Conservation Paleobiology: Leveraging Knowledge of the Past to Inform Conservation and Restoration

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Keywords

Abstract

Humans now play a major role in altering Earth and its biota. Finding ways to ameliorate human impacts on biodiversity and to sustain and restore the ecosystem services on which we depend are grand scientific and societal challenges. Conservation paleobiology is an emerging discipline that uses geohistorical data to meet these challenges by developing and testing models of how biota respond to environmental stressors. Here we (*a*) describe how the discipline has already provided insights about biotic responses to key environmental stressors, (*b*) outline research aimed at disentangling the effects of multiple stressors, (*c*) provide examples of deliverables for managers and policy makers, and (*d*) identify methodological advances in geohistorical analysis that will foster the next major breakthroughs in conservation outcomes. We highlight cases for which exclusive reliance on observations of living biota may lead researchers to erroneous conclusions about the nature and magnitude of biotic change, vulnerability, and resilience.

1. INTRODUCTION

Humans are now the principal architects of environmental and biotic change on planet Earth. In response, conservation paleobiology has emerged over the past decade as a powerful intellectual approach and effective tool for acquiring longer-term perspectives on changes in species, communities, and ecosystems, beyond the limited time frame of direct human observation, and applying this information to pressing conservation issues (Birks 1996, 2012; Delcourt & Delcourt 1998; Swetnam et al. 1999; Gorham et al. 2001; Flessa 2002; NRC 2005; Willis & Birks 2006; Froyd & Willis 2008; Gillson et al. 2008; Smol 2008; Dietl & Flessa 2009, 2011; Jackson & Hobbs 2009; Willis & Bhagwat 2010; Willis et al. 2010a,b; Vegas-Vilarrúbia et al. 2011; CPW 2012; Louys 2012; Lyman 2012a,b; Sayer et al. 2012; Rick & Lockwood 2013; Gillson & Marchant 2014). The overarching goal of conservation paleobiology is to use geohistorical analysis to develop knowledge, principles, and tools for conserving and restoring biodiversity and ecosystem services in the face of climate change and other human impacts (Dietl & Flessa 2011, CPW 2012).

Research in conservation paleobiology generally takes two approaches. A near-time approach uses the relatively young fossil record, primarily from the past 2 million years, to provide a context for present-day conditions, focusing largely on extant species. Such geohistorical records are used to (*a*) define baselines to compare conditions before and after disturbance, (*b*) examine the response of species and ecosystems to recent natural and anthropogenic perturbations, (*c*) develop a narrative of the historical range of variability, (*d*) set realistic targets for restoration, (*e*) differentiate between anthropogenic and nonanthropogenic change, and (*f*) recognize ecological legacies that can be explained only by events or conditions that are not present in the system today. A deep-time approach uses the much older geologic record as an archive of repeated natural experiments. This approach permits analysis of biotic responses to system perturbations of diverse kinds and magnitudes, some of which approximate present-day disturbances or those predicted for the near future, such as substantial climate warming and ocean acidification. The deep-time approach also permits testing of biotic responses under a broader array of conditions than is available in the modern world or its recent past. In particular, observation of consistent patterns involving now-extinct species at remote periods in the past can strengthen the ecological theory underlying conservation practice.

In this review, we illustrate how geohistorical analysis informs both the practice of conservation biology and our general understanding of biotic responses to stress. This review is drawn from a National Science Foundation–funded workshop, "Conservation Paleobiology in the Coming Decades," convened at the Paleontological Research Institution in Ithaca, New York, June 3–5, 2011, and its resulting report (CPW 2012).

2. ENVIRONMENTAL STRESSORS

Both near-time and deep-time approaches to conservation paleobiology are motivated by efforts to understand biological vulnerability and resilience. The most important direct drivers of current biodiversity loss and change in ecosystem services are habitat change (Section 2.1), climate change (Section 2.2), overexploitation (removal) of wild species (Section 2.3), spread of invasive species (Section 2.4), and disturbance or disruption of biogeochemical cycles (Section 2.5) (MEA 2005). Geohistorical analysis can address biotic response(s) to these stressors on timescales that are appropriate to the biological and environmental phenomena of concern (e.g., the long individual life spans of key forest and reef species and community assembly by migration), which are typically beyond the temporal reach of direct scientific observation.

2.1. Habitat Change

Humans have modified more than half of Earth's ice-free land (Hooke et al. 2012). Profound anthropogenic changes include deforestation for agriculture and urban development, damming and channelization of rivers, draining of wetlands, and armoring of coasts. In coastal and open seas, "dead zones" have spread globally since the 1960s and are now reported from 400 regions (Diaz & Rosenberg 2008). By the early 2000s, if the effects of fishing and by-catch are included, every square kilometer of ocean had been affected by an anthropogenic driver of ecological change (Halpern et al. 2008). Predicting biotic responses to anthropogenic habitat change using only direct observations has proved difficult because estimates of the timing and extent of biodiversity change have large uncertainties.

Paleoecological studies have revealed responses that could not have been predicted solely from modern ecological data and theory. For example, using the Quaternary fossil record from islands in the Gulf of California, Wilcox (1978) found that lizard species richness was determined more by the duration of island isolation than by island area, contrary to expectations from the species-area effect. Although islands became isolated and their habitable area became smaller with sea-level rise, lizard species richness did not decline to the theoretically expected values for such small areas for at least 10,000 years. Similar lagged responses have been documented for small alpine mammals, and century-scale lags (e.g., in birds) to millennial-scale lags (e.g., in conifer forests) have been detected or inferred (Ewers & Didham 2006).

Sediments from lakes, estuaries, and caves provide particularly useful geohistorical records for assessing the long-term effects of habitat change on biota. For example, raptor-concentrated bone assemblages from two caves revealed significant changes in small-mammal communities in response to land-use changes in the Great Basin of the western United States (Terry 2010). Community evenness and richness, as well as the identity of the most abundant species, have changed significantly since the mid-1960s in an area of Utah that became a military test site at that time but have remained unchanged over the past century in a relatively undisturbed counterpart area in Nevada.

Geohistorical analysis is especially important for restoration ecology, informing us about both what has been lost and what is required to restore altered ecosystems and their functions. Paleoecological studies, for example, documented the response of the delta ecosystem in the northern Gulf of California to habitat change driven by upstream damming of the Colorado River and diversion of water to cities and farms in the United States and Mexico (summarized by Calderon-Aguilera & Flessa 2009). Biotic responses include a 94% reduction in the population densities of the endemic Colorado delta clam, *Mulinia coloradoensis*. All that remains of this once abundant clam is a very small population of living individuals and an estimated two trillion empty shells, preserved in wave-generated beach ridges.

2.2. Climate Change

Biotic responses to recent climate changes have been studied largely using observational data on living plants and animals. Empirical and theoretical models that relate biotic responses to climate change, however, are difficult to validate using the limited range of recent climate variability. Geohistorical records provide unique information on the biological consequences of climate changes of different types, rates, magnitudes, and durations (MacDonald et al. 2008, Willis et al. 2010a).

For example, radiocarbon-dated records of pollen, charcoal, and macrofossils (e.g., plants, insects, mollusks, corals, and vertebrates) revealed both fast and slow biotic responses to climate changes over the Holocene, i.e., the past ~10,000 years. Some species maintained local populations

despite major climate changes, whereas other species shifted along local elevational, topographic, and microhabitat gradients (Jackson & Overpeck 2000, Dawson et al. 2011). The ranges of other species shifted at regional to subcontinental scales, with range displacement from the early to late Holocene spanning 10–1,000 km (Dawson et al. 2011). Studies of ancient DNA revealed climate-driven changes in population size or population replacement (de Bruyn et al. 2009, Kuhn et al. 2010), genetic erosion as populations isolated by climate change were overrun by a species with which they can hybridize (Cahill et al. 2013), and other climate-driven responses (Ramakrishnan & Hadly 2009).

Geohistorical records that extend to the limits of ^{14}C dating, i.e., the past 50,000 years, reveal biotic responses to glacial conditions and the complete deglacial period, which commenced ~20,000 years ago and included episodes of gradual and rapid warming and cooling (e.g., Younger Dryas cooling approximately 12,800–11,500 years ago). The period spanning the past 50,000 years was characterized in many regions by combinations of plants and animals that are different from any that exist today, that is, novel or no-analog assemblages (Jackson & Williams 2004), as well as by changes in species ranges (Birks & Willis 2008), population size (Blois & Hadly 2009), genetic diversity (from ancient DNA; Hadly & Barnosky 2009), and morphology (Bruzgul et al. 2005). The period was also characterized by different rates of community turnover (Birks & Birks 2008) and trophic dynamics (Gill et al. 2012).

Geohistorical records more than ~50,000 years old, i.e., beyond the reach of ^{14}C, are characterized by an even broader range of climate conditions. They can be dated by different methods (e.g., U/Th, ^{40}Ar/^{39}Ar, varve counting, orbital stratigraphy) and can be temporally correlated using event horizons such as regional volcanic ash layers, global isotope signatures, and sediment paleomagnetic properties. The range of rates and magnitudes of climate change over long time spans provides countless natural experiments for which ecological and evolutionary responses can be inferred (Willis & MacDonald 2011, Dietl 2013) to help constrain predictions and yield general insights into biotic response. For example, the body size of many mammals, including the early horse *Sifrhippus sandrae* (**Figure 1**), decreased by 30% or more over a time interval of less than 10,000 years, largely as an adaptive response to increasing temperature in western North America during the Paleocene–Eocene Thermal Maximum (PETM) ~56 million years ago (Secord et al. 2012). These trends are consistent with increasing evidence collected by biologists documenting a general pattern of reduced body size for a diversity of species living today, which is linked to a warming climate over the past century (Gardner et al. 2011).

Studies of biotic responses to large, past changes in temperature sometimes reveal clearer patterns than studies of modern systems. For example, there is growing concern that diverse tropical and subtropical crop pests and pathogens will expand poleward with global warming, but the signal is noisy, in part because of observation biases (Bebber et al. 2013). Warming during the PETM and later warm events in the Eocene are associated with abrupt, unambiguous increases in the frequency and diversity of insect damage to North American plants (Labandeira & Currano 2013). This finding makes it clearer that damaging insect outbreaks will likely increase in temperate and boreal habitats with further anthropogenic warming.

2.3. Exploitation (Removal) of Wild Species

The scarcity of well-documented time series, especially for periods before governmental mandates such as the US Endangered Species and Clean Water Acts of the early 1970s, poses a significant barrier to assessing the impact of human exploitation on species and ecosystems. Geohistorical records are rich and largely untapped archives of information on the effects of resource
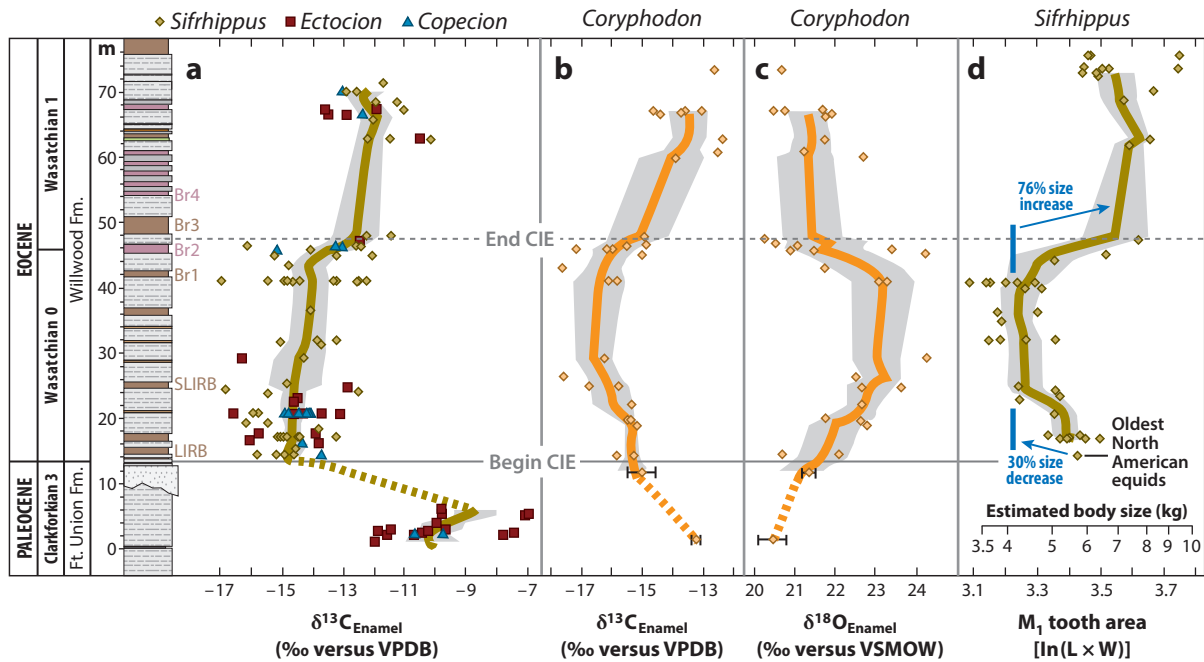
Paleocene–Eocene Thermal Maximum (PETM): <10,000-year period of exceptional and rapid global warming that occurred about 56 million years ago

Figure 1

Trends in climate change (inferred from stable carbon and oxygen isotopes) and body size of horses (*Sifrhippus*) during the Paleocene–Eocene Thermal Maximum (PETM) from the Cabin Fork area of the southern Bighorn Basin, Wyoming. (*a,b*) Carbon isotope trends in tooth enamel ($\delta^{13}C_{Enamel}$) of three common mammal genera (panel *a*) and *Coryphodon* (panel *b*), a large semiaquatic mammal, which show an abrupt negative carbon isotope excursion (CIE) that lasted ~175,000 years. (*c*) Oxygen isotope trends derived from tooth enamel ($\delta^{18}O_{Enamel}$) for *Coryphodon*. (*d*) Change in body size—indexed as log-transformed first lower molar area (length × width)—for *Sifrhippus*. Body size of *Sifrhippus* is negatively correlated with temperature derived from $\delta^{18}O_{Enamel}$ values in *Coryphodon*. Standards: VPDB, Vienna Pee Dee Belemnite; VSMOW, Vienna Standard Mean Ocean Water. Key marker beds: LIRB, lowest intermittent red bed; SLIRB, second-lowest intermittent red bed; Br, Big Red sequence. Modified from Secord R, Bloch JI, Chester SGB, Boyer DM, Wood AR, et al. 2012. Evolution of the earliest horses driven by climate change in the Paleocene-Eocene Thermal Maximum. *Science* 335:959–62 (Secord et al. 2012). Reprinted with permission from AAAS.

depression by humans on organismal behavior, body size, age structure, and abundance and on species composition of communities on land (Grayson 2001) and in the sea (Jackson et al. 2001).

For example, Edgar & Samson (2004) used down-core changes in shell assemblages to assess how the scallop-dredging industry affected molluscan populations in Tasmanian estuaries over the past century. Using ²¹⁰Pb and concentrations of metal pollutants to develop an independent age model, they found strong, otherwise undocumented declines in species diversity and raw abundance, coincident with the known history of commercial harvest of two scallop species. These geohistorical data corroborated the suspicions of local fishermen that dredging had been a primary driver of the collapse of the scallop fishery, and raised new questions about other effects on the ecosystem.

A long-term perspective on resource exploitation can also exonerate human agency. For example, Baumgartner et al. (1992) used fish scales from cores of annually varved marine sediment to establish that abundance variations of two key commercial species off the California coast (sardines and anchovies) were strongly cyclic and out of phase with one another on decadal scales over the past 1,700 years. These data suggested that sharp twentieth-century declines in one species and concomitant rises in the other, a pattern evident in commercial fishery data, probably reflected

natural climate oscillations or regime changes in the Pacific rather than alternating human over-exploitation of one species and then the other (see also lake records of mixed climate and fishing impacts on salmon biomass; Finney et al. 2000, 2002).

Paleobiological study of exploited species that declined and recovered reveals 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 about 1800 CE but attained high abundance following protection in the early twentieth century. Isotopic and demographic data from fossils revealed that the species was capable of greater flexibility in its reproductive strategies than is exhibited by extant populations, contributing to its adaptability (Newsome et al. 2007). Ancient DNA revealed that high dispersal rates and Arctic refugia prevented loss of genetic diversity in this marine mammal (Pinsky et al. 2010), also making it resilient to environmental changes. The fossil record also can be used to evaluate the success of species reintroductions by comparison with species composition, ecological interactions, or ecosystem processes in ancient systems. For example, isotopic analysis of bone collagen of reintroduced California condors showed that these endangered birds recently rediscovered marine carrion (whales and seals), a food source they exploited in the Pleistocene (Chamberlain et al. 2005).

2.4. Biological Invasions

Studies of human-assisted species invasions have focused mainly on the short-term biological consequences that have occurred over the past century, a timescale over which the process of invasion has probably not been fully realized, especially if evolutionary adaptation is considered (Vermeij 2005). The fossil record of past invasions can provide opportunities to explore the long-term consequences of invasion (Gillson et al. 2008, Dietl 2009), placing human-assisted invasion in a broader temporal context (Vermeij 2005).

For example, the deep-time fossil record shows that many successful invasions are highly asymmetric, with the predominant direction of invasion going from larger, biologically more diverse areas to smaller, less diverse areas (e.g., Beard 1998, Vermeij 2005). Paleontological evidence, however, suggests that prior or ongoing disturbance in a region can be important in regulating invasion intensity (Jablonski & Sepkoski 1996, Valentine et al. 2008), and that intrinsic features of invaders, such as body size and dispersal ability, can play a role in differential range expansion among clades (e.g., Roy et al. 2002, Jablonski et al. 2013). Such observations could help identify the likely direction of future, large-scale biotic interchanges—the spread of many species from one geographic area to another—as Earth's climate warms over the next century (Vermeij & Roopnarine 2008, Lawing & Polly 2011).

The fossil record also can be tapped to understand how natural selection affects both invaders and species in recipient communities (Vermeij 2005, Dietl 2009). For example, Kerfoot & Weider (2004) conducted genetic analysis on laboratory-hatched eggs of the cladoceran *Daphnia retrocurva*, which were extracted from sediment cores taken in Portage Lake, Michigan. They found that since invading the lake in the mid-twentieth century, *D. retrocurva* adapted to changes in the relative abundance of invertebrate and vertebrate (fish) predators by evolving morphological defenses such as spines. This kind of information is useful in predicting how interactions between the invader and the recipient biota will evolve over the course of an invasion (Gillson et al. 2008, Dietl 2009).

Geohistorical data have also proved helpful to refine the concepts of native and non-native species (Jackson 1997). For example, pollen data from the Galápagos Islands showed that several presumed non-native plant species that were widespread and difficult to control were in fact native (van Leeuwen et al. 2008, Coffey et al. 2011). Similarly, paleoecological studies indicate that some large herbivores, considered by management agencies to be deleterious invasives, may

in fact be returning natives, or are at the least assuming the role of now-extinct natives. Grazing of salt marshes on the east coast of the United States by feral horses, descended from Spanish herds, appears to promote higher bird diversity, crab density, and other outcomes that are considered positive (Levin et al. 2002). Native North American horses were members of the regional community from the PETM until the Late Pleistocene, just 11,000 years ago. Such empty niches may stem from relatively recent, perhaps human-driven extinctions. This realization has led to the idea of Pleistocene rewilding, especially for large-bodied herbivores and carnivores that, as a trophic group, are key components of food webs elsewhere (Donlan et al. 2005, 2006). Rewilding has sparked heated debate in North America. In contrast, 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 example, paleoecological records from Makauwahi Cave, Hawaiian Islands, demonstrated the prehuman presence of rails (*Gallirallus* spp.) and other birds, motivating a successful program of avian reintroduction (Burney & Burney 2007).

2.5. Biogeochemical Disturbance

Using only short-term, direct observation and experiment to understand biotic responses to human-induced biogeochemical disturbance has proved difficult because of scaling issues and inadequate characterization of the timing and magnitude of disturbance. These shortcomings are issues for both terrestrial and marine systems and are especially problematic at the regional scale of individual ecosystems, where global trends may or may not be evident.

Paleobiological archives such as ocean cores, lake sediments, deep-sea corals, and tree rings have revealed the timing and pervasiveness of anthropogenic biogeochemical perturbations. For example, the massive increases in reactive nitrogen release associated with Haber–Bosch fertilizer production and fossil fuel combustion have profoundly altered the global nitrogen cycle (Galloway et al. 2008). These impacts have been documented primarily near human population centers, but Holtgrieve et al. (2011) used nitrogen isotope records from boreal and high-altitude lakes in the Northern Hemisphere to show that substantial increases in nitrogen deposition began in remote ecosystems at the dawn of the twentieth century and accelerated after World War II. Many Arctic lakes have experienced large changes in species composition since 1850 (Smol et al. 2005), but partitioning the impacts of multiple stressors on these systems (e.g., climate change versus pollution) requires more work.

Deep-time records provide an unparalleled view of the biogeochemical consequences of rapid carbon addition and high-CO_2 worlds. For example, the rapid ($<$10,000 years) injection of massive amounts ($>$5,000 pedagrams) of new carbon into the atmosphere-ocean-biosphere system at the PETM led to dramatic ocean acidification, manifested by dissolution of seafloor carbonates and a decrease in carbonate export production, followed by an even larger pulse of biogenic carbonate accumulation during the recovery, which appears to signal carbonate oversaturation associated with enhanced silicate weathering under hot, and perhaps wet, climate conditions (Zachos et al. 2008). More troubling with respect to future scenarios for fossil fuel combustion, the recovery from such massive CO_2 injections into the atmosphere takes tens of millennia, as is also predicted from carbon cycle models. The message for the future from the distant past is very clear—if humans continue to emit large amounts of new carbon into the atmosphere-ocean-biosphere system, that carbon will remain at Earth's surface for a period much longer than the entire past history of human civilization (Caldeira et al. 2013).

The biogeochemical and biotic consequences of high pCO$_2$ and ocean acidification have been explored in a number of systems. For example, Hannisdal et al. (2012) used fossil coccolithophores to predict the future biotic response of calcifying marine phytoplankton to rising pCO$_2$ and ocean

acidification. Their data show that coccolithophores were more abundant, more widespread, larger, and more heavily calcified in the world's oceans during the greenhouse conditions of the Eocene than they are today. These results are consistent with theory, experiments, and observations on coccolithophores over the past two centuries (Halloran et al. 2008, Irie et al. 2010), all of which suggest that these key producers of open-ocean carbonate have the capacity to adapt to changes in ocean pH.

Surprising biotic responses to past biogeochemical disturbances have also been observed in terrestrial ecosystems. For example, ecological theory predicts that changes in the availability of resources such as nitrogen should lead to changes in plant community composition as a consequence of different species-specific nutrient requirements. On the basis of paleoecological data on forest species composition over an 8,000-year interval that was interrupted by abrupt climate warming, Jeffers et al. (2011) found that disturbance of the nitrogen cycle did not drive secondary succession from a coniferous to a deciduous forest, contrary to expectations.

3. MULTIPLE ENVIRONMENTAL STRESSORS

Most modern ecosystems are subject to multiple human and natural stresses, and their present states probably reflect complex cumulative or relay histories of stress and stress release. Interactions among multiple stressors are thought to lead to biological outcomes that are qualitatively and quantitatively different from those produced by single stressors (Christensen et al. 2006, Brook et al. 2008, Crain et al. 2008, Darling & Côté 2008). Without knowing how stressors interact with one another across relevant scales, however, we will not be able to develop effective adaptation strategies (sensu Dearing et al. 2012) that enhance resilience to future environmental change.

In this respect, geohistorical records contain abundant data relevant to conservation biology. Such records contain information needed to (*a*) identify thresholds in system histories that may presage collapse or interfere with recovery, (*b*) reveal feedbacks that stabilized systems in the past, (*c*) recognize interactive effects among multiple stressors, which may amplify or dampen impacts of individual environmental stressors, (*d*) gain insights into the duration of lag effects in ecosystem response, (*e*) assess controls on "slow" processes in ecosystems, and (*f*) quantify effects and frequencies of rare events in ecosystems and the time needed to recover from them. Conservation paleobiology can address these issues in unique ways.

Geohistorical records provide the long-term perspective needed to identify past threshold events, i.e., sudden changes in the state of an ecosystem after prolonged stability, despite sustained or intensifying stress (Folke et al. 2004, Scheffer 2009). For instance, abrupt loss of submerged aquatic vegetation in tributaries of the upper Chesapeake Bay in the early 1970s was unexpected because water quality changes (e.g., nutrient stress) had been occurring in the estuary for more than a century. Biologists speculated that the reduction in submerged aquatic vegetation represented natural population fluctuations. Seeds preserved in estuarine sediment cores over the past 2,000 years, however, showed that this ecological shift was a threshold response to land-use changes (e.g., heavy use of fertilizer for agriculture), which began two centuries earlier and intensified in the mid- to late nineteenth century (Brush & Hilgartner 2000).

Geohistorical time series provide a means for testing whether increased variability (Carpenter & Brock 2006) or slower rates of recovery from disturbance (van Nes & Scheffer 2007, Scheffer et al. 2009) can serve reliably as early warnings of impending major changes in ecosystems at local, regional, and global scales (Gorham et al. 2001, Barnosky et al. 2012, Hughes et al. 2013). For example, Wang et al. (2012) combined diatom assemblage data from sediment cores of a eutrophic lake in Yunnan, China, with a mathematical model to show that flickering—the back and forth switching between alternative states in response to environmental stress—may be an early warning

signal of a critical transition. The abrupt shift to an alternative, stable, eutrophic lake condition in the early 2000s was preceded by increasing variance coupled with decreasing autocorrelation and skewness in the diatom data since the early 1980s, which may have been related to the interaction of multiple environmental stressors (e.g., increased nutrient loading and climate change). The 10–30-year interval of flickering recorded in the sediment cores contrasted with nearly 750 years of relatively low variability in the composition and diversity of the diatom community (Wang et al. 2012).

Geohistorical time series also have been used to identify feedbacks involved in threshold events. For example, Ireland & Booth (2012) used core-derived paleoecological data to show that upland deforestation by European settlers triggered an ecosystem state shift in an adjacent wetland area in Pennsylvania. Land clearance increased rates of wind erosion of exposed soils and transport of nutrients to the wetland. The wetland plant community shifted from largely *Sphagnum* moss to vascular plants, coincident with nutrient enrichment. The decomposition rate, estimated from the proportion of highly decomposed plant material in the cores, was higher in postsettlement vascular plant communities than in presettlement *Sphagnum*-dominated communities, perhaps because nutrient enrichment stimulated microbial decomposition, which is typically limited in nutrient-poor wetlands. The higher rates of decomposition suggest that more rapid nutrient cycling provided a feedback mechanism to sustain the new, postsettlement ecosystem state.

Geohistorical data have proved valuable for discriminating the multiple stressors and their interactions involved in abrupt ecosystem changes. For example, according to direct observations, Caribbean reef corals have suffered a dramatic decline since the 1980s, with the onset and intensification of coral bleaching and disease events attributed to (anthropogenic) climate change (Harvell et al. 1999, Donner et al. 2007). Sediment cores demonstrate how unprecedented these changes are over the past several thousand years, in most instances, and can reveal the role of the other contributing or more important stressors. In Panama back-reef communities, for example, high-sediment and high-nutrient runoff from agricultural lands is the more likely driver of a shift to a new dominant coral (*Agaricia*), following millennia of dominance by *Porites*, and to a much simplified food web (Cramer et al. 2012), with the threshold crossed perhaps as recently as the 1970s (Aronson et al. 2014). Similarly, Virah-Sawmy et al. (2009) used a multiproxy approach to show that the combined effects of aridity and sea-level rise were required to achieve a threshold shift from closed littoral forest to open *Erica*-dominated heathland along the coast of Madagascar during the late Holocene (**Figure 2**).

Geohistorical data can also provide insights into the duration of lag effects in ecosystem response. For example, meta-analyses of historical trajectories in coastal ecosystems found that the collapse of trophic webs—that is, the functional extinction of apex predators, large herbivores, or habitat-forming engineers—may occur several decades to centuries after the onset of intense exploitation of an ecosystem (Jackson et al. 2001, Lötze et al. 2006). Such collapses seem to require multiple stressors, for example, urban-sourced eutrophication in addition to exploitation, but appear to be slowed by numerous ecologically redundant species in each trophic level, which compensate for the loss of other species.

Many controls on slow processes (sensu Carpenter & Turner 2001) in ecosystems that occur over geological timescales can be understood only by using geohistorical records (NRC 2005). For example, Seddon et al. (2011) used sediment cores to investigate the ecological resilience of coastal mangrove communities in the Galápagos Islands over the past 2,700 years. They found that a combination of fast and slow processes, such as increased aridity stress from precipitation changes over annual to decadal timescales and slowly falling sea level over centuries (attributed to isostatic processes), eroded community resilience and drove a threshold response to an alternative stable state, whereby the mangrove community was replaced by microbial mats.

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Multiproxy approach: use of more than one proxy to reconstruct past environmental conditions
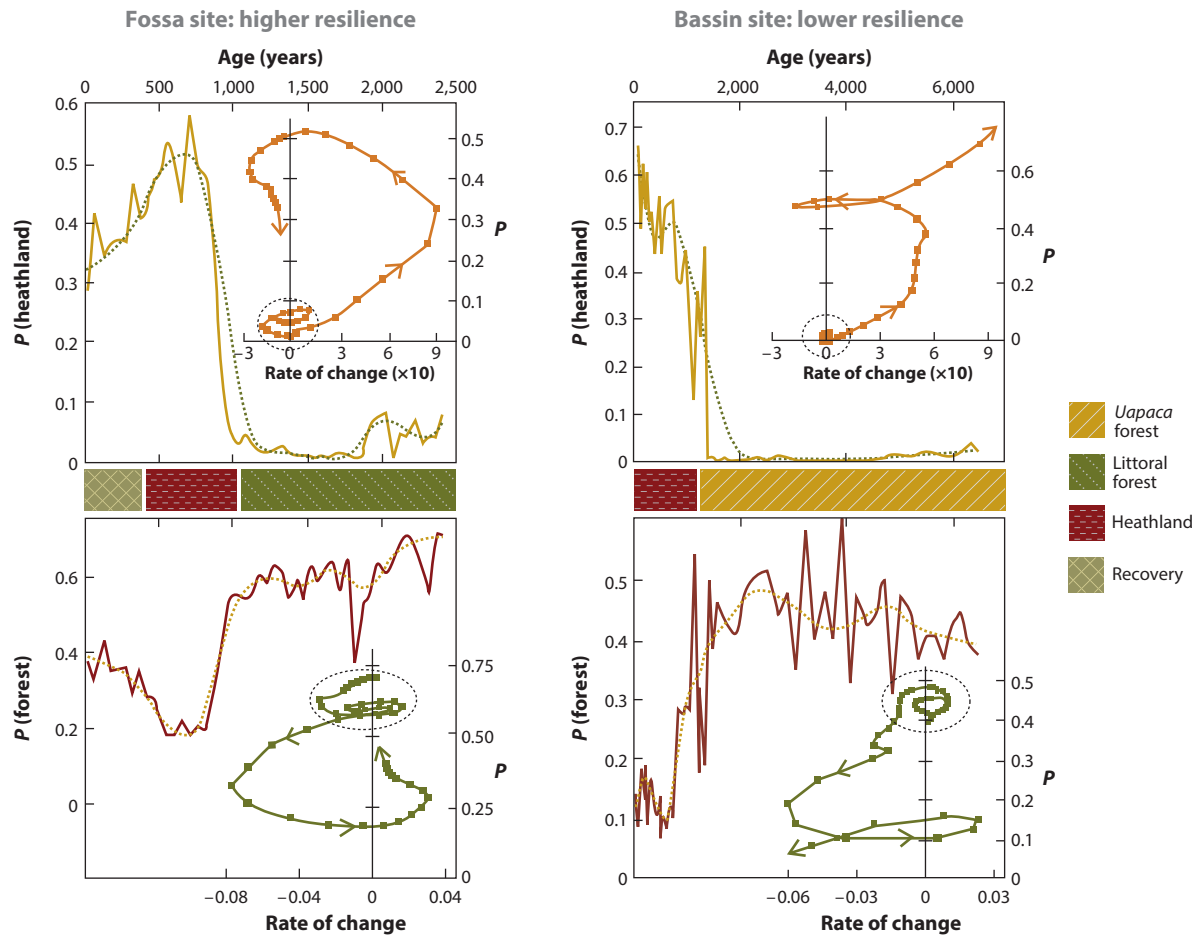
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Figure 2

Response of vegetation (*P*, relative pollen abundance) at two sites, Fossa and Bassin (Madagascar), to environmental stress (sea-level rise and climatic aridity) about 1,000 years ago. Both sites experienced a threshold shift from forested conditions (littoral forest tree species and open *Uapaca* forest tree species) to heathland (*Erica*, Asteraceae, and grass species) in response to the combined effects of arid climate and sea-level rise. The vegetation state at the Fossa site subsequently recovered toward the earlier forested condition (high resilience), whereas at the Bassin site there is no sign of recovery (low resilience). The proximity of points along lines in phase plots (*insets*) indicates the rate of change in system state; arrows indicate the direction of time, and dashed ovals enclose the stable (forest) state prior to environmental stress (>1,200 years ago). Modified from Willis KJ, Bailey RM, Bhagwat SA, Birks HJB. 2010. Biodiversity baselines, thresholds and resilience: testing predictions and assumptions using palaeoecological data. *Trends Ecol. Evol.* 25:583–910 (Willis et al. 2010a). Copyright 2010, with permission from Elsevier.

A long-term perspective also is needed to study the effects on ecosystems of large, infrequent disturbances such as droughts, floods, hurricanes, and wildfires (Turner & Vale 1998). For example, Urquhart (2009) used various signals of hurricane disturbance in sediment cores to assess posthurricane regeneration of forests along the coast of Nicaragua over the past 8,000 years. Pollen data and a radiocarbon-based age model indicate that ~500 years was required for forests to recover after a major hurricane 3,300 years ago.

These examples highlight that conservation paleobiology research is entering a new era, building on a foundation of advances in basic and applied use of geohistorical records to understand the

effects of single environmental stressors on biota. The interrelated topics we outline above require increased research effort if we are to improve understanding of the dynamics of interactions among multiple stressors and their consequences in biological systems.

4. DELIVERABLES

Conservation paleobiology has demonstrated its utility to conservation biologists and resource managers. Indeed, paleontological studies increasingly influence decisions regarding priorities and challenges in conservation and restoration. We focus here on cases for which erroneous conclusions about the nature and magnitude of biotic change, vulnerability, and resilience would be reached if only direct observations of living biota and environmental conditions were used.

4.1. Identifying Invasive Species

Distinguishing native from non-native taxa is a first-order challenge for conservation and restoration efforts. However, the flora and fauna that characterized an area prior to human colonization are poorly known. Paleoecology has documented precolonization biota and revealed many surprises, including that some species assumed to be exotic are in fact native. For example, although *Pandanus tectorius* (screw pine) and *Cordia subcordata* were thought to have been introduced into the Hawaiian Islands by colonizing Polynesians, pollen and seed evidence 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.

4.2. Measuring Historical Variability

Resource managers on federal lands in the United States and in other countries use the historical range of variability (HRV) as a dynamic management target (Keane et al. 2009). Paleoecological records with relatively high—i.e., annual to decadal—resolution (with minimal time-averaging per sampled assemblage) 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 trend (Willard & Cronin 2007, Smol 2010). For example, Wolfe et al. (2001) studied sediment cores from two alpine lakes in the Colorado Front Range and showed that an increase in the abundance of mesotrophic diatoms and increasingly ^{15}N-depleted sediments were responses to excess nitrogen derived from agricultural and industrial sources since the 1950s. The rate and magnitude of these shifts far exceeded 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 (Jackson 2012a).

4.3. Quantifying Past and Present Biodiversity

Paleontological studies indicate that estimates of species richness and diversity made using only live-collected organisms can be deceiving, because modern ecosystems are often so disturbed that biodiversity estimates can be compromised by both the presence of exotic species and the commonly unrecognized loss of endemic taxa. For example, the bone assemblage in a Madagascar cave showed that the vertebrate community of the surrounding semiarid spiny bushlands was much more diverse only a few millennia ago than it is today. Many key guilds are now missing as a consequence of human-caused extinctions or range contractions (Burney et al. 2008). Additionally,

Historical range of variability (HRV): variation in past ecological conditions over time and space that is relevant to resource management

without evidence provided by the plant fossil record, extinction of the aquatic fern *Azolla nilotica* in Egyptian Nile Delta lakes, as recently as the 1960s, would not have been recognized (Birks 2002). Furthermore, the likely causes of its extirpation—a change from year-round inflow of fresh irrigation water and a rise in the freshwater table as a consequence of inadequate drainage—would have remained obscure.

4.4. Detecting Recent Shifts in Species Abundance

Declines in a species population that fall short of local extinction can be difficult to detect without dedicated, continuous monitoring. Most knowledge of temporal trends of abundance is limited to presence-absence or semiquantitative estimates. 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, Hawaii, to show that rare plant species now restricted to remote montane habitats on the island were widespread in coastal lowlands before human colonization. Discordances in the presence and relative abundances of species between living communities and time-averaged death assemblages collected from surficial sediments are also well-established signs of recent changes in the living community. Rather than signifying postmortem bias in preservation, large "live-dead" differences reflect recent, decadal- to centennial-scale changes in the composition and richness of living communities, often driven by eutrophication, climate and habitat change, introduction of invasives, and exploitation (Kidwell 2007, 2013; Western & Behrensmeyer 2009; Terry 2010; Miller 2011; Yanes 2012; for review, see Kidwell & Tomasovych 2013).

4.5. Predicting Shifts in Species Geographic Range

Predicting changes in species' distributions under different scenarios of climate change is a major objective in conservation biology. Paleoecological data can be used to detect shifts in geographic distribution of species in response to recent climate change. For example, bones from now-abandoned breeding sites of Adélie penguins on Anvers Island, Antarctic Peninsula, show that these sites were occupied exclusively by that species back through the Little Ice Age (~1400–1850 CE) and that the gentoo and chinstrap penguins now breeding there have expanded their ranges to this region only within the past 50 years, presumably in response to climate warming (Emslie et al. 1998). The fossil record is also sometimes the sole means to indicate where species occurred in the past, beyond their present-day geographic range. For example, Greenstein & Pandolfi (2008) used fossil occurrences in seacliffs along the coast of Western Australia to document how reef-building coral species shifted their distribution in response to climate change since the Late Pleistocene. This understanding enabled them to forecast coral response to future climate warming. Tropical-adapted coral species are predicted to migrate south along the coast of Western Australia and persist in temperate refugia. Knowing where and which coral species might migrate is critical to developing effective management practices that enhance their chances of survival in an era of climate warming.

4.6. Assessing Changes in Genetic Diversity and Identity

Ancient DNA (aDNA) technology has opened new opportunities for assessing the genetic consequences of population bottlenecks and other effects of human stressors and environmental changes in general (Ramakrishnan et al. 2005, Leonard 2008, de Bruyn et al. 2011). For example, working on fossil bones from Macquarie Island in the southwest Pacific Ocean, Heupink et al. (2012)

found that the king penguin (*Aptenodytes patagonicus*), which was nearly driven extinct by human exploitation in the 1800s, has recovered more than 85% of its past genetic diversity in response to recent conservation efforts. Vilà et al. (2003) also used aDNA to confirm that a population of Scandinavian wolf (*Canis lupus*) was founded by migration of wild individuals, not by illegally reintroduced zoo animals, and thus was subject to legal protection.

4.7. Documenting Shifting Baselines

Scientists and nonscientists alike are trapped in the present. Our expected norms for biodiversity and ecosystem services are set by what we experience, and thus, with each successive generation, the expectation is altered and usually diminished. Explicit effort is required to counteract this so-called shifting baseline phenomenon (Pauly 1995), using historical information to inform experiential norms (Jackson et al. 2011). Paleobiological studies are useful to (*a*) recognize that ecological conditions have in fact changed, (*b*) establish the timing of the change and thereby disentangle possible anthropogenic from natural drivers, and (*c*) in the best cases, establish "what was natural" or at least what biological conditions prevailed at some specified time in cultural history (see Swetnam et al. 1999, Jackson 2001, Willis & Birks 2006).

Although "natural" is a moving target when viewed through the lens of geohistorical records (e.g., Jackson & Hobbs 2009), paleoecological analyses reveal the deep roots of human and natural alteration of landscapes, coastlines, and even the open sea (Jackson et al. 2001, Jackson 2012a). Such analyses can have direct value for management. For instance, paleontological evidence shows that progressive diversion of Colorado River water in the twentieth century had major impacts on the productivity of the northern Gulf of California. These impacts include the functional extinction of a key bivalve species and suppressed growth rates in the iconic fish *Totoaba macdonaldi*, among other faunal effects, and yielded the first science-based estimates of the water flow across the US-Mexico border that will be needed to restore some modicum of marine ecosystem services (Zamora-Arroyo & Flessa 2009). Indeed, these assessments of environmental needs, along with estimates of flows required to sustain riparian habitats (Zamora-Arroyo et al. 2005), played an integral role in a newly signed international agreement to provide water for the delta's environments (Flessa et al. 2013).

4.8. 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 for which change was detected within a single human generation. As noted above, geohistorical analysis often has sufficient temporal, spatial, and taxonomic acuity to resolve this issue. One superb and early example involved direct pH measurements of lake waters from the northeastern United States during the 1970s and 1980s, which suggested widespread acidification. The timing and magnitude of change, and the extent to which industrial emissions were responsible, however, remained controversial. Calibration of relationships between living diatom communities and lake pH permitted paleoecologists to infer pH history from lake-sediment cores upwind and downwind of industrial sources, demonstrating that acidification occurred only in downwind lakes and coincided with an increase in anthropogenic sulfate and nitrate emissions, not with other potential drivers (Charles & Smol 1990).

4.9. 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 an increasing role in ecological restoration efforts (Steadman 1995, Burney & Burney 2007, Willard & Cronin 2007), and they contribute to discussions regarding feasible restoration targets in a changing environment (Jackson & Hobbs 2009). For example, Volety et al. (2009) used geohistorical baseline data from Holocene oyster (*Crassostrea virginica*) reefs off the coast of south Florida to establish that populations diminished largely as a consequence of reduced freshwater discharge from the Everglades. These data are now used by resource managers to identify suitable areas for oyster reef development under different flow conditions associated with Everglades restoration.

4.10. Evaluating Extinction Risk

Understanding why some species are more vulnerable to extinction than others is a central goal of conservation. Conservation paleobiology can help disentangle the relative importance of intrinsic (e.g., ecological traits) versus extrinsic (abiotic) factors in determining extinction risk. For example, Boyer (2009) used classification (regression) trees that integrated fossil and modern bird species occurrence data from Pacific islands to discover that intrinsic ecological traits (e.g., endemism, body size, and diet) were better predictors of extinction risk than were extrinsic factors such as island size and isolation. This analysis suggests that species that are currently classified as unthreatened but share the traits of extinct species deserve closer examination for extinction risk, which may well be underestimated.

4.11. Informing Decisions on Rewilding

Conservation biologists now realize that some approaches to restoration—in particular, proposals to replace ecosystem functions lost when critical species underwent extinction, by introducing related or ecologically similar extant species (Donlan et al. 2006)—can benefit from detailed information about extinct species and their ecosystems. Geohistorical analysis can be used to identify recently extinct species and reconstruct their functional traits (Burney & Burney 2007, Hansen 2010). Such information is critical for selecting suitable candidates for rewilding projects. For example, paleoecological analysis showed 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 most extinctions occurring on islands (Hansen et al. 2010). This knowledge has led to proposals—and some success—for rewilding extant tortoises in order to restore ecosystem functioning (Hansen et al. 2010, Burney 2011; see also the example of feral horses mentioned in Section 2.4).

4.12. Strategies for the Design and Selection of Reserves

Biologists are taking a more systematic approach to conservation planning, which involves identifying sites for biological reserves where biodiversity and ecosystem services might persist (Margules & Pressey 2000, Hannah et al. 2007, Langford et al. 2011). Conservation paleobiology can improve the utility and reliability of these planning methods. For example, biologists currently design reserve networks by predicting where species will move with projected climate change, building on niche models of the present-day distribution of species. Williams et al. (2013) evaluated the predictive power of this approach using fossil data from the last glacial period of rapid warming (approximately 21,000–15,000 years ago): Would a biologist have been able to place reserves in ways to correctly anticipate the shifting distributions of plant species across North America? They

found that the predictive ability of the niche-based strategies was limited, with only moderate to low correlations between predicted reserve ranking and actual reserve ranking. This result suggests that the tools currently used to design reserve networks should be considered as only rough guides to identifying areas of future conservation value.

4.13. Establishing Conservation Priorities

Conservation biologists recognize that resources are insufficient to save all threatened populations and species, leading to debates about setting conservation priorities. Although conservation triage remains as controversial now (Jachowski & Kesler 2009, Parr et al. 2009) as in the early days of environmental science (Hardin 1968, 1985), it is increasingly accepted in light of human population growth, ongoing changes to natural systems, finite funds, and lack of political will (Bottrill et al. 2008, 2009). Conservation paleobiology can inform these discussions. For example, meta-analysis of paleontological and other historical data on key plant and animal guilds permits ecosystems to be ranked according to their state of degradation and potential for remediation (**Figure 3**) (Pandolfi et al. 2003; Lötze et al. 2006). Cavin & Kemp (2011) discussed the impact fossils had in providing objective grounds to determine the conservation status of *Neoceratodus forsteri*, a threatened lungfish
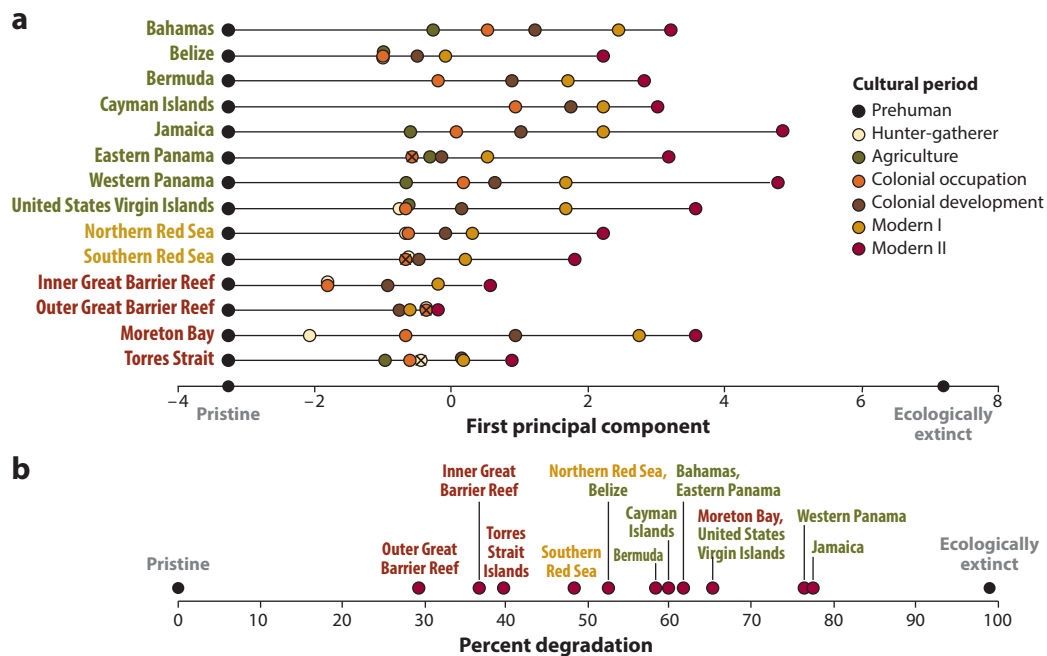

Figure 3

History and present state of seven guilds (corals, large herbivores, large carnivores, suspension feeders, small herbivores, seagrass, and small carnivores) found in 14 coral reef regions around the world over seven cultural periods. (*a*) Historical trajectories (along the first principal component) of each reef start in the pristine state (no evidence for human use or damage) and end in the ecologically extinct state in which members of each guild are rarely observed. The majority of reef regions show an increasing level of ecological degradation through time, except where noted with an *x* in the filled circle, which denotes a minor reversal in reef degradation. (*b*) Present ecological state of reef regions, as indicated by relative distance along the first principal component between pristine and ecologically extinct extremes. Oceanic regions are color-coded: red, Australia; yellow, Red Sea; green, western Atlantic. Modified from Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, et al. 2003. Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301:955–58 (Pandolfi et al. 2003). Reprinted with permission from AAAS.

in Australia. Inclusion of fossil information in a phylogeny for living lungfishes emphasized the originality (sensu Pavoine et al. 2005) of this lineage and helped improve current conservation practices.

Proxy: a physical, chemical, or biological variable from the geologic record that can substitute for direct measurement of an environmental variable

5. CHALLENGES

As a cross-disciplinary science, conservation paleobiology deals with complex environmental processes and biotic responses at multiple spatial and temporal scales. Realizing the full potential of the conservation paleobiology approach, therefore, depends on the continued development and improvement of tools and methods to integrate neontological and paleontological data (Section 5.1), especially across the spectra of data scales (Section 5.2), and develop and calibrate proxy indicators of physical, chemical, and biological characteristics of past environments (Section 5.3).

5.1. Analysis of the Near-Time Fossil Record

Actualistic studies of modern death assemblages, using pollen, mollusks, mammals, and corals, have generated a wealth of insights into the temporal and spatial resolution of biotic remains and established their generally high fidelity to the living communities that produced them (for a recent review, see Kidwell 2013). Such data help establish protocols for sampling and biological interpretation of very young, not-yet-buried fossil records and permit modeling of the dynamics of fossilization. Other key groups and habitats, however, need to be evaluated, most notably finfish, freshwater fauna, and high-latitude sites, all of which are under elevated stress from human exploitation and/or climate change.

Quantifying the resolution and fidelity of fully buried fossil assemblages represents another challenge (Jackson 2012b, Kidwell 2013). Does burial below the uppermost mixed layer of the landscape or seabed simply "freeze in" the qualities of death assemblages? Or does temporal resolution coarsen and bias from differential preservation increase, under the combined influences of diagenesis and diminished input of newly dead individuals? Comparisons among living, recently dead, and young but fully buried fossil assemblages are scarce and yield varied results. For example, death assemblages can resemble fossil assemblages more closely than they resemble the local living community if that community has been altered by recent human activities (e.g., Greenstein 2007, Erthal et al. 2011). Systematic analyses, down-core studies in areas where the ecological history of the past century is well known, and modeling are needed to evaluate this critical formation process in fossil records.

5.2. Scaling Issues for Merging Neo- and Paleobiological Data

A challenge that arises when comparing geohistorical and neontological data is that the two types of data commonly encompass different spatial and temporal scales (Bennington et al. 2009, Polly et al. 2011, Bennington & Aronson 2012, Birks 2012). For example, in contrast to the fine temporal and spatial resolution of a census of living individuals, naturally accumulated assemblages of dead or otherwise shed remains of organisms are typically temporally and/or spatially averaged to some degree (Kidwell 2013). Such death assemblages may integrate multiple generations at a site, and they usually encompass multiple patches or habitats, owing to short-term fluctuations in environmental conditions, habitat migration, and random variability in living communities during the window of time-averaging. Postmortem transport of remains may also be important and, for some groups such as pollen, may involve considerable distances. Such time- and space-averaged assemblages dominate the fossil record.

Modeling and meta-analysis of "live-dead" data sets show that time-averaging leads to predictable effects on biological information (Kidwell & Tomasovych 2013). For example, with progressive temporal pooling at a site, richness increases, largely through the capture of rare species, and evenness increases, owing to switching among short-term dominants (Tomasovych & Kidwell 2009a, 2010a). Such temporal averaging improves the ability of death assemblages to estimate the richness and abundance structure of the regional species pool (Terry 2010). The spatial averaging that is associated with time-averaging reduces between-site differences (β-diversity), but spatial gradients evident in the living communities are usually still captured. In molluscan death assemblages, for example, bathymetric gradients are preserved because rare species tend to be habitat specialists (Tomasovych & Kidwell 2009b), and in land-mammal assemblages, seasonal habitat use, such as for overwintering or calving, is detected because multiple years of mortality are summed (Miller 2011, Miller et al. 2013; see also Western & Behrensmeyer 2009).

This damping of temporal and spatial variability has both advantages and disadvantages. On the one hand, for example in paleolimnology, decadal time-averaging reduces interannual variability, yielding better records of average conditions and longer-term trends (e.g., Smol 2008, 2010). On the other hand, the centennial time-averaging in some coastal cores will cause the true range of past variation to be underestimated, making present-day conditions and recent variability seem unprecedented (Tomasovych & Kidwell 2010b).

Knowledge of scaling effects allows investigators to compensate when comparing past and present conditions, disentangle these effects from postmortem and diagenetic processes, and devise protocols to avoid—or take advantage of—scaling effects. For example, when species that possess preservable skeletal hardparts are present alive but absent in a local death assemblage, a new community state or biotic invasion is suspected (e.g., Yanes 2012). Similarly, when abundant dead individuals of a species are found but no living individuals are encountered, local extirpation is suspected. Building a mechanistic understanding of postmortem preservation, including quantifying the key rates of loss to burial and disintegration, is a primary basic research challenge.

5.3. Proxy Development for Environmental and Biotic Conditions

New and refined proxies for environmental conditions have continued to emerge over the past several decades. Increasingly, paleoenvironmental conditions can be inferred from independent sedimentary, geochemical, and molecular evidence, liberating fossil material for use in evaluating biotic responses to environmental change (NRC 2005). Proxy records, however, are only rarely calibrated to the accuracy and precision of instrumental data (Seddon et al. 2014). A transfer function, or calibration function (Birks et al. 2010), is the quantitative relationship between a proxy variable in modern sediments (the youngest part of a geohistorical record) and a modern environmental variable of interest. It enables inference of past values of the environmental variable from the proxy variable in the deeper (older) sedimentary record. Transfer functions are standard tools in paleoecology but are sometimes subject to considerable error when used to infer past conditions because of the effects of strongly correlating variables on the response function (Birks & Birks 2006, Saros 2009, Sayer et al. 2010, Birks et al. 2012, Jackson 2012b). Inability to separate the effects of multiple stressors across an irregularly sampled time series also makes it difficult to determine the key driver or drivers of change (Anderson et al. 2006). Teasing apart the roles of interacting drivers poses an important but tractable challenge, requiring integration of the best available taphonomic, ecological, and paleoecological knowledge using multiple data sources, analytical tools, and models.

SUMMARY POINTS

1. Conservation paleobiology is a rapidly developing field that applies the theories and methods of paleontology to the conservation and restoration of biodiversity and ecosystem services.

2. Conservation paleobiology studies have provided valuable insights into the ecological and evolutionary responses of species, communities, and ecosystems to environmental stressors—habitat change, climate change, exploitation (removal) of wild species, biological invasions, and disturbances in biogeochemical cycles—acting in the past and today.

3. A critical next step for advancement of conservation paleobiology is quantification of the effects of multiple environmental stressors and their often unexpected and complex interactions in space and time on biodiversity and ecosystem services.

4. Conservation paleobiology methods have already moved from academic development to application by agencies and nongovernmental organizations.

5. The momentum needed to cross research frontiers and translate research results into conservation outcomes requires continued development and improvement of tools and methods to compare neontological and geohistorical data across scales and to calibrate proxies that accurately reflect environmental conditions.

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