REVIEW SUMMARY

CONSERVATION

Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems

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BACKGROUND: The pace and magnitude of human-caused global change has accelerated dramatically over the past 50 years, overwhelming the capacity of many ecosystems and species to maintain themselves as they have under the more stable conditions that prevailed for at least 11,000 years. The next few decades threaten even more rapid transformations because by 2050, the human population is projected to grow by 3 billion while simultaneously increasing per capita consumption. Thus, to avoid losing many species and the crucial aspects of ecosystems that we need—for both our physical and emotional well-being—new conservation paradigms and integration of information from conservation biology, paleobiology, and the Earth sciences are required.

ADVANCES: Rather than attempting to hold ecosystems to an idealized conception of the past, as has been the prevailing conservation paradigm until recently, maintaining vibrant ecosystems for the future now requires new approaches that use both historical and novel conservation landscapes, enhance adaptive capacity for ecosystems and organisms, facilitate connectedness, and manage ecosystems for functional integrity rather than focusing entirely on particular species. Scientific breakthroughs needed to underpin such a paradigm shift are emerging at the intersection of ecology and paleobiology, revealing (i) which species and ecosystems will need human intervention to persist; (ii) how to foster population connectivity that anticipates rapidly changing climate and land use; (iii) functional attributes that characterize ecosystems through thousands to millions of years, irrespective of the species that are involved; and (iv) the range of compositional and functional variation that ecosystems have

exhibited over their long histories. Such information is necessary for recognizing which current changes foretell transitions to less robust ecological states and which changes may signal

Fewer than 900 mountain gorillas are left in the world, and their continued existence depends upon the choices humans make, exemplifying the state of many species and ecosystems. Can conservation biology save biodiversity and all the aspects of nature that people need and value as 3 billion more of us are added to the planet by 2050, while climate continues to change to states outside the bounds that most of today's ecosystems have ever experienced?

benign ecosystem shifts that will cause no substantial loss of ecosystem function or services.

Conservation success will also increasingly hinge on choosing among different, sometimes mutually exclusive approaches to best achieve three conceptually distinct goals: maximizing biodiversity, maximizing ecosystem services, and preserving wilderness. These goals vary in applicability depending on whether historical or novel ecosystems are the conservation target. Tradeoffs already occur—for example, managing to maximize certain ecosystem services upon which people depend (such as food production on farm or rangelands) versus maintaining healthy populations of vulnerable species (such as wolves, lions, or elephants). In the future, the choices will be starker, likely involving decisions such as which species are candidates for managed relocation and to which areas, and whether certain areas should be off limits for intensive management, even if it means losing some species that now live there. Developing the capacity to make those choices will require conservation in both historical and novel ecosystems and effective collaboration of scientists, governmental officials, nongovernmental organizations, the legal community, and other stakeholders.

OUTLOOK: Conservation efforts are currently in a state of transition, with active debate about the relative importance of preserving historical landscapes with minimal human impact on one end of the ideological spectrum versus manipulating novel ecosystems that result from human activities on the other. Although the two approaches are often presented as dichotomous, in fact they are connected by a continuum of practices, and both are needed. In most landscapes, maximizing conservation success will require more integration of paleobiology and conservation biology because in a rapidly changing world, a long-term perspective (encompassing at least millennia) is necessary to specify and select appropriate conservation targets and plans. Although adding this long-term perspective will be essential to sustain biodiversity and all of the facets of nature that humans need as we continue to rapidly change the world over the next few decades, maximizing the chances of success will also require dealing with the root causes of the conservation crisis: rapid growth of the human population, increasing per capita consumption especially in developed countries, and anthropogenic climate change that is rapidly pushing habitats outside the bounds experienced by today's species. ∎

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Conservation of species and ecosystems is increasingly difficult because anthropogenic
impacts are pervasive and accelerating. Under this rapid global change, maximizing
conservation success requires a paradigm shift from maintaining ecosystems in idealized
past states toward facilitating their adaptive and functional capacities, even as species
ebb and flow individually. Developing effective strategies under this new paradigm will
require deeper understanding of the long-term dynamics that govern ecosystem
persistence and reconciliation of conflicts among approaches to conserving historical
versus novel ecosystems. Integrating emerging information from conservation biology,
paleobiology, and the Earth sciences is an important step forward on the path to success.
Maintaining nature in all its aspects will also entail immediately addressing the overarching
threats of growing human population, overconsumption, pollution, and climate change.

Local and global stress on ecosystems, species, and populations—already severe—will intensify in the near future as the number of people, land use, and consumption of natural resources increase and as anthropogenic climate change continues ([1–4]). Even now, it is no longer possible to effectively manage most ecosystems to maintain them in a historical state, as has been prevailing practice and theory in conservation biology ([4–6]). Rather, a paradigm shift is under way, with new conservation goals aiming to maximize the capacity of ecosystems to adapt to current and impending changes ([4–11]).

Recent work highlights that achieving such goals will require understanding how ecological dynamics play out over time scales much longer than a human lifetime ([12]). Such information has long been known to be available from historical, paleobiological, and geological records ([10], [13]). However, scientists and land managers are still grappling with how to more fully integrate paleobiological information into conservation theory and decisions (Fig. 1).

The current conservation landscape

More than half of Earth's ice-free land has been converted for human use ([14]), tens of thousands of species have been transported around the globe ([15]), and species and populations are going extinct at highly elevated rates ([16]). As a result, much if not most of the planet is now covered by novel ecosystems (Fig. 1D) ([6])—that is, those with assemblages of species or other characteristics that did not exist before preindustrial times, which human activities have created, either intentionally or inadvertently. Here, we include as novel ecosystems cropland, pastureland, timber plantations, and land modified by logging and human-caused erosion and sedimentation, in total covering ~47% of ice-free land ([14]). Urban and rural communities, roads, reservoirs, railways, and mining areas account for an additional ~7% ([14]).

Historical ecosystems are defined loosely as those presumed to be operating as they have for at least centuries (Fig. 1B) ([6]). They include some national parks and other large tracts of land that are often protected to some degree and are at most lightly inhabited by people. Although all historical ecosystems exhibit signs of human modification, ranging from millennia of manipulation by indigenous people to present-day anthropogenic climate change, their dynamics and species compositions seem to closely resemble those present for at least centuries and to be more heavily influenced by nonanthropogenic

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processes than by humans. Here, we regard historical ecosystems as those that still have at least 70% of the habitats that were present 500 years ago and that contain fewer than 5 people/km^2 (*17*). A subset of historical ecosystems retains at least ~90% of habitats that have characterized them over at least the past five centuries and contain <1 person/km^2 (*17*). We refer to these places as wilderness; such wilderness comprises ~26% of ice-free land (*17*).

Conservation efforts typically target at least one of three key goals: maximizing biodiversity, maintaining ecological structure and function, and/or maximizing ecosystem services. In attempts to conserve historical ecosystems, achieving all three goals simultaneously—with the approach typically being to minimize human impacts—is usually implicitly or explicitly intended and can be very successful. A case in point is preserving intact tropical forests, which support the majority of Earth's terrestrial species, retain a general ecological structure that has persisted for at least tens of thousands of years (even considering the long integration of indigenous peoples into such systems), and as a result offer myriad ecosystem services ranging from carbon sequestration, to purifying water and air and provisioning food, to providing diverse aesthetic, emotional, and wilderness experiences for people.

In contrast, in novel ecosystems, particularly under conditions of rapid global change, the conservation goals of maximizing biodiversity, maintaining particular ecological structures and functions, and provision of particular ecosystem services can diverge substantially (*6*, *18*), although in most cases, the three goals exhibit at least some overlap (Fig. 1E). For instance, rescuing a species threatened by climate change or habitat loss may require manipulating its genetic diversity (Fig. 1, example E1) (*19*) and/or managed relocation into a geographic region and ecosystem in which the species has never lived (Fig. 1, example E2) (*20*). Although effective in conserving biodiversity and perhaps promoting certain ecosystem services, such as tourism, such actions contradict other goals—for example, the philosophy of maximizing wilderness attributes (*21*). Less nuanced examples include zoos, botanic gardens, and well-designed urban landscapes, which will be essential in maximizing biodiversity but which completely replace wilderness. At another end of the spectrum are agricultural landscapes, which maximize a necessary ecosystem service (food production) and can either severely depress biodiversity relative to pre-anthropogenic conditions, as in the case of monoculture farming, or help maintain biodiversity if designed to do so, as in some coffee farms in Costa Rica (Fig. 1, example E3) (*22*, *23*). Thus, in novel landscapes, deciding which goal to optimize can engender much debate among stakeholders, as can the very decision about whether a given landscape should be regarded as historical or novel (Fig. 1A).

Such concerns lead to conflicting opinions about the relative importance of preserving large landscapes with minimal human impact (*24*–*26*) versus designing human-dominated ecosystems

in ways that maximize particular conservation goals (*27*). In practice, the two schools of thought both recognize a gradient of human impacts, that conservation only works when human values are articulated by multiple stakeholders to guide any given effort, and that threatened species and special landscapes and ecosystems should be preserved (*18*, *28*, *29*). Nevertheless, the different viewpoints have led to developing and implementing a diverse menu of conservation approaches (*18*), some of which appear contradictory or even mutually exclusive (Table 1). Yet when put in the

context of making choices (Fig. 1) that recognize both historical and novel ecosystems and rapid global change, most have a place.

Critical information from paleobiology

Under current global change, successful conservation outcomes for most approaches (Table 1) depend on meaningful comparisons between modern conditions and long-term histories. The emerging discipline of conservation paleobiology (*10*, *30*) is supplying necessary data, insights, and techniques through (i) specifying long-term, fluctuating
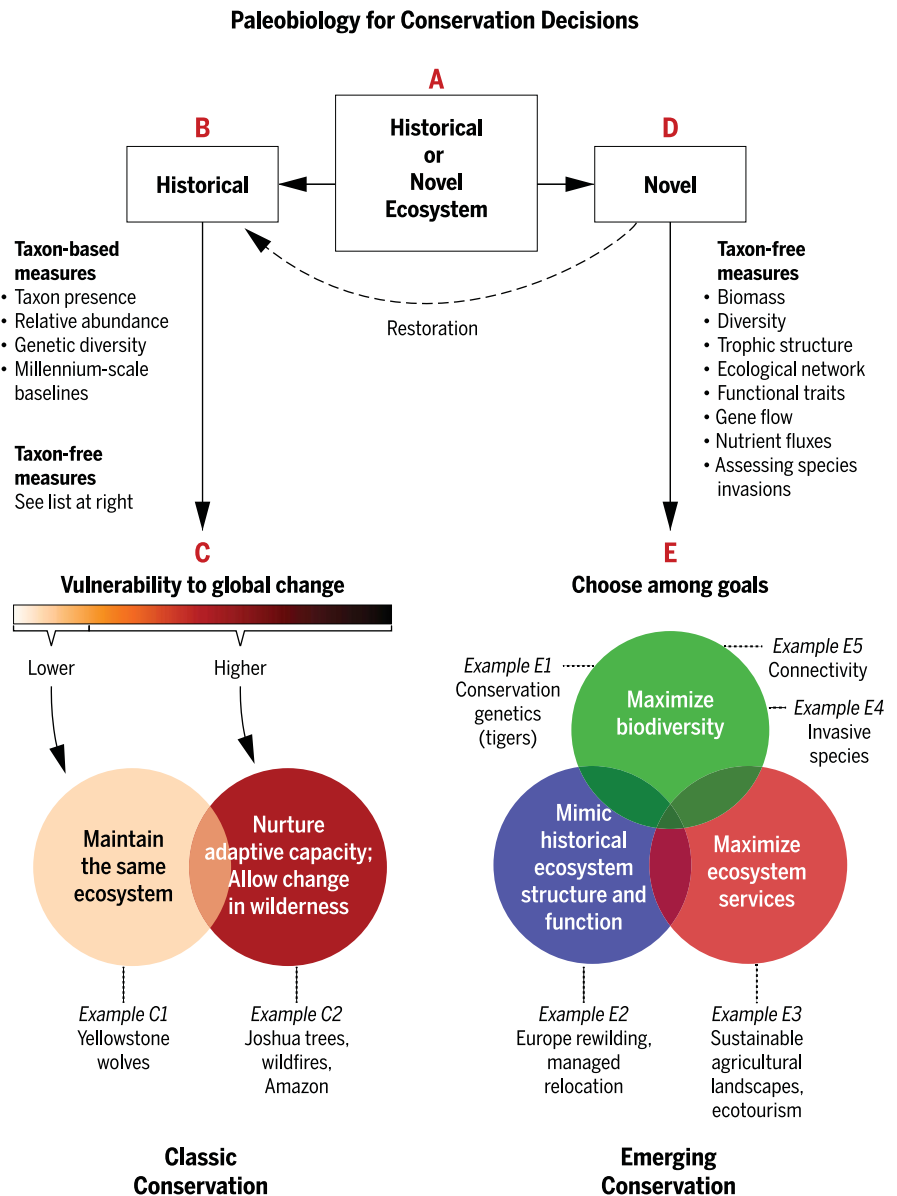

Fig. 1. Critical conservation decisions. (**A** to **E**) Decision points at which data from paleobiology are essential. Here, "biodiversity" refers to all levels of the biological hierarchy. Novel ecosystems can serve to maximize biodiversity, particular ecosystem services, or ecosystem structure, which can be mutually exclusive or overlap to varying degrees. The overlap of these conservation goals is typically broad in historical systems. For conserving historical ecosystems, taxon-based methods from paleobiology have already proven essential, and taxon-free methods also are useful. For novel ecosystems, taxon-free methods hold much potential for linking past, present, and future to help formulate effective conservation programs.

baselines required to understand how ecosystems, communities, species, populations, and genetic structure vary naturally through time and space and how they respond to major perturbations (*10*, *31–36*); (ii) identifying scalable taxon-free metrics that allow attributes of ecosystems to be tracked over seasons, decades, centuries, millennia, and millions of years (*10*, *37*); (iii) dem-onstrating biotic outcomes of many "natural experiments" in global change (*30*), ranging from major extinctions (*10*, *16*, *29*, *38*) to rapid climate change (*10*, *39*, *40*) to species invasions (*10*, *41*); (iv) testing and refining models of biotic response to future environmental change (*10*, *35*, *42*); and (v) tracking the long-term dynamics of ecosystems in ways relevant to assessing continued potential for ecosystem services (*12*, *43*, *44*) and early warn-ing signs of ecological state-shifts (*10*, *45*).

The kinds of fossils that have provided such insights most commonly include phytoplankton and zooplankton, many kinds of plants (repre-sented by fossil pollen, seeds, leaves, and wood), invertebrate animals with hard parts (such as mollusks), and vertebrate animals (represented by bones and teeth) (Fig. 2). Depositional envi-ronments in which these taxa commonly are fos-silized include lakes, river valleys, rock shelters, and caves. The fossil samples recovered from such deposits are particularly useful because they often show high fidelity to the living commu-nities from which they were drawn in terms of taxonomic composition and relative abundance, as demonstrated by taphonomic studies that as-sess how the same sampling vectors that build fossil assemblages sample modern communities (*10*, *46–49*). Some of these favorable depositional environments occur in most biomes, opening possibilities to use paleobiological data in many conservation settings; therefore, it should not be assumed that paleontological information is not available if there has not been targeted explora-tion for appropriate fossil sites.

Less available for conservation uses are species restricted to areas where fossilization potential is low (such as upland areas lacking lakes, rivers, caves, or rock shelters), those whose taphonomy is not well understood (*10*, *50*), and those whose body parts are too fragile to fossilize on a regular basis, such as most insects and birds. Even so, some taxa with low fossilization potential are informative for conservation efforts when they are present; for instance, beetles found in lake sed-iments and peat illustrate a response to climate change that differs from the mammalian response (*51*), and bones of California condors have been critical in identifying their pre-anthropogenic diet (*10*). In general, Quaternary fossils (Pleistocene and Holocene) have proven especially informa-tive for addressing conservation questions, but useful information has also come from much older fossil deposits, reaching back millions of years (*34*, *37*).
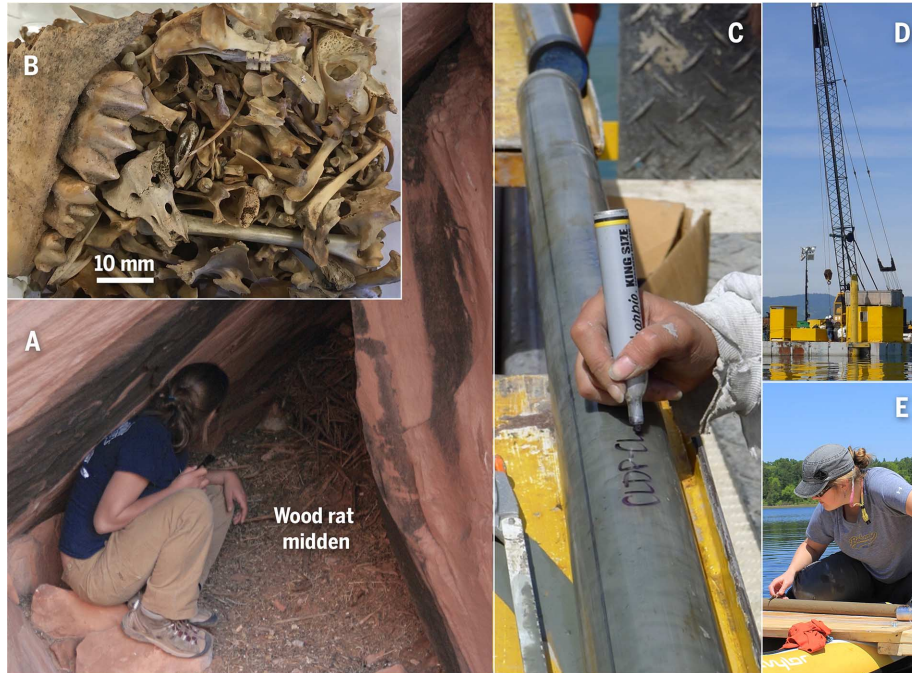

Fig. 2. Tracking community fluctuations through millennia. (**A**) Deposits accumulated by wood rats (*Neotoma* spp.) as they drag bone-laden carnivore scat and raptor pellets into their middens are par-ticularly useful in sampling the vertebrate and plant community with high fidelity to taxonomic composition and relative abundance (*46–48*). Such records can provide successive snapshots of taxon presence, absence, and abundance through thousands to millions (*33*) of years and genetic variation (*73*) through thousands of years. Wood rat middens occur through much of North America; species in genera other than *Neotoma* construct paleoecologically useful middens elsewhere. (**B**) Bones excavated from a wood rat midden, after being concentrated by screening and sorting. (**C**, **D**, and **E**) Sediment cores from lakes contain fossil pollen and spores that allow reconstruction of vegetation changes through hundreds to hundreds of thousands of years (*10*).

Table 1. Multiple conservation approaches.

Approach	Examples
Address root causes of conservation crisis through reducing the human footprint	(*96*)
Increase the number of national parks and other protected areas and connections between them	(*26*)
Quantify ecosystem services regionally and globally and value them in economic terms	(*97*)
Abandon the idea of "pristine wilderness" and maintain high biodiversity (at genetic, population, and species levels) in cultural landscapes	(*27*)
Triage species interventions according to importance, specificity, or likelihood of success	(*98*)
Relocate species, populations, or genotypes whose habitats are disappearing in one place but emerging in another, especially where corridors are lacking	(*8*, *20*)
Reconstruct or restore damaged or extinct ecosystems	(*99*)
Manipulate populations and genetics of endangered species to enhance their survival	(*19*, *100*)
Create ecosystems that simulate long-past conditions, such as Pleistocene rewilding	(*65*)
Produce facsimiles of extinct species through emerging techniques in molecular biology, such as "de-extinction" (which is not considered a viable conservation strategy in this Review)	(*29*, *75*, *76*)

The analytical methods that allow comparing present with past fall into two main categories: taxon-based and taxon-free. Taxon-based methods are those that rely on the presence, absence, or abundances of certain taxa and their underlying diversity, including genetic or phylogenetic differentiation. Taxon-free methods use metrics that reflect ecosystem function rather than structure; examples used in modern systems include assessing ecological network structure (52) and measuring biomass (53), functional traits (54), nutrient flow (43), net primary productivity (55), or ecosystem services (7, 43). Quantifying taxon-based and taxon-free attributes in the present alone does not capture the full range of conditions under which a given ecosystem can thrive because most ecosystems (at least those that have not been created by humans) have persisted for thousands to millions of years. The taxon-based approach to link conservation paleobiology and biology has been used most so far, but current efforts to develop and use taxon-free methods hold considerable promise. Depending on the availability of fossils and the type of conservation question being asked, one or the other approach may be more appropriate.

Historical or novel

Taxon-based paleontological data are critical in deciding whether a given so-called "natural" landscape represents a historical or a novel ecosystem (Fig. 1A). These methods rely on direct comparisons of the taxa that occupied a region in the past to those living there presently. By using superposed, taphonomically understood and well-dated fossil samples (Fig. 2) to reconstruct successive snapshots of the past, it is possible to outline the range of taxonomic and relative-abundance variation that characterizes ecosystems as they fluctuate over thousands to tens of thousands of years, sometimes much more.

For a modern ecosystem to be considered historical (Fig. 1B), its taxon assemblage and their abundances should fall within the range of past millennial-scale variation. For example, in the world's first national park, Yellowstone National Park, USA, paleontological data influenced critical management decisions by demonstrating that Yellowstone preserves a historical ecosystem. Fossil deposits verified that the area proposed in 1995 for the reintroduction of the gray wolf (Canis lupus) had indeed harbored wolves (up to their extirpation in the 20th century) for more than 3000 years, that a principle prey species—elk—used the area for calving thousands of years ago as they still do today, and that almost all of the mammal species that had occupied the region for millennia are still present (Fig. 1, example C1) (13). In this case, the conservation question arose first: Were wolves and elk native to the region before the park was established? Exploration for the requisite fossil sites, previously unknown, ensued as part of the data-gathering exercise before management actions. Further verification that Yellowstone still represents a historic ecosystem came from assessing impacts of climate change on small mammals: Ancient DNA obtained from fossil rodents confirmed that although genetic diversity, population sizes, and gene flow had fluctuated through time in response to climatic conditions, genotypes in the park now have been there for millennia (56). From the botanical perspective, palynological (fossil pollen) records show that the current vegetation has persisted with only minor fluctuations in abundance of dominant taxa for at least 8000 years (57).

Assessing whether historical ecosystems can be maintained

A critical question for many historical ecosystems is whether they will be able to persist in the same states in which they have existed for thousands of years, given rapid, intensifying environmental changes (Fig. 1C). The taxon-based approaches summarized above provide useful answers through establishing the range of variation that taxon-based attributes exhibit through the perturbations an ecosystem experiences over thousands of years. The nature and magnitude of the perturbations can be assessed from the contemporaneous geologic record—for example, isotopic proxies for temperature, lake-level or tree-ring analyses for precipitation, or charcoal records in alluvial deposits and lake cores to track fire frequency. Modern-day changes in the taxon-based metric or in the suspected perturbing agent (for instance, climate change) that exceed the variation evident through millennia or longer may warn that a shift to a new ecological state is imminent. In such cases, the management choice is to either attempt to hold the system to historical conditions, which would require ever-more intensive interventions and may be impossible, or manage the system for "adaptive capacity" (4). Adaptive capacity in this context is the ability of an ecosystem to "re-configure without significant changes in crucial functions or declines in ecosystem services" (58). Put another way, adaptive capacity is the ability of an ecosystem to avoid collapse as it makes the critical transition from its historical ecological state to a new state and to be as resilient in its new state as it was in its previous state.

Robustly assessing adaptive capacity requires combining information about prehistoric conditions,
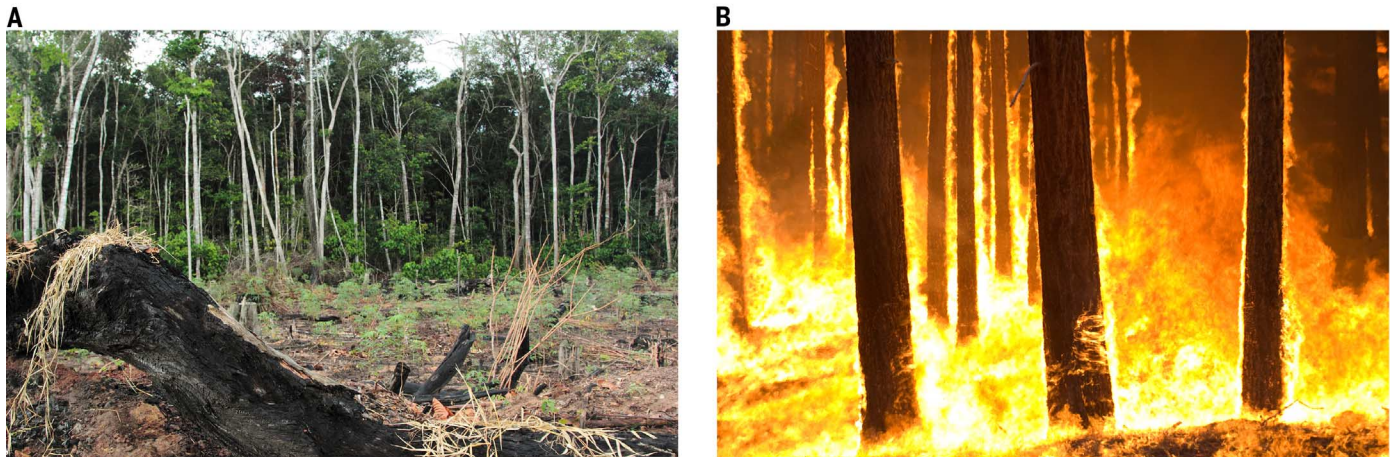
Fig. 3. Transformation of historical ecosystems. (A) Near Parque Nacional de Anavilhanas, Brazil. Palynological data revealed that increased precipitation coincided with southern expansion of Amazon rainforest ~3000 years ago to its early 20th-century position (85). Reduced rainfall across two thirds of the rainforest related to changes in the El Niño–Southern Oscillation (86), combined with deforestation (87), have recently contributed to shifting the rainforest-savanna border northward, reducing vegetative productivity (88), increasing fire frequency, and lengthening the fire season (89). Climate models suggest that future transformation of vast areas of Amazon rainforest may be imminent (90, 91). **(B)** Las Conchas Fire near Bandelier National Monument, New Mexico, USA. Paleontological data show that western North American forest ecosystems depend on high-frequency, low-severity fires and that wildfire frequencies increased with drought (92, 93). Fuel buildup from fire suppression and anthropogenic climate change increased fire frequencies in the late 20th century (94), and climate projections suggest that by 2100, fire frequency may increase to levels far above those to which historical and current vegetation have adapted (91). These considerations have been used to justify prescribed burning to preempt catastrophic crown fires (95).

modern and historic observations, and future projections. An illustrative example is the conservation of Joshua trees (*Yucca brevifolia*) in and around Joshua Tree National Park, California (Fig. 1, example C2). The distribution of Joshua tree fossils preserved in wood rat middens (Fig. 2) and in the dung of extinct Shasta ground sloths (*Nothrotheriops shastensis*) demonstrated the sensitivity of the trees to increased temperature and aridity ~11,700 years ago and also revealed that dispersal of the species occurred only slowly: ~1 to 2 m/year (*59*). Today, Joshua trees are only rarely reproducing within the park because of increased temperatures and drought, and climate projections under a medium greenhouse gas emissions scenario indicate that 90% of their suitable habitat in the park could be lost by 2100 (*59*). Climatically suitable areas may shift northward and upslope, but the slow migration rate of Joshua trees limits their ability to track their suitable climate space, especially because one of their dispersal agents—Shasta ground sloths—is extinct. In this case, the fossil information implies that conserving Joshua Tree National Park in its present

ecological state may not be possible because of climate-triggered species turnover, including loss of its namesake species and colonization by currently exotic species. The implication is that conserving Joshua tree ecosystems may require more active management in protected areas outside the national park, acquisition of new lands, and perhaps targeted planting. This landscape-scale management of Joshua trees could nurture the adaptive capacity of the species across its range, even if the national park loses its suitable habitat, while still maintaining the wilderness character of Joshua Tree National Park if wilderness character depends more on the low level of local human impacts than on the presence of Joshua trees.

Paleontological data show that other historical ecosystems have already begun to change and are vulnerable to future change, including fire-dependent ecosystems across western North America and Amazon tropical rain forests, the latter of which can rapidly shift to savanna (Fig. 3). Comparisons of species dispersal rates to past and present velocity of climate change—the distance per unit of time that a species would need to

move to remain in its current conditions of temperature or other climate variables (*60*)—have also proven useful in determining areas and species most at risk of ecological transformations. In general, such studies reveal that the speed at which species will need to move over the coming decades far outstrips the pace at which they actually did move in response to the most rapid climate change documented in the fossil record, the transition from the last glacial period into the Holocene (*60*). Such information indicates that the need to manage historical ecosystems for their adaptive capacity will increase, mandating increased use of taxon-free metrics to assess how well that management is proceeding.

Conservation in novel ecosystems

Landscapes that already fall outside historical norms (Fig. 1D)—which in many cases is evident even without consideration of fossil data (*6, 14*)—may be candidates for restoration to a desired historical state if the kinds of data described above verify that the system has not been pushed irreparably beyond its millennial-scale variation in
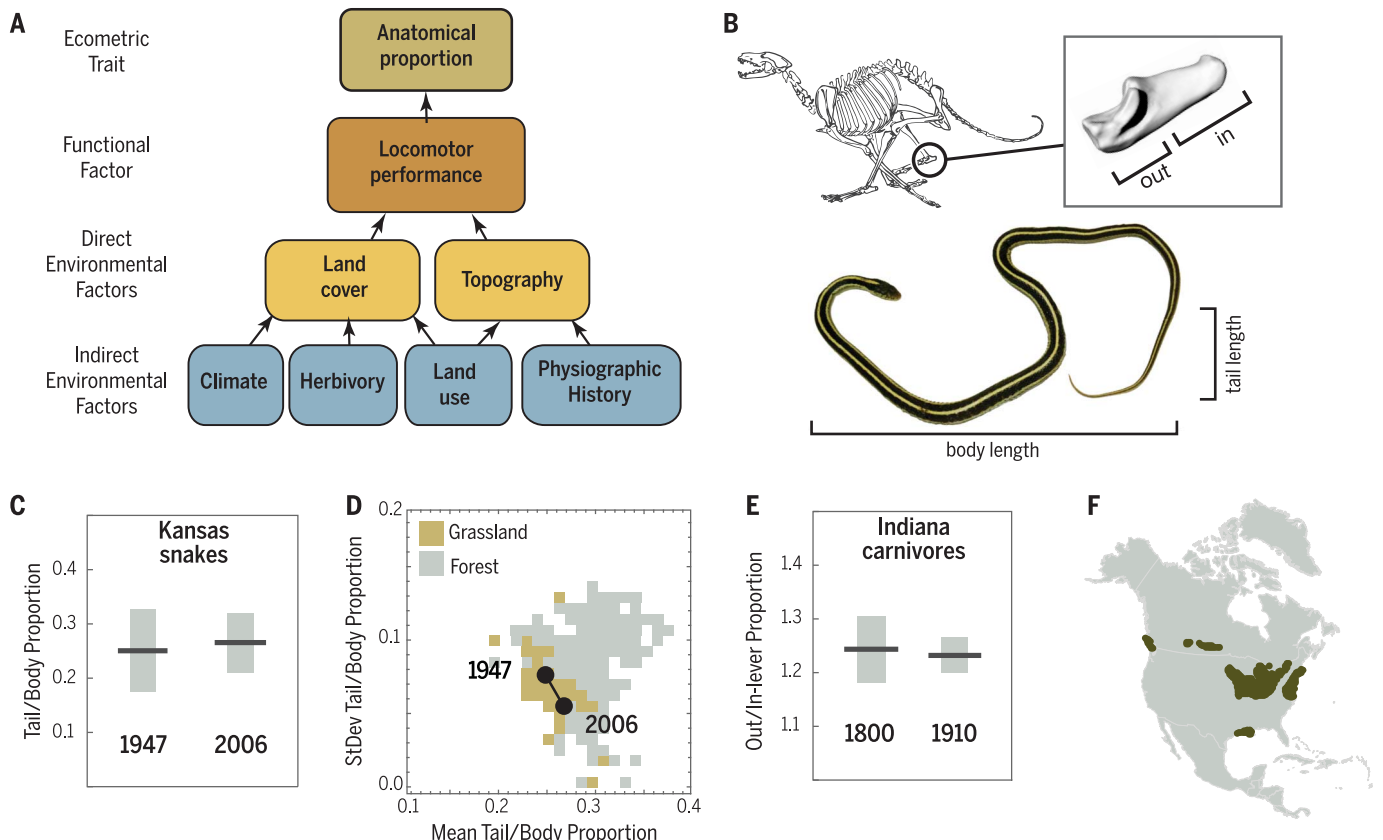

Fig. 4. Ecometrics in paleobiology. (A) Proportions of certain bones are linked to land cover, land use, and topography through locomotor performance. **(B)** In mammalian carnivore communities, locomotor diversity can be measured by using the in- and out-levers of the limbs and is linked to vegetation cover (*68, 70*); in snakes, the same relationship can be measured with the ratio of tail to body length (*67*). **(C)** Changes in the variance and mean of these traits can be assessed for congruence with changes in community composition and land cover. For example, when land acquired by the University of Kansas was allowed to revert from agricultural grassland to forest between 1947 and 2006, turnover in the herpetofauna changed the mean (black line) and standard deviation (gray bar) of tail-to-body length ratios. **(D)** The change illustrated in (C) was congruent with ecometric values associated with grassland and forest ecosystems elsewhere (*67*). **(E)** Conversely, 19th-century deforestation of Indiana extirpated many large mammalian carnivores, resulting in a loss of locomotor diversity, measured as the standard deviation (gray bars) of the out-to-in-lever ratio. **(F)** The loss of locomotor diversity can be mapped to identify other regions (dark gray shading) that may have been similarly affected (*68*).

taxonomic composition and abundance (*10*). This may be the case, for example, if the current system can be returned to its long-term state by reintroducing key taxa or genotypes. Where restoration is not possible or desirable (Fig. 1E)—the situation for perhaps most of the ecosystems on the half of the planet that humans have transformed and that are changing even more under current anthropogenic pressures—novel ecosystems also provide many conservation opportunities (*6*). By definition, novel ecosystems are distinct with respect to past ecosystems in terms of taxonomic composition; thus, in these cases taxon-free instead of taxon-based approaches provide the most effective applications of paleontological data to inform conservation strategies.

For example, paleontological analyses have shown that certain body-mass distributions (*34*), biomass patterns (*29*), numbers of species within trophic and size categories (*33, 34*), abundance patterns (*61*), and ecological networks (*62, 63*) are characteristic of mammal communities that persist for thousands to millions of years, irrespective of the constituent species. This knowledge can answer critical questions, which abound, about the design and long-term viability of novel ecosystems by considering the constituent species primarily in terms of ecological function rather than taxonomic identity. In urban settings, for example, do domestic cats carry out the function of extirpated or extinct meso-predators, keeping rodent and bird populations in check, which would indicate healthy ecological function, or is their impact greater than previously present meso-predators, which might degrade ecosystem health? In ranchlands, is the biomass of livestock within the bounds of long-term megafauna variation, which once included mammoths and other extinct large mammals, or is the biomass of livestock presently greater? In managed relocation experiments, how will the transferred species affect trophic structure and ecological networks of the target ecosystems? And in rewilding initiatives—which can range from replacing "missing" taxa with the same species [for example, wolves in Yellowstone and the Rewilding Europe effort (*64*)] to building ecosystems from scratch by using functional analogs of extinct species (*65*)—what trophic structures and ecological networks will maximize biodiversity and ecosystem services and yield a system that is functionally robust to perturbations, thus keeping maintenance costs at a minimum?

Because taxon-free metrics can often be related to environmental parameters with statistical significance, they offer opportunities for understanding which kinds of species are likely to thrive in which regions as biota adjust to rapidly changing environmental conditions (Fig. 4). Such measures have been applied in modern community ecology (*54, 66*). In conservation paleobiology, they have been called "ecometrics" (*37, 67–69*) and include studies of both plants and animals, with a focus on functional traits that are frequently preserved in the fossil record. For plants, this includes leaf size and shape (reflects precipitation patterns), stomatal index (measures equilibrium

with atmospheric carbon dioxide), and phytolith shape (a proxy for resistance to herbivore use and whether or not the leaf wax hardened in a sunny or shady environment). Animal-based traits include dental morphology (which is a proxy for diet), locomotor attributes (which show distinct differences in different environments) (Fig. 4), and body size (which can reflect climate variables and nutrition). By focusing on such traits, it becomes possible to assess the ability of taxa to persist in particular places under particular scenarios of rapid environmental change. This in turn helps in identifying suitable candidates and locations for managed relocation, restoration, and rewilding programs (Fig. 1, example E2).

For example, in mammalian carnivore communities, locomotor diversity is known to be linked to vegetation cover (*68, 70*), which provides a valuable predictor of which carnivore species will be best suited to areas where climate change or other human impacts substantially alter plant communities, and also a metric by which to identify ecologically impoverished systems (Fig. 4). The application of such techniques requires that the linkage between a given trait

and environmental parameter be firmly established, which so far has only been done for relatively few traits, especially in vertebrate animals. Future research that expanded the suite of useful traits would be valuable.

Taxon-free paleontological measures can also reveal whether the potential for delivery of ecosystem services is being sustained in novel ecosystems by tracking metrics that reflect ecological processes over centennial to millennial time scales, such as nutrient cycling, biomass, crop production, water supply, climate regulation, timber, and coastal protection (*43*). Geologically based proxies can track nutrient cycling, soil formation and stabilization, and erosion (*43*). As an example, a suite of 50 paleoenvironmental proxies demonstrated that since the year 1800, rapid economic growth and population increases since the mid-20th century coincided with environmental degradation in the lower Yangtze Basin, China (*44*).

Last, taxon-free paleontological data are critical for understanding whether certain ecosystems are approaching ecological thresholds (*10, 45*)—so-called "tipping points," as demonstrated by analysis of diatoms, pollen, and sediments from lake
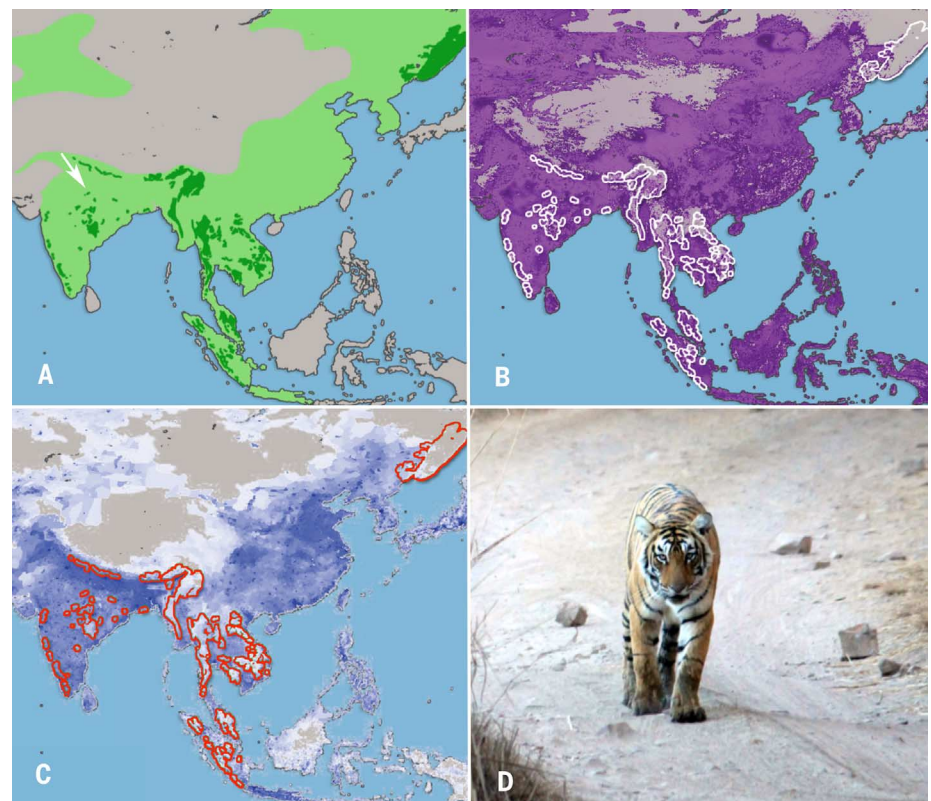

Fig. 5. Pressures affecting wild tigers. (**A**) Only ~3800 wild tigers remain, confined to only 7% (dark green) of their historic (light green) geographic range (the white arrow shows the region of Ranthambore National Park). (**B**) Present geographic range of wild tigers (white outline) overlain on a map of crop and pasture lands (darker shades of purple indicate more intensive agricultural use), and on (**C**) (red outline) a map of human population density, where darker blues indicate higher density, ranging from ≤1 person/km² in the lightest colored regions to >10,000 people/km² in the darkest. (**D**) Tigers remain mainly in the least densely populated areas, or in reserves located in novel ecosystems, such as this individual in Ranthambore National Park, India. By 2050, at least one half billion more people are projected to populate regions that include tiger reserves.

cores, which identified a match between mathematical models and an ecological state-shift in Yunnan, China. Another example comes from Pennsylvania, USA, where feedbacks that caused deforestation in one area triggered an ecological state-shift in an adjacent area (10).

The utility of such taxon-free approaches for conservation paleobiology and predictive ecology has been demonstrated over the past decade by many case studies (71). A challenge going forward will be to develop a coherent theoretical framework that takes into account such important relationships as the underlying trait distribution, performance filters that define trait fitness in varying environments, how traits will perform as environments change (71), spatial and temporal scaling and demography, and inter- and intraspecific variability in trait distribution and performance (72).

Emerging conservation applications for paleobiology
Conservation genetics

Conservation genetics is now being enhanced through studies of ancient DNA (56, 73). Besides establishing the long-term range of genetic diversity, population fluctuation, and gene flow as noted above for Yellowstone rodents (Fig. 1, example E1) (73), paleontological studies also have resulted in new methods applicable to contemporary conservation problems, notably coalescent simulation analysis. This technique was developed to understand the relative contributions of gene flow and population size in explaining observed fluctuations in genetic diversity chronicled in ancient DNA (73, 74) but is now informing conservation strategies for presently threatened species. A case in point is one of the world's iconic mammals, tigers (*Panthera tigris*) (Fig. 5). Most tigers live in zoos and other captive situations; only ~3800 remain in the wild, and many of those are confined to novel ecosystems such as Ranthambore National Park, which has been heavily used by humans for more than a thousand years. Such small reserves can support just a few individuals, which has led to dwindling genetic diversity within populations. It has been unclear whether such bottlenecks presage extinction of tigers even in the few remaining habitats set aside for them. Coalescent simulation analyses used to forecast into the future instead of interpreting the past indicate that without substantial gene flow between reserves, reduced diversity will likely imperil tigers by the next century, but that diversity can be maintained and perhaps even enhanced by aggressively maintaining functional connectivity, physically moving individuals, and prioritizing breeding among reserves worldwide (19). Global conservation efforts thus far, however, tend to prioritize tiger numbers over connectivity, or focus on maintaining the "purity" of the genetic composition of tiger subspecies.

Fossils have also figured prominently in experimentation with so-called "de-extinction" (75)—efforts to reconstruct facsimiles of species that humans have driven to extinction either recently (passenger pigeons) or in the deeper past (mammoths).
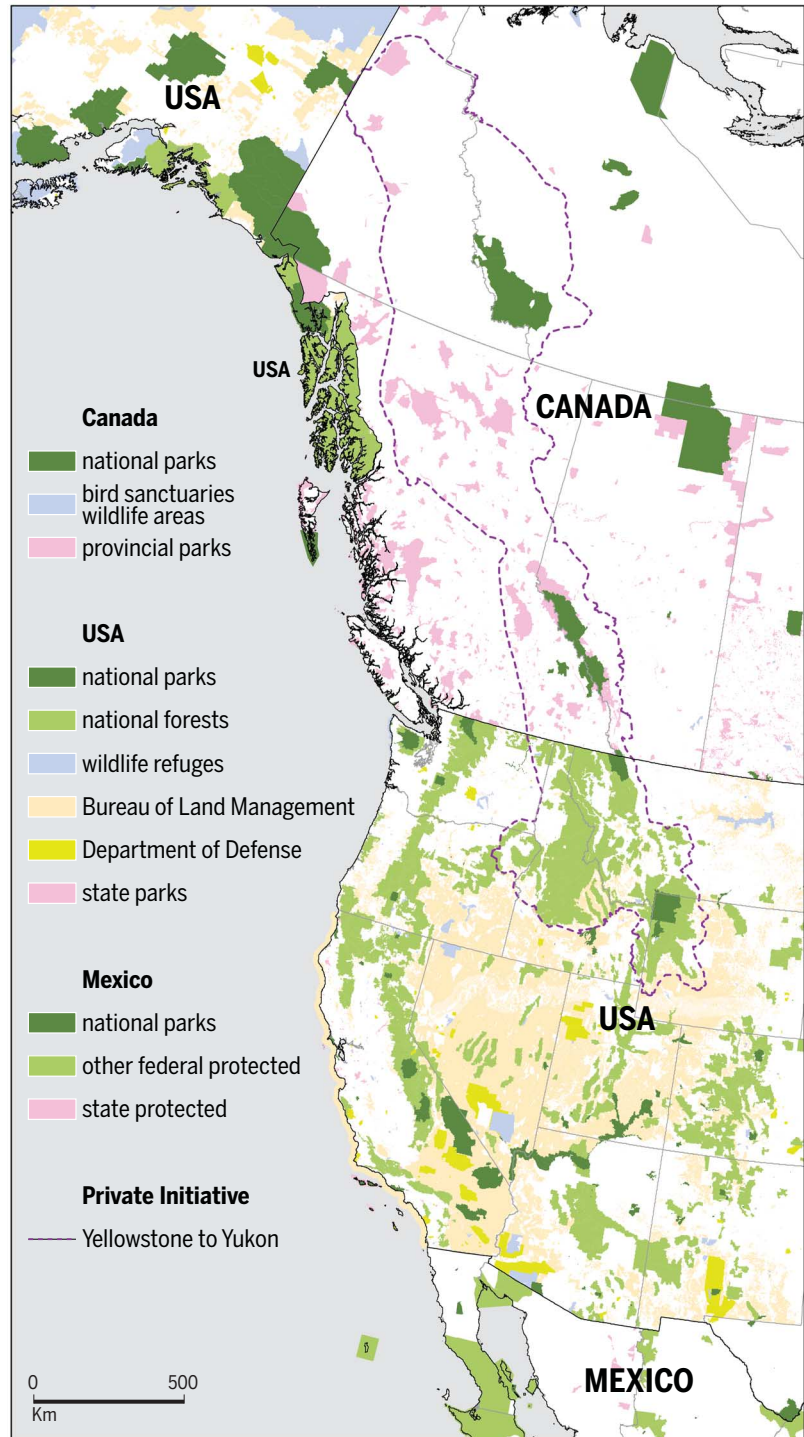
Fig. 6. The importance of conservation corridors. Climate change and jurisdictional differences challenge corridor design. The Yellowstone to Yukon Conservation Initiative (purple outline) spans ecosystems rapidly transforming from increasing wildfire frequency and forest mortality, both triggered by global climate change, and two nations where private land confers varying property rights and federal protected areas are managed by different government agencies. Although multiple jurisdictions complicate enhancing connectivity, such diversity can also contribute to success when the goals of maximizing biodiversity, ecosystem services, and preserving wilderness come into conflict because each stakeholder may choose to optimize a different goal, while still contributing to the overall effect of providing a piece of the corridor.

Although such efforts may eventually create scientific curiosities, their conservation applications are at best limited (*29*), given that (i) the created genomes would be mostly composed of the base pairs of the nearest living relatives of the extinct species; (ii) epigenetic effects are not yet well understood; (iii) only a few individuals of a given species could be engineered because the process is both time-consuming (because of gestation times) and very expensive; (iv) imparting the learned behavior that offspring gain from parental teaching would be impossible, because that knowledge went extinct with the lost species; (v) the ecosystems that supported many extinct species no longer exist, so survival outside of captivity would be difficult or impossible; and (vi) preventing the extinction of extant species and habitats numbering in the thousands already is challenging, so the prospects of sustaining "de-extincted" species are poor at best. Genetic engineering to simulate extinct life also raises ethical and legal concerns for many (*76*).

Invasive species

Whether invasive species substantially alter ecological structure and function is a critical conservation question that can only be answered with a paleontological perspective. For instance, in California grassland ecosystems, historic cattle introduction transformed historic ecosystems into novel ones; as cattle populations grew, grazing megafauna biomass rose far above prehistoric levels, precipitating a functional shift in grazing pressure that favored replacement of native annual grasses by invasive species (Fig. 1, example E4) (*77*). The fossil record also can help inform controversial management decisions (*41*), such as whether wild horses on western North American ranch lands are invasive because they have been absent for most of the Holocene, or native because they evolved in those regions and were for millions of years an integral component of the ecosystems in which they are now thriving.

Enhancing connectivity

Corridors designed to connect protected areas, such as the Yellowstone to Yukon Conservation Initiative (Fig. 6), are critical today (*4, 78*) and will be become even more so in the near future because one tenth to one half of global terrestrial area is highly vulnerable to biome shifts in the 21st century (*79*), whereas refugia in existing protected areas cover only 1 to 2% of global land (*78*). Therefore, a new perspective is that effective corridor design (Fig. 1, example E5), besides taking into account present land-use, will need to identify key areas that have served as refugia in prehistory (*80*) and anticipate ecological changes that will inevitably take place as climate changes (*81*).

Anticipating the future efficacy of corridors generally uses species distribution modeling (*82*). Most species distribution models rely on matching present or near-historic occurrences of a given species with nearby climatic parameters to estimate the ecological niche. Recent work that uses the same models combined with paleontologic, geologic, and paleoclimatic data

to hindcast where species could have occurred over the past several thousand years (*35, 42*) reveals that in many cases, existing models do not adequately project where species may move in the future. In addition, incorporating prehistoric distributional information helps quantify the probability of errors (*10*). Using the fossil record to refine species distribution models requires parameterizing the climate models with appropriate boundary conditions as well as adequate dating control, which is now routinely achievable with accelerator mass spectrometry radiocarbon dates that place the age of critical fossils within decades.

The paleobiological approach can further improve species distribution models by incorporating information on trait-environment connections and/or persistent associations of taxa—that is, groups of two or more taxa that co-occur in fossil localities distributed widely through time and space. Current models rely primarily on climatic parameters alone to estimate niche space. Such paleontologically enhanced species distribution models can also be helpful in informing efforts to relocate species into suitable environments, ranging from managed relocation experiments that aim to save threatened species to choosing which trees to plant in urban and suburban landscaping in order to jump-start dispersal in anticipation of future climatic conditions.

Even with ideal corridors, however, species will not all respond in concert as climate changes, a lesson made clear by the fossil record (*10*). Some species will move quickly, some slowly, and some not at all, and species will key on different aspects of global change, such as temperature, humidity, or biotic interactions. Effective corridors will maximize the opportunities for such natural adjustments to proceed, even though the end result will be species assemblages almost certainly different than current or historical ones.

Conservation policy implications

Laws and governmental policies have played a critical role in conservation. Examples are numerous, ranging from the court-mediated Endangered Species Act in the United States, to extremes such as the "shoot-to-kill" policy for poachers in South Africa and Kenya. An open question under very rapid global change, however, is whether existing policies and laws are adequate to facilitate managing for the adaptive capacity of ecosystems, as opposed to simply mandating the presence of certain species (*9, 83, 84*). Answering that question will require concerted interactions among conservation biologists, paleobiologists, and the policy and law communities nationally and internationally. A key challenge for paleobiologists and conservation biologists will be identifying ecological metrics that are meaningful for legislation.

Conclusions and outlook

Effective conservation of biological resources now involves understanding and anticipating change in ecological systems in terms of adaptive capacity and ecosystem structure and function, knowledge that will become even more impor-

tant in the future. The path forward requires enhanced use of information from the fossil and rock records in conservation planning and practice, combined with the coordination of conservation efforts situated in historical and novel ecosystems. Future efforts need to clearly differentiate between historical and novel ecosystems, identify key resiliencies and features of past ecosystems that may be generally applicable to the future, and characterize the functional interactions that persist in ecosystems for at least thousands of years. All of these tasks require integrating information from paleobiology, Earth sciences, and conservation biology through use of both taxon-based and taxon-free analyses that allow parallel characterization and comparison of contemporary and past ecosystems. Taxon-free methods—which allow comparisons of functional attributes of past, present, and future ecosystems, regardless of the species involved—may prove especially useful for conservation efforts in novel ecosystems and for calibrating the extent of functional change that historical ecosystems will experience under ongoing and future global pressures. In addition to implementing these new approaches to conservation, it will be essential to deal with the root causes of the conservation crisis—rapid human population growth, overconsumption of goods and resources, and climate change—in order to keep nature diverse, adaptive, and able to fulfill the needs of the billions of people for whom Earth is the only home.

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Science

Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems

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Looking back to move forward

The current impacts of humanity on nature are rapid and destructive, but species turnover and change have occurred throughout the history of life. Although there is much debate about the best approaches to take in conservation, ultimately, we need to permit or enhance the resilience of natural systems so that they can continue to adapt and function into the future. In a Review, Barnosky *et al.* argue that the best way to do this is to look back at paleontological history as a way to understand how ecological resilience is maintained, even in the face of change.

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