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Looking Back for the Future: The Ecology of Terrestrial Communities Through the Lens of Conservation Paleobiology

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Abstract

Terrestrial ecosystems encompass a vast and vital component of Earth's biodiversity and ecosystem services. The effect of increased anthropogenic dominance on terrestrial communities defines major challenges for ecosystem conservation, including habitat destruction and fragmentation, climate change, species invasions and extinctions, and disease spread. Here, we integrate fossil, historical, and present-day organismal and ecological data to investigate how conservation paleobiology provides deep-time perspectives on terrestrial organisms, populations, communities, and ecosystems impacted by anthropogenic processes. We relate research tools to conservation outputs and highlight gaps that currently limit conservation paleobiology from reaching its full impact on conservation practice and management. In doing so, we also highlight how the colonial legacies of conservation biology and paleobiology confound our understanding of present-day biodiversity, ecosystem processes, and conservation outlooks, and we make recommendations for more inclusive and ethical practices moving forward.

1. INTRODUCTION

Ecosystem service:

an ecological function within an ecosystem that benefits human society

Anthropogenic: caused by human activity

Ecosystem engineer:

an organism that significantly modifies, maintains, or creates habitats and modulates resource availability in ecosystems

Functional diversity:

the range of ecological functions offered by organisms in a community Encompassing nearly 30% of Earth's surface, terrestrial ecosystems host 80% of Earth's species (Grosberg et al. 2012), serve as significant reservoirs of carbon and nutrients (Keenan & Williams 2018), and provide a wealth of ecosystem services (**Figure 1**) (Jiang et al. 2021). At present, humans directly affect more than 70% of the global, ice-free land surface, and at least one-third of this area represents land converted for grazing, crops, and forestry (Shukla et al. 2019). Land-use change is linked to habitat loss and climate change, both of which disrupt the diversity, distributions, and interactions of species. Human activity in terrestrial ecosystems also impacts coastal and marine ecosystems, which are sensitive to pollution from agricultural runoff, mining, and fossil fuel extraction. While natural habitats have been fragmented, the establishment of anthropogenic biomes (Ellis & Ramankutty 2008) has also increased the connectivity of geologically and biologically distinct biomes, leading to introductions of invasive species and further eroding biodiversity due to disease, competition, and predation (Pereira et al. 2012). As these phenomena continue to intensify, there is an urgent need to expand biodiversity conservation practices.

A central aim of conservation is the preservation of biological diversity, often with priority given to landscapes seen as pristine and wild with minimal human impacts. Indeed, Western conservation is rooted in the notion of terra nullius (land belonging to no one), which emerged during European colonialism and propelled European nations to claim ownership of Indigenous lands, as Indigenous people were seen as part of the fauna instead of active ecosystem engineers (Hendlin 2014). However, archaeological data indicate human habitat conversion occurring on a traceable scale as early as 10,000 years ago and a significant global distribution of habitat conversion by 3,000 years ago (Stephens et al. 2019). Today's biodiversity is contingent on the entire history of human utilization and manipulation of ecosystems, as well as the abiotic drivers of biodiversity change (e.g., climate change, sea level fluctuations, tectonic activity) that shape ecosystems in perpetuity. Wild and pristine are therefore misnomers, and conservation science must draw upon deeper temporal data in conservation management that include both long-term human-ecosystem interactions and long-term abiotic drivers of biodiversity change if it hopes to be successful in conserving biodiversity and ecosystem services. Conservation paleobiology rises to that challenge, using fossil and associated geohistorical data to inform conservation policy. The long-term perspective offered by conservation paleobiology provides more scientifically robust data for the conservation, restoration, and management of biodiversity and ecosystem services than historical data can provide (Dietl & Flessa 2011). Indeed, paleobiological perspectives have called for a paradigm shift in conservation science that will foster dynamism on a changing planet, including facilitating ecosystem connectivity, nurturing the adaptive capacity of ecosystems, and managing ecosystems to maintain functional diversity (Barnosky et al. 2017).

Much of biodiversity research and conservation is future facing, so it might seem counterintuitive to look at the past, as conservation paleobiology does. However, past insight is essential for addressing present-day and future problems. The past documents changing ecosystems over geologic timescales, revealing the long-term trajectories of biodiversity with and without human influences. The fossil record provides the only window into the lives of long-extinct species and the impacts of these losses on species interactions and ecosystem processes. Here, we highlight the utility of paleobiological data sets and tools for elucidating the ecology of terrestrial communities. By examining patterns and processes across levels of ecological organization, we emphasize methods commonly used in conservation paleobiology that have utility for managing and disentangling anthropogenic and natural impacts. To conclude, we reflect on the human dimension of conservation paleobiology, including the effects of long-term human activity on biodiversity worldwide and the colonial legacy of paleobiology that confounds our understanding of present-day biodiversity and conservation outlooks.



Biomes

- Boreal forests/taiga
- Deserts and xeric shrublands
- Flooded grasslands and savannas
- Mangroves
- Mediterranean forests, woodlands, and scrub
- Montane grasslands and shrublands
- Temperate broadleaf and mixed forests
- Temperate conifer forests
- Temperate grasslands, savannas, and shrublands
- Tropical and subtropical coniferous forests
- Tropical and subtropical dry broadleaf forests
 Tropical and subtropical grasslands, savannas and shrublands
 Tropical and subtropical moist broadleaf forests
 Tundra
 Not applicable

Biodiversity hotspots

- Hotspot area
- ---- Outer limit



Biodiversity hotspots

---- Hotspot area

Protected areas

 Terrestrial and inland waters protected areas
 (Caption appears on following page)

а

Figure 1 (Figure appears on preceding page)

The global distribution of terrestrial ecosystems and protected areas. (*a*) Global map of terrestrial biome classifications, overlaid with biodiversity hotspots. (*b*) Global map of terrestrial and inland waters protected areas from the World Database on Protected Areas. Projection for both maps is in world geodetic system 1984 geographic coordinate system. Maps in panels *a* and *b* modified from Dinerstein et al. (2017) (CC BY 4.0) and Protected Planet (UNEP-WCMC & IUCN 2023), respectively. Biodiversity hotspots reproduced from Conservation International based on Mittermeier et al. (2004).

2. LEVELS OF ECOLOGICAL ORGANIZATION AND INVESTIGATIVE TOOLS

Conservation paleobiology relies on fossil specimens and the data that are generated from them. At a minimum, these data include locality and specimen identity, but additional data obtained directly from the specimen (e.g., skeletal morphology, biomolecules) and its geological and environmental context (e.g., stratigraphy) help reconstruct how the organism interacted with its biotic and abiotic environment. Thus, conservation paleobiology can clarify patterns and processes at different ecological levels of organization, from the individual to the population, community, or ecosystem level. While the individual-represented by an individual specimen-is the fundamental unit of ecological systems, it is not emphasized as a unit of study, even though data are gathered from individuals for studies at more macroscopic scales. Historically, the population level has been prioritized in conservation and paleoecology. Inventories like the International Union for Conservation of Nature (IUCN) Red list of Threatened Species (IUCN 2022) use parameters such as population size, growth rates, and geographic area size to inform status designations of threatened species, and paleoecologists routinely reconstruct population abundance using fossil data. The community level brings attention to the interactions of multiple populations through dynamics such as mutualisms, predation, and competition. Communities are also heavily emphasized in conservation because changes in one population can have cascading effects on other populations. At the ecosystem level, we see how communities interface with their abiotic environment (e.g., temperature, precipitation, soil type). Given how integrated organisms are with their abiotic environment and the drastic changes seen in abiotic factors worldwide, the ecosystem is of utmost concern in conservation. The geological and environmental context of fossils serves as a powerful tool for reconstructing past terrestrial ecosystems and quantifying the resilience of ecosystems to abiotic processes such as climate change.

In this review, we highlight several core tools commonly employed in characterizing fossil specimens (**Figure 2**) and the populations, communities, and ecosystems that they are a part of. Importantly, these tools not only have conservation relevance but can also be applied to modern ecosystems, allowing researchers to connect the past to the present. In recognition of the destructive nature of several of these tools, we present them in order of generally least invasive to most destructive, a chronology that might guide researchers who intend to gain multiple types of data from a single specimen.

2.1. Morphology

Identifying fossil material of past organisms using morphology is often the first step for palaeoecological and evolutionary analyses and creates a bridge linking the past to the present. Pairing morphology with ecology provides a method for understanding changes in populations, communities, and ecosystems through space and time. Therefore, morphological data facilitate conservation strategies that are cognizant of long-term patterns of diversification and extinction, species distributions and turnover, and community responses to climatic and environmental changes.

A specimen's locality and taxonomic identity can elucidate how the range of a species is impacted by environmental change. Analysis of fossil polar bear remains in the arctic documented



Figure 2

Investigative tools of conservation paleobiology research. Input data for paleobiological research are obtained from excavations and include fossils, sediments, phytoliths, and pollen. These data represent the start of a workflow that can provide multiple types of information about ancient terrestrial communities. While research can start with any of the illustrated tools, we recommend starting data collection and analysis with morphology (blue; see Section 2.1), as morphological methods tend to be less invasive than stable isotopes (purple; see Section 2.2) and paleogenomics (magenta; see Section 2.3), which both require physical destruction of all or part of a sample. Techniques such as photogrammetry and computed tomography scanning allow researchers to create a digital record of morphology that can exist in perpetuity. Isotopes provide further information on the individual specimen, such as its age or trophic position, and paleogenomics yields genetic information that can confirm or refine morphological identifications. The data generated from these tools are often integrated into ecological and evolutionary models (orange; see Section 3) that reconstruct community dynamics, quantify extinction risk, model projected species distributions, etc. While any of these tools can be used individually to inform conservation, combining multiple tools produces more holistic interpretations of the past for application to conservation. Photos provided by Tianyi Xu (top), Molly Moroz (center left), Alexis M. Mychajliw (center), Melissa E. Kemp (center right).

extralimital occurrences and revealed how the ranges of polar bears shifted with ice extent while reaffirming the importance of polynya habitat for polar bears since the late Pleistocene (Crockford 2022). Past species interactions can also be gleaned using fossils, sometimes leading to novel guidance for modern conservation management practices. Presence and absence data from fossil sites, for example, provided strong evidence that the endangered black-footed ferrets' dietary specialization for prairie dog prey items may be a more recent phenomenon (Owen et al. 2000). This information is useful for determining how and where to focus black-footed ferret reintroduction efforts. We can also use fossil evidence to examine the role humans have played in shaping terrestrial ecosystems through past utilization, translocation, and domestication of

No-analog community: an

ecological community that is compositionally different from all present-day communities

Phytolith:

a microscopic silicate structure found in plant tissues

Ecomorphology:

the study of how morphological variation is related to ecological traits species. A reassessment of fossil material, including morphometric analysis, led to the discovery that wild boar were introduced to Cyprus over 11,400 years ago and were likely managed on the mainland prior (Vigne et al. 2009).

The temporal dimension of the fossil record provides evidence for how populations, communities, and ecosystems are impacted by and respond to environmental changes. One response relevant for physiological, ecological, and evolutionary processes is body size change. Tomé et al. (2022) used scaling relationships to estimate body mass for fossil woodrats from Central Texas. They found a trend of decreasing body size over the last 22,000 years, which was hypothesized to be related to changes in biotic interactions such as predation pressure and resource competition. Morphological analysis of fossils can demonstrate shifts in features associated with ecologically relevant traits. In a study of bat fossils from Quaternary paleontological sites across central Texas, Moroz et al. (2021) found that changes in mandible shape of *Myotis velifer* were linked to precipitation changes and likely associated with dietary shifts. These data suggest that the range-restricted *M. velifer* may quickly adapt to climate change, which is useful knowledge for conservation practitioners who often prioritize range-restricted species over widespread species.

At the community level, serial paleobiological data sets facilitate reconstructions of communities before and after specific environmental changes such as human settlement (Burney et al. 2001). Fossils allow for the discovery of paleocommunities composed of species whose ranges do not overlap today. These no-analog communities point to and further our understanding of individualistic responses of populations to environmental change (Graham et al. 1996). Conversely, fossil material may also indicate long-term stasis in a community, as was demonstrated in the ecomorphological structure of the anole community on Hispaniola (Sherratt et al. 2015). Within a community, fossil assemblages are useful for examining guilds and their interactions. For example, identification of plant remains including pollen and phytoliths from a late Quaternary fossil site in Central Texas (Cordova & Johnson 2019) documented changes in the vegetation over an 18,000 year period. Insights into communal change through time and how communities responded to disturbances provides modern conservation practitioners with a baseline by which to contextualize modern communities and a framework for making predictions for the future. This information is relevant for increasingly common conservation strategies focused on preserving ecosystem diversity and functionality.

Ecomorphology is useful for examining the roles that organisms play in an ecosystem. Extending ecomorphological analyses to the fossil record enables us to examine how functionality in an ecosystem has changed through time. For example, by reconstructing ecological functional diversity in paleocommunities, Lundgren et al. (2020) demonstrated that introduced species often fill functional roles that were lost during the late Pleistocene due to the extinction of large mammals.

Also at the ecosystem level, functional traits are a primary means of relating communities and abiotic factors across space and time and can act as proxies for paleoenvironmental reconstructions. These traits directly influence and mediate the interactions between organisms and their environments and can link data from the past and present for deep time studies that are unobservable using only modern data sets (Short & Lawing 2021). By examining a combination of morphological traits, functional groups, and ecological niches represented in organisms, we find evidence for how organisms at individual to community levels and at local to regional scales interact with their environment. These methods, often grouped under a taxon-free or taxon-independent umbrella, are so named because they do not require detailed taxonomic identification outside of inherent phylogenetic constraints yet are critical to examining ecological principles that cross taxonomic, geographic, and temporal boundaries (Louys 2012).

One particularly promising category of taxon-free methods links ecomorphological traits with bioclimatic and environmental factors over geological time scales and enables us to examine how functionality in an ecosystem or community has changed through time. These methods, known in paleobiology as ecometrics (Eronen et al. 2010), have been employed for a variety of organismsincluding mammals, reptiles, birds, and plants-to better understand interactions with bioclimatic and environmental factors over geological time scales (Vermillion et al. 2018). For example, Polly & Head (2015) used carnivoran hind limb locomotor morphology (calcaneum gear ratio) and herbivore tooth crown height (hypsodonty) to reconstruct topography, vegetation cover, precipitation, and volcanism across North America. While some ecometric studies may be used primarily for paleoenvironmental reconstruction, extending these studies through geological time allows us to consider how the distributions of these traits have shifted over time and how they might be expected to change given potential future environmental trajectories. The application of ecometrics to fossil and living data sets can therefore inform conservation and management efforts, for example, by determining the effects of vegetational or bioclimatic shifts at local to continental scales (Lawing et al. 2012, 2016; Žliobaitė et al. 2016). Ecometrics, in addition to other types of taxon-free analysis, informs the characterization of processes that cannot be predicted or observed using neontological perspectives alone, including the likelihood of extinction, adaptation, range shifts, species invasions, ecological succession, or population fragmentation under changing environmental conditions and shifting biomes (Polly et al. 2016, Polly & Sarwar 2014).

Our ability to use morphological data to identify and interpret fossils is largely determined by our current understanding of patterns of morphological variation and evolution; however, there are substantial knowledge gaps for some taxonomic groups. Detailed knowledge about morphological variation in ancient and modern mammals often permits species-level reconstructions of fossil populations and communities, whereas knowledge of squamate osteological variation is more limited, which is an obstacle for interpreting patterns from fossils (Bell & Mead 2014). Further study, including additional sampling of modern populations and computed tomography scanning of existing alcohol-preserved museum collections, can help fill gaps in our knowledge of variation. Rapidly advancing quantitative morphological methods like geometric morphometrics further our understanding of patterns of variation and show fine-scale morphological patterns (Bochaton et al. 2017). The application of these novel techniques to morphological research promotes the utilization of fragments of the past to reconstruct community composition, functional diversity, and responses to environmental change, all of which can better direct conservation practices.

2.2. Stable Isotopes

Stable isotopes are used to quantitatively analyze the life history and ecology of species and are tractable in both ancient and present-day populations. Diet, migration patterns, habitat preference, ecological tolerance, and chronologies for when a species occupied an area can be extracted from a specimen using stable isotopes. Stable isotopes are also helpful with paleoclimate reconstruction, using either fossils or associated materials [e.g., speleothems (McDermott 2004)]. An array of isotopes exist, enabling ecosystem reconstruction at various temporal and spatial scales (Koch 2007). Here, we focus on isotopes commonly used in Quaternary research, in which human impacts can be detected and disentangled from natural processes.

The high precision of accelerator mass spectrometry ¹⁴C dating can pinpoint potential drivers of extirpation and extinction, especially in relation to human impact and recent climate change. Pairing radiocarbon dates and environmental niche models, Soto-Centeno & Steadman (2015) found that many Caribbean bat extinctions previously thought to be associated with climate change at the last glacial–interglacial transition occurred much later. While climate and humans acted synergistically to trigger the extinction of South American megafauna (Villavicencio et al. 2016), radiocarbon dating directly implicated humans in extinctions in other systems (Cooke et al.

Ecometrics:

the quantitative study of functional traits at the community level and how they sort temporally and spatially

Geometric

morphometrics: the quantitative morphological analysis of shape and size variation using landmark-based data 2017). These results highlight the complexities of late Quaternary extinctions. Radiocarbon dating can also clarify the timing of species introductions, facilitating the identification of prehistoric species introductions and their impacts on native communities (Giovas et al. 2012).

The long-term impacts of humans on the dietary ecology of natural populations can also be studied using stable isotopes, providing insight into the ability of organisms to adapt to human disturbance. For instance, Baumann et al. (2020) used carbon and nitrogen isotopes to reconstruct the isotopic space of Pleistocene foxes and found a growing commensalism between humans and foxes as human populations increased. Commensalism has been implicated in biodiversity loss (Hulme-Beaman et al. 2016), so detailed analysis of the ecological and evolutionary origins of anthropogenic commensalism may help mitigate the spread of such relationships.

Strontium isotopes (⁸⁷Sr/⁸⁶Sr) are particularly adept at addressing questions about mobility and land use, which is useful for understanding individual home range size. While morphological characters and life history traits may predict dispersal capabilities and range sizes, strontium isotopes provide empirical data on exactly how an organism traverses its landscape. Indeed, Crowley & Godfrey (2019) showed that large-bodied, extinct lemurs had small home ranges comparable to extant, small-bodied lemurs, despite the tendency for large-bodied primates to be highly mobile (Milton & May 1976). Furthermore, including information from other isotopes can further clarify the factors leading to extinction. For example, using strontium and carbon isotopes, Fannin et al. (2021) concluded that a reduction in suitable grassland habitat and large body size contributed to the extinction of all but one species of *Theropithecus* monkey across North Africa. Yanes et al. (2011) analyzed snail shells from the Canary Islands using morphology, carbon isotopes, and oxygen isotopes to compare changes in paleoenvironment over the last 50,000 years, revealing an overall decrease in relative humidity and the proportion of C4 plants and a corresponding decline in snail abundance and diversity.

In recent years, isotope use in paleoecology has increased and broadened to include novel applications of isotopes of hydrogen, sulfur, and zinc (Bourgon et al. 2020, Clementz 2012) and heavier elements like calcium, since it is minimally affected by diagenesis compared to other isotopes (Martin et al. 2018). Methodological innovations such as laser ablation and mass spectrometer advancements are creating new avenues for less destructive extraction and finer analysis of individual amino acids, carbohydrates, and other smaller molecules (Badgley et al. 2017, Clementz 2012, Martin et al. 2017). While further studies with each of these isotopes will provide richer data on the paleoecology of communities, the need for modern proxies remains highly relevant and should be considered in order to draw connections to the modern day and to better inform conservation practices for terrestrial communities (Merceron et al. 2021).

2.3. Paleogenomics

Paleogenomics, broadly defined as the analysis of ancient DNA (aDNA), and its sister field paleoproteomics, the study of ancient proteins (Lindqvist & Rajora 2019), are rapidly advancing fields that have proven to be useful for modern day conservation. The extraction of aDNA and proteins from fossils, as well as older museum specimens, can play a direct role in the taxonomic component of conservation as it can shed light on species delimitation in cases of taxonomic uncertainty and thereby help shape conservation policy and protection status. Kearns et al. (2016), for example, used aDNA extracted from historical museum specimens to recognize and elevate the Norfolk Island Robin as a distinct species deserving of appropriate conservation protections. Paleogenomics also explicates the evolutionary patterns that influence extinction and losses of genetic diversity. Using proteomic methods on fossils, Buckley et al. (2020) recovered evidence for lost species diversity among extinct Caribbean island shrews that previously inhabited islands of the Greater Antilles and reconstructed their evolutionary histories. Using aDNA, Larsson et al. (2019) found that both climate change and human exploitation led to a loss of genetic diversity in arctic foxes that may lead to increased vulnerability with future environmental change.

Indeed, paleogenomic research plays an increasingly pivotal role in examining evolutionary responses of organisms and whole communities to environmental changes over long timescales. For example, ancient mitochondrial and nuclear DNA revealed that several species of moas were not in decline prior to human colonization of New Zealand, further implicating humans in the extinction of these taxa (Allentoft et al. 2014). Paleogenomics can also uncover nuanced and sometimes individualistic responses of communities and species to climatic change. Clarke et al. (2019) analyzed sedimentary aDNA and found long-term persistence of an arctic-alpine plant community's composition until warmer temperatures led to a decrease in diversity because of encroachment by woody vegetation. Additionally, Baca et al. (2020) used aDNA from common vole remains across Europe to show patterns of population extirpation and replacement, lending insight into how species are impacted by abrupt environmental changes such as those following the last glacial maximum.

Paleogenomics can also shed light on the ancient biodiversity of entire communities, capturing taxa that do not fossilize well. For example, Seersholm et al. (2020) used bulk-bone metabarcoding of highly fragmented bones and nondiagnostic bones in conjunction with sedimentary aDNA to detect 100 vertebrate taxa and 45 plant taxa at Hall's Cave in Texas. Their work was concordant with previous morphology-based studies, but they also identified several taxa not previously described and were able to provide lower taxonomic resolution in some cases than that provided by osteology-based identification methods. Increased fossil identification through methods like bulk-bone metabarcoding and sedimentary aDNA can help establish temporal biodiversity baselines and characterize the suite of ecological functions and taxon interactions within ancient communities.

Although paleogenomics has shown great applicability for investigating past organisms and communities with implications toward conservation, it has not been applied equally to all taxonomic groups or geographies, in part due to preservation challenges (Reed et al. 2003). Recent methodological innovations have seen an increase in studies in tropical regions (Gutiérrez-García et al. 2014) and on understudied taxa like insects. Smith et al. (2021) performed high-throughput shotgun sequencing on insect fossils obtained from packrat middens in Joshua Tree National Park, California, and identified the fossils as *Philolithus actuosus*, a beetle that is still found in the area today. As insects are often used as bioindicators of climate change and environmental conditions, future studies of insect aDNA have great potential to provide key information on long-term environmental dynamics that terrestrial ecosystems encounter.

3. ECOLOGICAL AND EVOLUTIONARY MODELING

Models are often the culmination of integrating data generated from the aforementioned approaches with abiotic data, such as climatic variables, and have the power to inform long-term ecological and evolutionary patterns across varied spatial scales. There is a broad array of modeling techniques that incorporate paleobiological data or inform our understanding of past systems, but here, we focus on a subset of approaches with direct relevance to conservation.

3.1. Ecological Niche Modeling and Species Distribution Modelling

A fundamental goal in conservation is to measure the extent of a taxon's geographic distribution and identify the environmental factors that shape it. Ecological niche models (ENMs) and species distribution models (SDMs) are essential tools for prioritizing conservation areas, predicting

Biodiversity baseline:

a reference state of biodiversity measured at a given time and place

Ecological niche model (ENM):

a model using associations between species occurrences and environmental data to approximate fundamental niche parameters as potential geographic distributions for species

Species distribution model (SDM):

a model combining geographic distributions with environmental estimates to understand environmental influences on species' occurrence or abundance and to perform ecological forecasting **Climate envelope:** the range of suitable climatic conditions for a species

Phylogenetic comparative methods (PCMs): methods that use phylogenies and

temporal information to test evolutionary hypotheses on lineage diversification, lineage history, and trait evolution responses to environmental change, and mapping biological invasions (Schwartz 2012). It should be noted that the terms SDM and ENM are often used interchangeably in the scientific literature (Peterson & Soberón 2012). Although they can share similar applications, the goal of SDMs is to model actual geographic distributions, while ENMs examine the biotic and abiotic interactions that shape distributional patterns (for a detailed review, see Peterson & Soberón 2012). However, these models are most often parameterized solely on contemporary observations. Geohistorical records can complement modern data in ecological models to inform the past distribution of species outside of their present range and help improve forecasts for species. For example, Davis et al. (2014) found that hindcasting models for the distribution of several small mammals had a consistent prediction bias toward more southern distributions when compared to the fossil record for those organisms, which could cause even more bias when forecasting the future distributions of organisms. They found that the addition of deep-time fossil data helped calibrate niche models used in conservation planning. A paleobiological perspective of a species' biogeography improves our understanding of the long-term processes that shape present-day diversity and distribution patterns (Svenning et al. 2011).

Our interpretation of deep-time biogeography is complicated by lower spatial and temporal occurrences in the fossil record, fewer models of paleoclimate, and the need to consider evolutionary change. Lawing (2021) discussed the progression of SDMs and ENMs, including the application of climate envelope models to the fossil record, and described a framework for paleophylogeographic SDMs. This framework incorporates phylogenetic relatedness, fossil occurrences, and paleoclimate from general circulation models in deep time to infer past hotspots of species diversification and past geographic responses of species to environmental change. For example, Lawing & Polly (2011) applied paleophylogeographic data to map the ancestral climate envelopes of North American rattlesnakes through Pleistocene glacial-interglacial transitions and found that the rate of displacement for rattlesnakes in the future may be magnitudes greater. Similarly, Rödder et al. (2013) reconstructed Quaternary range shifts of Nearctic chelonians and were able to reconstruct past geographic changes, identify geographic processes that may have caused genetic bottlenecks. and predict threats from anthropogenic environmental change in the future for 59 turtle species. These studies escalate our ability to apply biogeographical, area-based metrics to pinpoint both past and present challenges to specific regions and species (geographic and anthropogenic environmental change, habitat fragmentation), and even populations or communities (genetic, functional, and taxonomic diversity; range shifts). In turn, these studies can be harnessed not only to make more robust predictions of future threats from environmental change but also to identify what types of challenges we can immediately or preemptively address.

While area-based metrics using the fossil record will continue contributing to the enhancement of ENM and SDM models, there has been a considerable push to improve protected area design and effectiveness beyond area-based metrics (Maxwell et al. 2020, Rodrigues & Cazalis 2020). Research shows that protected areas may have higher species richness but equal rates of decline when compared to nonprotected areas (Cooke et al. 2023), indicating a need to account for shifting environmental variables. Investigating the effects of environmental change through deep time on species distributions and richness will help to both enhance models and develop a more holistic implementation of protective efforts.

3.2. Macroevolutionary Modeling

Phylogenetic comparative methods (PCMs) are used to quantify the diversification of clades, evolutionary patterns of traits, and species biogeography. Although PCMs are most often used at the macroevolutionary level, an increasing number of researchers have recognized the advantages of applying these methods to conservation (Condamine et al. 2013, Lamsdell et al. 2017, Lawing 2021, Pyron & Pennell 2022). For instance, using phylogenies to estimate speciation and extinction rates and clade age can help us understand the vulnerability and evolutionary potential of species or clades (Condamine et al. 2013, Pyron & Pennell 2022). These estimations will help identify species or clades that are more prone to extinction due to high extinction rates or low speciation rates. In turn, we can tease apart whether a declining species was already on a trajectory toward extinction or declining due to anthropogenic impacts. For example, PCMs and the fossil record have shown that cycad diversity has declined since the Late Cretaceous (Condamine et al. 2015, Crisp & Cook 2011). However, cycad extinction is amplified by anthropogenic impacts such as habitat destruction and harvesting, resulting in over 66% of extant cycad species being listed as vulnerable, endangered, or critically endangered on the IUCN Red List (IUCN 2022). Using PCMs and biogeographical approaches, conservation biologists recommended protecting five hotspots to maintain cycad diversity (Yessoufou et al. 2017). Diversification rates also help identify areas with high speciation rates or low extinction rates; species in these localities may exhibit the greatest chance of recovering from anthropogenic impacts. For example, species found in mountains exhibit much higher speciation rates than species found in topographically less complex habitats (García-Rodríguez et al. 2021). Similarly, diversification models can help conservation paleobiologists examine temporal changes in species geographic ranges across deep evolutionary time and determine whether these changes were influenced by natural climatic and environmental changes or were human induced (Lamsdell et al. 2017, Lawing 2021). For example, temperature-dependent models reveal that the diversification and distribution of temperate and tropical lacertid lizards are associated with changes in paleoclimate, particularly in the past 10 million years of progressive global cooling. However, lineage-specific thermophysiology may prevent species from adapting to current anthropogenic climate change, thus explaining local lizard extinctions, especially in cool and humid climates (Garcia-Porta et al. 2019). Altogether, diversification analyses can inform conservation management toward protecting areas with high speciation rates for their evolutionary potential and identifying areas with low extinction rates that might be more resistant and resilient to biodiversity loss.

Trait-dependent models [e.g., state-dependent speciation–extinction models (Maddison et al. 2007)] and adaptive models [e.g., Ornstein–Uhlenbeck models (Butler & King 2004, Hansen 1997)] also provide researchers tools to examine how phenotypes impact speciation and extinction. Phenotypic and ecological specialization can often lead to extinction (Cardillo et al. 2005, Day et al. 2016, Nolte et al. 2019). Therefore, modeling relationships between phenotypes, ecologies, and diversification across phylogenetic time can help conservation scientists predict how changing phenotypes or ecologies influence future changes in populations.

The integration of the fossil record in PCMs remains a challenge for their use in conservation paleobiology primarily because phylogenies composed of both extinct and extant species tips are difficult and time intensive to reconstruct. Consequently, diversification rates are often estimated using timetrees reconstructed using only extant species. However, there has been considerable debate surrounding the reliability of inferring speciation and extinction rates with just extant phylogenies (Beaulieu & O'Meara, Louca & Pennell 2020). Similarly in trait evolution, incorporating the fossil record in macroevolutionary analyses dramatically improves the model selection of trait evolution (Hunt & Slater 2016, Slater et al. 2012). Nevertheless, the continued development of models and the integration of expertise across broad disciplines (Liow et al. 2022, Wright et al. 2022) plus the rise of aDNA to place fossil taxa into phylogenetic contexts (Oswald et al. 2019) will enable conservation paleobiologists to utilize PCMs in our understanding of anthropogenic impacts across deep time and provide guidance for conservation practice and management for mitigation.

3.3. Biodiversity Modeling

Serial computation of biodiversity indices allows us to evaluate taxonomic richness, turnover, and cooccurrence structures that inform the stability of ecological communities over time and the impact of environmental stressors on taxa. For example, by calculating the Jaccard similarity index for North American mammalian assemblages from the late Pleistocene to the present, Fraser et al. (2022) showed a 100-fold increase in biotic homogenization over the past 10,000 years. The facts that the onset of biotic homogenization in this system coincides with megafaunal extinction 10,000 years ago and that homogenization then continued to increase rapidly during a period of human population growth and agricultural intensification that occurred 2,000-1,000 years ago underscores the long-term role of humans in altering mammalian communities and their ecosystems. By analyzing abundances of the coprophilous fungi Sporormiella in conjunction with pollen and charcoal from a lake sediment core, Gill et al. (2009) showed that megaherbivore declines occurred prior to increased fire regimes and the development of plant no-analog communities, suggesting that ancient megaherbivores played a keystone role in ecosystem structure. Such findings inform the long-term role of keystone species-which are often prioritized in conservation planningin ecosystem functioning and underscore the need to support plans that seek to conserve these species.

While taxon-based biodiversity assessments are valuable for conserving specific taxa, quantifying biodiversity change through the lens of functional diversity is needed to conserve ecosystems—or suites of ecological functions—more broadly. Paleobiology is particularly poised to assess functional diversity over long timescales and across taxonomic groups, as species-level analyses are not always tractable in the fossil record. Functional diversity can also clarify functional similarities between extinct and introduced species, which may inform restoration practices and habitat prioritization. Functional diversity is often a target of restoration ecology (Cadotte et al. 2011). As humans have been introducing species outside of their native range for millennia, researchers have wondered whether introduced species restore ecological functions lost through extinction. However, many emerging data sets suggest that introduced species are not functional replacements of extinct ones, indicating that anthropogenic extinctions and introductions are selecting for different suites of traits. In a study of 1,302 bird species, Sayol et al. (2021) showed that while introduced bird species increase species richness and make up for extinctions in terms of the numbers of species in a biota, the introduced species possess a narrower set of functional traits than extinct species possessed, which may also translate into the introduced species performing a narrower set of ecological functions. A similar pattern is seen in Caribbean reptile assemblages, where extinct species and introduced species were shown to occupy different areas of functional trait space (Kemp 2023). Functional richness can also provide insight into factors that contribute to ecosystem resilience. In the same study, Kemp (2023) used functional entities—groupings of species with the same trait character combinations-to examine functional redundancy across different islands of the Caribbean and quantify functional diversity loss over the Quaternary. While small islands ($<2,000 \text{ km}^2$) lost on average 5.4% of their native functional richness, functional redundancy on large islands served as a buffer to significant functional diversity loss (Kemp 2023). These differences in biodiversity loss are due in part to differences in evolutionary history: Large islands not only have higher species richness but also higher rates of in situ diversification, which may lead to the presence of multiple species with similar functional traits. Interestingly, several small islands retain high levels of functional diversity roughly equivalent to those of large islands in part due to minimal human impacts, having had consistently low human populations and minimal habitat conversion for agriculture. Functional trait diversity-combined with knowledge of historical human land use-highlights aspects of human activity that might promote

biodiversity retention and resilience, as well as functional traits that are particularly vulnerable to loss.

4. LIMITATIONS AND AREAS FOR GROWTH

Paleobiological data hold great promise for conservation, but there are several critical knowledge gaps and methodological limitations that stymy conservation paleobiology from reaching its full potential in affecting change in terrestrial ecosystems. Most strikingly, methods have not been applied equally across taxa, resulting in differential impact. Of terrestrial vertebrates, mammals have been the most widely studied (Dillon et al. 2022), although research in birds and reptiles is increasing. Ancient amphibian communities, on the other hand, are poorly characterized. Amphibians are severely impacted by anthropogenic global change in recent years (Wake & Vredenburg 2008), with an estimated 40% of species threatened with extinction (IUCN 2022). As habitat destruction, climate change, and disease are the principal drivers of modern extinction, paleobiological data can provide pivotal information about past responses to these phenomena and traits that underlie resiliency.

There is also a disconnect between what conservation practitioners want to prioritize and what conservation paleobiology can inform, given limitations in our ability to characterize fossil data. This outcome is particularly acute at certain scales of ecological organization and for certain taxonomic groups. When species-level or genus-level identifications of fossil material are infeasible, conservation paleobiology cannot deliver the long-term population-level data that might be desired by practitioners. As discussed in Section 2.1, this likely does not affect many mammal species but would certainly hinder paleobiology-informed conservation plans for squamate species.

Several of the methods featured here were initially developed in other disciplines and applied only recently to paleobiology, and we are likely to see a growth in case studies in conservation paleobiology as a broader array of researchers learn the techniques and develop creative use cases. Studies of ancient disease transmission could further clarify the impacts of human colonization and introduced species on native communities and facilitate long-term characterization of immune evolution in species that are vulnerable today. This emerging research area has largely focused on humans but is likely to expand to other organisms (Stone & Ozga 2019). As technological innovations in disciplines like paleogenomics continue to break new ground in retrieving sequences from older specimens (van der Valk et al. 2021) and localities with poor preservation (Nieves-Colón et al. 2020), it is of utmost importance that researchers use specimens responsibly, taking care to record aspects of a specimen that might be lost through destructive sampling, using the most minimally invasive sampling techniques, and leaving material for future work that may be situated on unknown research frontiers (Fox & Hawks 2019). As fossils are a rare, nonrenewable resource, researchers must weigh future research opportunities alongside the benefits of immediate specimen analysis. Preservation is a constant consideration that may preclude some analyses from taking place, though we highlight a few pathways for moving forward, such as going straight to paleogenomic analyses with highly fragmented fossil material that may be hard to identify morphologically. While we highlight genomic data in this review, paleoproteomic data may be more tractable for some taphonomic contexts and can answer similar questions to paleogenomic data, albeit with lower taxonomic resolution (Buckley 2018).

The investigative tools we highlighted contribute directly to conservation practice and management, and using several of these methods in tandem results in more robust and nuanced interpretations of the past that one method alone cannot articulate. Approaches that synthesize multiple lines of evidence are necessary to combat biodiversity loss in complex socioenvironmental systems and encapsulate the spirit of conservation paleobiology, which integrates



* Morphology * Stable isotopes * Paleogenomics

Figure 3

Contributions of paleobiological tools to conservation. Conservation paleobiology is uniquely poised to provide data that informs multiple aspects of conservation research, practice, and management. For each of the scenarios listed, we indicate whether morphology, stable isotopes, paleogenomics, or ecological and evolutionary modeling contributes relevant data using a colored square. Some methods are relevant only when used in conjunction with other data; the type of additional data required is indicated by an appropriately colored asterisk.

diverse tools and knowledge from geohistorical data for direct application to conservation practitioners, scientists, and other stakeholders. We implore researchers to consider how the tools they use contribute to conservation and to explore the feasibility of integrating additional research methods into their scientific practice (**Figure 3**).

Related to our last point, the conservation paleobiology community needs to engage more deeply and meaningfully with the larger conservation community to ensure that priorities are aligned for maximal impact on policy and management. Conservation paleobiologists are not

THE MOST SIGNIFICANT QUESTIONS FOR TERRESTRIAL ECOSYSTEM CONSERVATION: A CONSERVATION PALEOBIOLOGY PERSPECTIVE

Conservation paleobiologists often struggle to integrate with the broader conservation community. When representatives from 24 international organizations convened to identify the 100 most significant questions for biodiversity conservation (Sutherland et al. 2009), no conservation paleobiologists were included. Unsurprisingly, conservation paleobiology is uniquely positioned to address several of the identified questions, including the following:

- 1. "What was the condition of ecosystems before significant human disruption, and how can this knowledge be used to improve current and future management?" (p. 562)
- 2. "Do critical thresholds exist at which the loss of species diversity, or the loss of particular species, disrupts ecosystem functions and services, and how can these thresholds be predicted?" (p. 561)
- 3. "Which elements of biodiversity in which locations are most vulnerable to climate change, including extreme events?" (p. 561)
- 4. "What, and where, are the significant opportunities for large-scale ecosystem restoration that benefits biodiversity and human well-being?" (p. 562)
- 5. "What spatial pattern of human settlement (e.g., clustered versus dispersed) has the least impact on biodiversity?" (p. 562)
- 6. "What information is required to enable responsible authorities to decide when and how to manage nonnative species?" (p. 564)

always at the table when other conservation scientists are brainstorming and prioritizing urgent issues in biodiversity conservation, even though conservation paleobiology data types are uniquely equipped to address many issues that have been raised (see the sidebar titled The Most Significant Questions for Terrestrial Ecosystem Conservation: A Conservation Paleobiology Perspective). Climate change poses a profound threat to global biodiversity, and paleobiologists are uniquely positioned to study the impacts of climate at all ecological levels of organization, from reconstructing individual physiologies to the adaptive capacities of populations, communities, and ecosystems. However, in a recent survey of both conservation paleobiologists and the literature, climate data were employed rarely in the published literature (1.2% of reviewed papers) and used only by 9.2% of responding conservation paleobiologists (Dillon et al. 2022). Most of the data that appear in the literature and were collected by survey respondents were presence-absence and abundance data, which are mostly useful for population and community level work. While trait data are used to a lesser degree, more implementation of trait-based approaches by the conservation paleobiology community may increase the relevance of findings, as conservation scientists are realizing that ecological function may be more important than taxonomic identity in maintaining resilient communities and ecosystems. Given high taxonomic turnover rates in many paleobiological assemblages as well as varying levels of taxonomic uncertainty in the fossil record, paleobiological data sets are uniquely positioned to characterize changes in trait diversity, and researchers should capitalize on these features instead of viewing them as flaws.

5. HUMAN DIMENSIONS TO CONSERVATION PALEOBIOLOGY

Conservation paleobiology and allied fields (archaeology, paleoecology, historical ecology) have contributed pivotal data on long-term biodiversity change and the role that humans have played in shaping ecosystems. Long-term human activity also has implications for terrestrial biodiversity

at all scales of ecological organization. Intensive, direct harvesting of individuals triggers population declines, leading to extinction. The loss of keystone flora and fauna can reverberate in communities and ecosystems, causing additional population declines, extinction cascades, and altered ecosystem function (Dirzo et al. 2014). Globally, defaunation and habitat loss have resulted in a 53% decline in food web links of terrestrial mammals (Fricke et al. 2022). Deforestation is one key contributor to population decline in the endangered Hispaniolan solenodon, which fossil evidence indicates was widespread across the island prior to human colonization; human population density was found to be negatively correlated with and the most important predictor of its present-day distribution (Gibson et al. 2019). Anthropogenic changes to community structure can also elicit evolutionary responses, such as reduced seed size in palm populations where large avian frugivores have been extirpated for decades (Galetti et al. 2013). Furthermore, the introduction of nonnative fauna over millennia has led to biotic homogenization in many biodiversity hotspots (Kemp et al. 2020), further disrupting species interactions and ecosystem services.

Paleobiology has enormous potential to continue clarifying human impacts, given the deep temporal perspective that it provides. Whereas ecological studies are limited to decadal and centennial scales, paleobiology can provide critical baseline data on populations, communities, and ecosystems before human impacts and inform how different human cultural practices impact biodiversity. Identifying human settlement patterns that are least impactful on biodiversity is a significant goal of conservation (Sutherland et al. 2009) that paleobiological data sets can clarify (Kemp 2023). Furthermore, phenotypic data (e.g., morphology and isotopes) and genotypic data derived from fossils can explicate whether species of conservation concern have exhibited adaptive responses to past anthropogenic perturbations, allowing for more robust predictions of future resiliency.

Humans are effective allogenic ecosystem engineers (Jones et al. 1994), and conservation science is an act of ecosystem engineering whereby humans modify ecosystems to restore, maintain, and guide biodiversity in an uncertain future. The establishment of protected areas (**Figure 1***b*), targeted species eradication, and species reintroductions have yielded significant conservation gains. Educational programming offered by park systems, museums, nature reserves, and other venues helps to emphasize the urgency of conservation and natural resource management. With the present-day emphasis placed on conservation, conservation paleobiology is primed to recruit new researchers and practitioners who seek to integrate historical and paleoecological data to predict organismal responses to future environmental changes; establish biodiversity baselines, restoration targets, and conservation priorities; and implement eradication, restoration, and reintroduction plans based on long-term scientific data.

While conservation paleobiology holds immense potential, it also runs the risk of excluding and harming vulnerable human populations, an aspect of the discipline that has not been explored as deeply as its positive impacts and potential. We consider some of the ethical issues pertaining to the derivation of paleobiological data and the implementation of conservation (Section 5.1) and outline ways in which conservation paleobiology can contribute to equity and inclusion in the conservation sciences and paleobiology (Section 5.2).

5.1. Colonial Legacies of Paleobiology and Conservation

Though paleobiology and conservation science have made significant contributions to advancing our knowledge of the changing world and to protecting biodiversity, these disciplines are heavily rooted in colonialism and remain deeply intertwined with their colonial legacies. The backbone of paleobiological research, fossil data collection, has been entrenched in colonialist practices and narratives since its inception (Monarrez et al. 2022, Raja et al. 2022), and funding in this field

is largely tied to the extraction of nonrenewable resources (Monarrez et al. 2022). Sampling and collection of fossils are largely conducted by a handful of countries and skewed toward certain regions of the world. Much of the earliest collections were extracted by foreign scientists in the Global North and originate from countries that were once under colonial control or countries with limited socio-economic or political power to prevent extractive collecting. In the widely used Paleobiology Database, 97% of all fossil occurrence data comes from scientists in high and upper-middle income countries (Raja et al. 2022). This collection history created sampling biases and perpetuated inequities that hamper scientific progress and conservation development, especially in biodiversity hotspots, which are disproportionately situated in the Global South.

Additionally, conservation science is rooted in colonialist land protection policies that have been fraught with the displacement of Indigenous peoples, the dispossession of their land, and the exclusion of local peoples from decision-making. Frequently, the protected areas that are a result of these policies are seen as pristine or untouched. However, this way of viewing conserved lands ignores precolonial use of the land and has historically been used as justification for colonialist occupation and exploitation (Hendlin 2014). Furthermore, conservation is not a new Western concept; Indigenous peoples were the first practitioners of conservation and land stewardship and possess relationships with land that stand in contrast to settler colonial land relationships that still drive modern-day conservation (Eichler & Baumeister 2021, Hendlin 2014).

For decades, the colonial legacies in these fields have limited the scope of conservation paleobiology research and biased both sampling and our subsequent understanding of ecological and evolutionary processes (Mohammed et al. 2022). This colonial history has impacted the targets of conservation prioritization, the stakeholders involved, the aims of conservation planning, and the policy enacted to meet these aims. This results in poorly informed conservation policies and practices that suffer from a lack of local and Indigenous knowledge and are biased toward specific regions of the world.

5.2. An Equitable Conservation Paleobiology

Moving toward a more equitable and inclusive future for the parent fields of conservation paleobiology is of paramount importance and is long overdue, and conservation paleobiologists must work conscientiously to avoid perpetuating inequities as the field continues to grow. To effectively reach this goal, actionable steps must be taken at all levels (e.g., personal, institutional, governmental). Previous papers have outlined a series of implementable best practices and changes to achieve this in paleobiology (Klymiuk 2021, Mohammed et al. 2022, Monarrez et al. 2022, Raja et al. 2022) and conservation (Domínguez & Luoma 2020, Eichler & Baumeister 2021, Hendlin 2014). Here, we highlight a subset of these best practices with the aim of promoting effective, immediate, and lasting impact in conservation paleobiology.

First, researchers, institutions, and funding agencies alike must accept and acknowledge their colonial legacies and enact policies to remedy the damage caused by past and ongoing actions. While it may be difficult, these institutions must reframe their own historical narratives by offering transparency about their history, their continued complicities in colonialist practices, and the harm this has caused. Only then can they truly fulfill and represent the purposes they seek to serve (i.e., preservation of collections, research, outreach, and education). There are myriad ways in which individuals, institutions, and funding agencies can rectify past wrongs, and the most appropriate response will involve open dialogue with impacted communities. Some pathways forward include training scientists from historically excluded communities who call the research area home, enacting and enforcing explicit guidelines about collaborating as a component for funding and permitting, and repatriating specimens to enable local research.

Second, we call for the abolition of parachute science by involving local experts and community members as project members at all project stages and depositing samples in local repositories whenever possible. Translating research findings into conservation management has been a recurring challenge for conservation paleobiologists, who are often not in dialogue with local communities, local stakeholders, land managers, government agencies, or other conservation researchers (Dillon et al. 2022). Community-engaged conservation paleobiology may be one way in which the field can achieve its goal of having on-the-ground conservation impact. By centering the needs and values of stakeholders, particularly those from vulnerable sectors of society, a community-engaged conservation paleobiology would yield greater buy-in from affected constituents who are given a voice in the direction of research. While these recommendations may require considerable self-reflection and reorganization of research programs, we are confident that they will yield more inclusive and impactful research outcomes.

6. CONCLUSIONS

Humanity depends on terrestrial ecosystems, which are at risk of continued land degradation and biodiversity loss, threatening critical ecosystem services that we depend upon. There is an urgent need to quantify recent biodiversity loss, characterize existing biodiversity, and determine how species and ecosystems will be impacted by ongoing and future global change. The fossil record provides unprecedented geohistorical data about ancient terrestrial communities during periods of environmental stasis and change, holding great promise for directing conservation practices moving forward. However, safeguarding terrestrial ecosystems, their biodiversity, and the services that they provide requires ingenuity and equitable collaboration across all sectors of society, overcoming our past to engineer a vibrant, resilient, and better future for us all.

SUMMARY POINTS

- 1. Conservation practitioners and researchers can gain a deeper perspective on preserving terrestrial communities by exploring long-term patterns and processes using historical, archaeological, and paleobiological data.
- 2. Humans have played an important role as ecosystem engineers over thousands of years, and conservation paleobiology has the potential to disentangle natural versus anthropogenic impacts on ecosystems.
- 3. There are many tools that conservation paleobiologists employ, and each provides specific conservation outputs. However, when used together, they can produce a more holistic and robust perspective for understanding past and present-day biodiversity and ecosystem services.
- 4. Currently, conservation paleobiology is heavily reliant on presence–absence and abundance data, but the community might increase engagement with conservation practitioners and other conservation scientists by employing more trait-based data that could inform community and ecosystem resilience in their research.
- 5. While paleobiological data provide deep temporal knowledge about biodiversity change, they are not an unlimited resource, and conservation paleobiologists must carefully consider the destructive nature of some data types when planning projects. Efforts should be made to preserve as much specimen information as possible—even if it is not related to the current project—to enable future research.

6. Conservation science and paleobiology are deeply intertwined with colonialism, and conservation paleobiologists must actively commit to pursuing equitable research and conservation practices. This includes becoming transparent about colonial histories, involving community members in research and conservation efforts, eliminating parachute science, and repatriating data and scientific findings.

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