhance facilities and improve methods of high-resolution geological and biological analysis.

Fostering cross-disciplinary research and training in *Conservation Paleobiology* is a challenge that is best addressed by NSF. Participants who attended the "Conservation Paleobiology in the Coming Decades" workshop represent the cross-disciplinary mixture needed to advance the field. It was from that mixture that our vision for the future emerged. We seek to change how we address fundamental scientific questions and how we can better "translate" our science as a community, rather than as individual researchers. We seek to develop the best science to address pressing national needs.



Vertebrate bone assemblage on beach, Baja California, Mexico, by Gregory Dietl.

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CONSERVATION PALEOBIOLOGY: OPPORTUNITIES FOR THE EARTH SCIENCES

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WORKSHOP STEERING COMMITTEE

Gregory Dietl, Paleontological Research Institution (Co-chair)
Karl Flessa, University of Arizona (Co-chair, not present)
Stephen Jackson, University of Wyoming
Susan Kidwell, University of Chicago
Paul Koch, University of California, Santa Cruz

ADDITIONAL PARTICIPANTS AT WORKSHOP

Mark Brenner, University of Florida
David Burney, National Tropical Botanical Garden
Paul Dayton, Scripps Institution of Oceanography
Kate Freeman, Pennsylvania State University
Elizabeth Hadly, Stanford University
David Jablonski, University of Chicago
Brian McGill, University of Maine
John Pandolfi, University of Queensland
Beth Shapiro, Pennsylvania State University
Bob Steneck, University of Maine
Tom Swetnam, University of Arizona
Mark Vellend, University of Sherbrooke
Kathy Willis, University of Oxford

INVITED BUT COULD NOT ATTEND

James Estes, University of California, Santa Cruz
Mikael Fortelius, Helsinki University
Malcom Hunter, Jr., University of Maine
David Lodge, University of Notre Dame
Heike Lotze, Dalhousie University
Taylor Ricketts, World Wildlife Fund
Kaustuv Roy, University of California, San Diego
Dov Sax, Brown University
John Smol, Queen's University

REPORT WRITING COMMITTEE

Gregory Dietl, Paleontological Research Institution (Co-chair)
Susan Kidwell, University of Chicago (Co-chair)
Mark Brenner, University of Florida
David Burney, National Tropical Botanical Garden
Karl Flessa, University of Arizona
Stephen Jackson, University of Wyoming
Paul Koch, University of California, Santa Cruz

REPORT CONSULTING AUTHORS

Kate Freeman, Pennsylvania State University
Elizabeth Hadly, Stanford University
David Jablonski, University of Chicago
Brian McGill, University of Maine

For more information on *Conservation Paleobiology*,
see <http://www.conservationpaleobiology.org>.



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PHOTO CREDITS & ENDNOTES

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Figure 1 photo credits: From top, clockwise: Paraguay's Chaco forest being cleared for cattle grazing (image by Peer V); Perito Moreno glacier calving, Santa Cruz Province, Argentina (image by Christof Berger); commercial fishing in South Naknek, Alaska (image by echoforsberg); gypsy moth caterpillar, the "number one forest and shade tree pest in the Northeast" (image by Scott Bauer, U.S. Department of Agriculture); applying nitrogen fertilizer to growing corn in Hardin County, Iowa (image by U.S. Department of Agriculture).

ENDNOTES

¹<http://www.earth-time.org/>.

²<http://www.neotomadb.org/>.

³<http://www.idigbio.org/>.

⁴<http://earthcube.ning.com/>.

⁵<http://www.dpc.ucar.edu/gepon/>.

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