Paleobiology

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Aligning paleobiological research with conservation priorities using elasmobranchs as a model

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Invited Article

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Non-technical Summary

We present an overview of conservation paleobiology and the directions in which the field could progress in the next 50 years to aid conservation. To do so, we use elasmobranchs (sharks, rays, and skates), one of the mostly highly marine endangered groups today, as a model. The perspectives we share are guided by current conservation priorities and recent advances in elasmobranch paleobiology and are developed around four main topics. For each topic, we outline knowledge gaps, discuss the potential of near- and deep-time records to contribute relevant information, highlight examples, and suggest research directions. Ultimately, we aim at focusing conservation paleobiology research agendas, encouraging collaborations across timescales, and distilling lessons that could be transferred to other threatened but understudied taxa in conservation paleobiology.

Abstract

Humans have dramatically transformed ecosystems over the previous millennia and are potentially causing a mass extinction event comparable to the others that shaped the history of life. However, only a fraction of these impacts has been directly recorded, limiting conservation actions. Conservation paleobiology leverages geohistorical records to offer a long-term perspective on biodiversity change in the face of anthropogenic stressors. Nevertheless, the field's on-the-ground contributions to conservation outcomes are still developing. Here, we present an overview of directions in which paleobiological research could progress to aid conservation in the coming decades using elasmobranchs (sharks, rays, and skates)—a highly threatened group with a rich fossil record—as a model. These research directions are guided by areas of overlap between an expert-led list of current elasmobranch conservation priorities and available fossil and historical records. Four research topics emerged for which paleobiological research could address open questions in elasmobranch science and conservation: (1) baselines, (2) ecological roles, (3) threats, and (4) conservation priorities. Increasingly rich datasets and novel analytical frameworks present exciting opportunities to apply the elasmobranch fossil record to conservation practice. A similar approach could be extended to other clades. Given the synthetic nature of these research topics, we encourage collaboration across timescales and with conservation practitioners to safeguard the future of our planet's rapidly disappearing species.

Introduction

Over the previous millennia, humans have dramatically transformed ecosystems and pushed species to the edge of extinction (Vitousek et al. 1997; Richardson et al. 2023). These anthropogenic impacts have accelerated since the 1950s (Steffen et al. 2015) and have potentially triggered a sixth mass extinction event comparable in magnitude to the other five that shaped the history of life (Barnosky et al. 2011; Dirzo et al. 2014; Ceballos et al. 2015). Change has progressed over different timescales on land and in the ocean, with marine impacts beginning more recently, so we sit at a critical moment where recoveries remain within reach (McCauley et al. 2015). Because resources are finite, decision makers must prioritize what and where to protect as well as which benchmarks to use when tracking progress toward conservation goals. Information about natural ecosystem states and vulnerabilities can help guide these decisions. However, human impacts often preceded the instrumental records and biological monitoring programs used to collect this information, shifting the reference points used for conservation (Pauly 1995; Jackson 2001).

The geological record captures a long-term view of environmental change that can inform conservation and inspire action. Geohistorical records (e.g., fossil records, sediment cores, tree rings, and archaeological middens) extend our understanding of ecosystem trajectories beyond the time frame of direct human observation (National Research Council 2005). They are

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commonly divided into near time (last 2.58 Myr, known as the Quaternary Period) and deep time (older than 2.58 Myr), which vary in scale, resolution, and completeness, and reflect different eco-evolutionary processes (Dietl and Flessa 2011; Fig. 1). Collectively, geohistorical records can be used to reconstruct natural variability before human disturbance (Willis and Birks 2006; Keane et al. 2009; O'Dea et al. 2020; Fig. 1C–G), document the patterns and drivers of biotic change over millennia to millions of years (Jablonski and Sepkoski 1996; Jackson and Blois 2015; Duda et al. 2020; Fig. 1A–G), estimate extinction risk (Harnik et al. 2012; Finnegan et al. 2015; Collins et al. 2018; Fig. 1B), and anticipate species' responses to future climatic conditions that have yet to be observed in the instrumental record (Davis 1989; Willis et al. 2010; Fordham et al. 2020; Fig. 1A). The potential for geohistorical records to tackle conservation challenges has accrued over decades (e.g., Martin and Wright 1967; Graham 1988; Smol 1992; Birks 1996; Swetnam et al. 1999; Jackson et al. 2001), setting the stage for conservation paleobiology to emerge as a named subfield in 2002 (Flessa 2002).

Conservation paleobiology aims to apply geohistorical records to the conservation, management, and restoration of biodiversity and ecosystem services (Dietl and Flessa 2011; Dietl et al. 2015). It integrates information from a variety of related disciplines, such as archaeology, paleoecology, historical ecology, and conservation biology (Louys 2012; Barnosky et al. 2017; Dillon et al. 2022b), and it has benefited from recent advances in paleontological and analytical methods (Dillon et al. 2023; Tomašových et al. 2023) as well as interdisciplinary collaborations (e.g., Conservation Paleobiology Network, https://conservationpaleorcn.org). Over the last two decades, conservation paleobiology has attracted a growing research community interested in leveraging geohistorical records to help address the climate and biodiversity crises (Dillon et al. 2022b). Examples of conservation paleobiology research in action are mounting: geohistorical records have supported caribou management in Alaska (Miller et al. 2021, 2023; Fig. 1C), forest restoration on Kaua'i (Burney et al. 2001; Fig. 1D), traditional clam gardening practices in British Columbia (Toniello et al. 2019; Fig. 1E), coral outplanting in Hong Kong (Cybulski et al. 2020; Fig. 1F), and freshwater flow

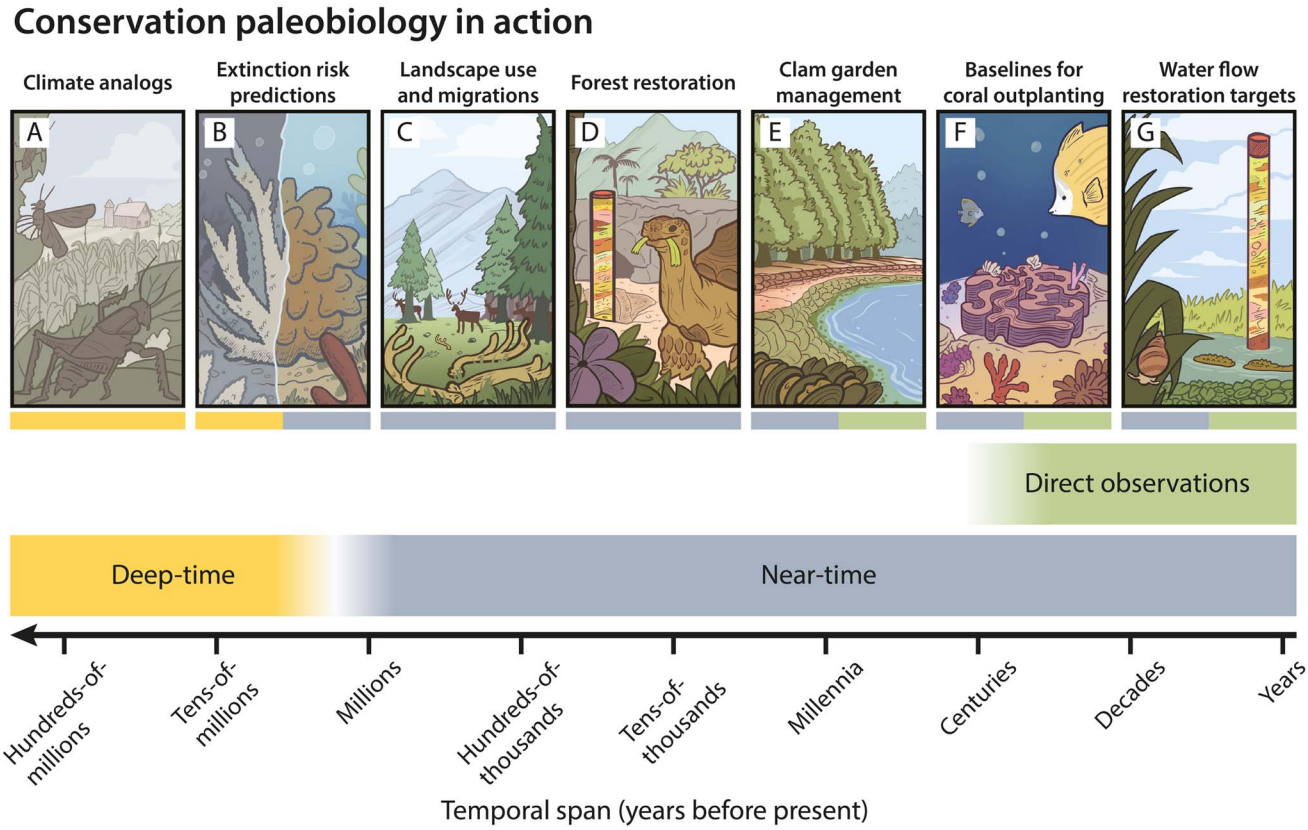


Figure 1. Examples of conservation paleobiology in action. Conservation paleobiology uses a variety of near-time (blue; last 2.58 Myr) and deep-time (yellow; older than 2.58 Myr) geohistorical records to extend the temporal span of direct observations (green; ca. last century). The application of deep-time geohistorical records to conservation practice remains unrealized, although it has promise: **A,** insect herbivory increased in North America during the Paleocene–Eocene thermal maximum (rapid global warming ca. 56 Ma), offering an analogue for how future warming might precipitate heightened insect damage to plants (Labandeira and Currano 2013); **B,** morphological traits of fossil Caribbean corals during the Plio-Pleistocene were used to predict the extinction risk of extant corals and validate their conservation status (Raja et al. 2021). Examples of conservation paleobiology studies resulting in tangible conservation outcomes are accumulating: **C,** caribou antlers exposed on landscapes dating back decades to millennia have supported spatial management plans (Miller et al. 2021, 2023); **D,** excavations from Makauwahi Cave Reserve on Kaua'i have informed forest restoration and the introduction of giant tortoises to fill lost ecological roles (Burney et al. 2001); **E,** intertidal death assemblages, archaeological shell middens, and modern clams have guided Indigenous-led ecosystem restoration goals and traditional clam gardening practices in the Salish Sea of British Columbia, Canada (Toniello et al. 2019); **F,** Holocene-age coral subfossils defined spatially explicit historical baselines for coral outplanting in Hong Kong (Cybulski et al. 2020); **G,** estimates of pre-alteration (before 1900 CE) hydrology reconstructed from pollen and mollusks were used to set salinity targets in the Florida Bay and manage freshwater flow through the Greater Everglades ecosystem (Marshall et al. 2014; Wingard et al. 2017). Illustrations by Ian Cooke Tapia (Cooked Illustrations).

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restoration in the Florida Everglades (Marshall et al. 2014; Wingard et al. 2017; Fig. 1G). These case studies have begun to instill optimism in the field's ability to "put the dead to work" (Dietl and Flessa 2011) and provide a framework for others to follow (Groff et al. 2023).

However, most geohistorical records do not influence conservation decisions. A review of the conservation paleobiology literature found that only ~10% of research resulted in tangible conservation outcomes, with all successful examples using near-time records of extant species (Groff et al. 2023). Although not all conservation paleobiology research needs to have direct real-world impacts, the field is still grappling with the research–implementation "gap" as it comes to terms with how applied it is, and should be, in practice (Boyer et al. 2017; Kelley et al. 2018; Savarese 2018; Dillon et al. 2022b). Implementation is, in part, impeded by disconnects between research and conservation priorities, such as when researchers collect data without first targeting a relevant conservation need or defining project goals with practitioners (Knight et al. 2008; Beier et al. 2017; Toomey et al. 2017). For example, conservation paleobiology research focuses on a few taxonomic groups, such that many taxa are underrepresented relative to their extinction risk (Dillon et al. 2022b). If conservation paleobiology aspires to increase its salience in conservation, reframing research agendas and collaborating with practitioners could bring the field closer to generating actionable science that is aligned with conservation needs.

One taxonomic group that has received little attention in conservation paleobiology research is marine vertebrates—in particular, the most threatened marine vertebrate group today: elasmobranchs (sharks, rays, and skates) (Dulvy et al. 2021; Dillon et al. 2022b; Sherman et al. 2023; Fig. 1). Elasmobranchs are found throughout all major marine (as well as some brackish and freshwater) ecosystems, where they play important ecological roles such as structuring food webs as upper trophic level consumers (Ferretti et al. 2010; Hammerschlag et al. 2019; Flowers et al. 2021; Heithaus et al. 2022; Fig. 2A). Elasmobranchs are also economically beneficial for ecotourism (Gallagher and Hammerschlag 2011; Cisneros-Montemayor et al. 2013), contribute to food security (Glaus et al. 2019), and have cultural significance (de Borhegyi 1961; Skubel et al. 2019; Fig. 2B). However, elasmobranchs are threatened by overfishing (Dulvy et al. 2021; Fig. 2C), which has drastically reduced their populations in the last decades (e.g., Pacoureau et al. 2021). If elasmobranch species go extinct, not only would biodiversity be lost but also millions of years of evolutionary history and ecological functions that could not be replaced (Stein et al. 2018; Pimiento et al. 2020, 2023). Despite how important they are to protect (Fig. 2D), elasmobranchs have only recently entered policy agendas (Dulvy et al. 2008, 2017; Fordham et al. 2022), so effective management is hindered by a lack of information about their biology, ecology, and conservation status (Jorgensen et al. 2022).

The elasmobranch fossil record is often overlooked when addressing these knowledge gaps. There has been a dwindling presence of paleobiological work at relevant biology conferences (Shiffman et al. 2020) and little buy-in for including geohistorical records in elasmobranch conservation assessments (McClenachan et al. 2012; Engelhard et al. 2016). Paleobiology has a lot to contribute to these conversations. First, elasmobranchs have a rich fossil record, with their teeth being the most abundant vertebrate fossil (Maisey 1984; Cappetta 2012). This is because their teeth

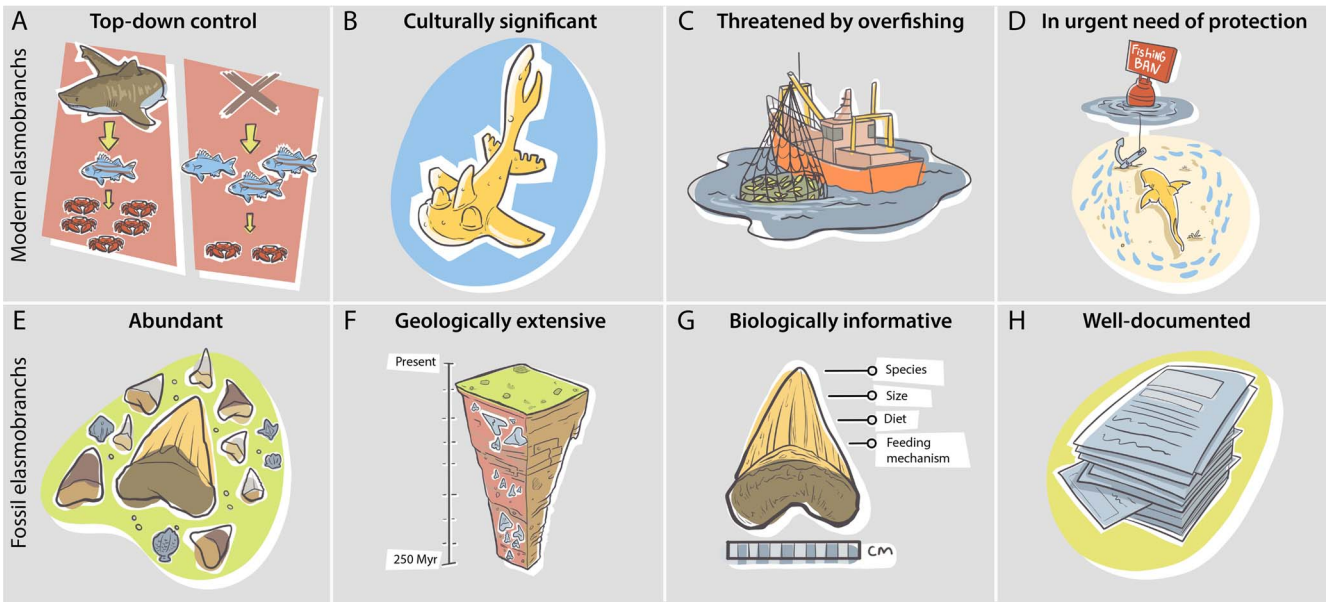


Figure 2. The potential of the elasmobranch fossil record to inform conservation. **A,** Elasmobranchs structure food webs, with their elimination potentially resulting in cascading effects (Heithaus et al. 2022). **B,** They are socioeconomically important, as they drive tourism (Cisneros-Montemayor et al. 2013) and are a source of protein for artisanal fishers (Glaus et al. 2019). They also hold cultural significance, as evidenced by archaeological artifacts and motifs found in Central America, among other regions (de Borhegyi 1961). **C,** Overfishing is the primary threat to elasmobranch populations (Dulvy et al. 2021). Given the antiquity of fishing, most systematic monitoring studies are predicated on a shifted baseline, so a long-term perspective is needed to reconstruct natural variation in elasmobranch communities. **D,** Elasmobranchs are the most threatened marine vertebrate group today (Dulvy et al. 2021) and need protection. **E,** Elasmobranchs have a rich fossil record because their teeth and dermal denticles are shed continuously and are composed of hard materials that easily fossilize. **F,** Modern elasmobranchs have a long evolutionary history, with extant taxa being well represented in the fossil record (Paillard et al. 2021). **G,** Fossil elasmobranch teeth can often be identified to the species level, and their morphological traits enable ecological inferences (Cooper et al. 2023). **H,** The elasmobranch fossil record is well documented in the paleontological literature. Illustrations by Ian Cooke Tapia (Cooked Illustrations).

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(and dermal denticles) are shed continuously and are composed of hard materials that easily fossilize (Fig. 2E). Second, the fossil record of modern elasmobranchs and their extinct relatives (Neoselachii) is geologically extensive, dating back to the Triassic (250 Ma; Maisey et al. 2004; Cappetta 2012; Fig. 2F). Importantly, many extant taxa are represented in the fossil record, including all orders, 88% of families, 75% of genera, and 10% of modern species (Pimiento and Benton 2020; Paillard et al. 2021). Third, elasmobranch fossils provide valuable biological information (Naylor and Marcus 1994; Cooper et al. 2023; Fig. 2G). Fourth, they are well-documented in the scientific literature, with around 17,000 occurrences in the Paleobiology Database (Fig. 2H). Finally, iconic specimens such as *Otodus megalodon* teeth capture the public's imagination and tell stories about ancient animals (Clements et al. 2022). Elasmobranchs therefore represent a ripe opportunity to incorporate geohistorical records into conservation practice (Fig. 2).

Here, we use the elasmobranch fossil record as an example to present research directions in which conservation paleobiology could progress to aid conservation in the coming decades. We share our perspectives as conservation paleobiologists working on elasmobranchs in the near- and deep-time fossil record. To frame our perspectives, we assessed the intersection between an expert-led list of current elasmobranch conservation priorities (Jorgensen et al. 2022) and available fossil and historical records (Table 1, Supplementary Material). Four broad topics emerged for which paleobiological research could address knowledge gaps in elasmobranch science and conservation: (1) baselines, (2) ecological roles, (3) threats, and (4) conservation priorities (referred to hereafter as Topics 1–4) (Fig. 3). We pose each as a question, discuss the potential of near- and deep-time records to contribute relevant information, and suggest how they could become more actionable. Our intent is to focus conservation paleobiology research agendas, encourage collaboration across timescales to inform elasmobranch conservation, and distill lessons that could be transferred to other threatened but understudied taxa in conservation paleobiology.

Topic 1: What Were Baseline Elasmobranch Abundances before and alongside Human Impacts?

Elasmobranch populations are severely depleted across many ecosystems today (MacNeil et al. 2020; Pacoureau et al. 2021; Simpfendorfer et al. 2023). Yet systematic monitoring has only captured the recent history of elasmobranch exploitation, so historical baselines preceding human impacts are scarce (Jackson

Table 1. The potential of near- and deep-time geohistorical records to address priority questions in elasmobranch conservation identified by Jorgensen et al. (2022). Three circles indicate a major contribution (e.g., relevant data are available and directly applicable); two circles indicate a minor contribution (e.g., some relevant data exist, but their application is less tangible or hindered by biases and/or mismatches in resolution); one circle indicates minimal contribution (e.g., few relevant data exist, but they could hypothetically contribute); and an empty cell indicates that no viable contribution is envisioned (e.g., no relevant data are available or the question is out of scope). A circle with a dotted outline indicates that the question could be reframed to incorporate geohistorical data but is not applicable as written. The bold numbers correspond to headings within the article (Topics 1–4) where examples are presented. See the Supplementary Material for the rationale behind each assessment.

Priority	Near-time	Deep-time
Status and threats		
How do we overcome data deficiency in elasmobranch population assessments? **(4)**	●●	●●
How can we improve life history estimations of elasmobranchs for fisheries management and conservation? **(2 & 4)**	●●	●●
What are the most effective and promising approaches for elasmobranch bycatch mitigation?	●	
How can we more accurately measure and monitor total global catch of elasmobranchs?	●	
Beyond fishing, what are the emerging threats to elasmobranchs? **(3)**	●●●	●●●
How can we reconstruct elasmobranch baselines to inform population decline estimations and recovery targets? **(1)**	●●●	●
Population and ecology		
What are the knowledge gaps in global abundance and diversity of elasmobranchs? **(1 & 4)**	●●●	●●●
How can tagging technologies be applied more effectively to inform elasmobranch research and conservation?	◌	◌
How can we more clearly define the ecological role of elasmobranchs? **(2)**	●●●	●●●
How can we improve knowledge of elasmobranch population structures?	●	●
Conservation and management		
What is the role of citizen science in elasmobranch conservation research?	●●	●●●
How can marine protected areas (MPAs) contribute to elasmobranch conservation? **(4)**	●●	●●
Under what conditions (ecological, environmental, social, political) can elasmobranch fisheries be sustainable? **(1)**	●●	
What is the socio-economic role of elasmobranch fisheries? **(1)**	●●	
How can we quantify ecosystem services provided by elasmobranchs? **(2)**	●●	
What is the role of vessel tracking in assessing and enforcing fisheries interactions with elasmobranchs?		
What are the relative impacts of small-scale, industrial, and recreational fisheries on elasmobranch populations? **(3)**	●●	
How can we reconcile public safety and healthy elasmobranch populations?	●	
What are the species composition and population impacts of the shark fin trade?	●	
What are the impacts of regulations across elasmobranch species and jurisdictional scales?		

Minimal ● Minor ●● Major ●●●

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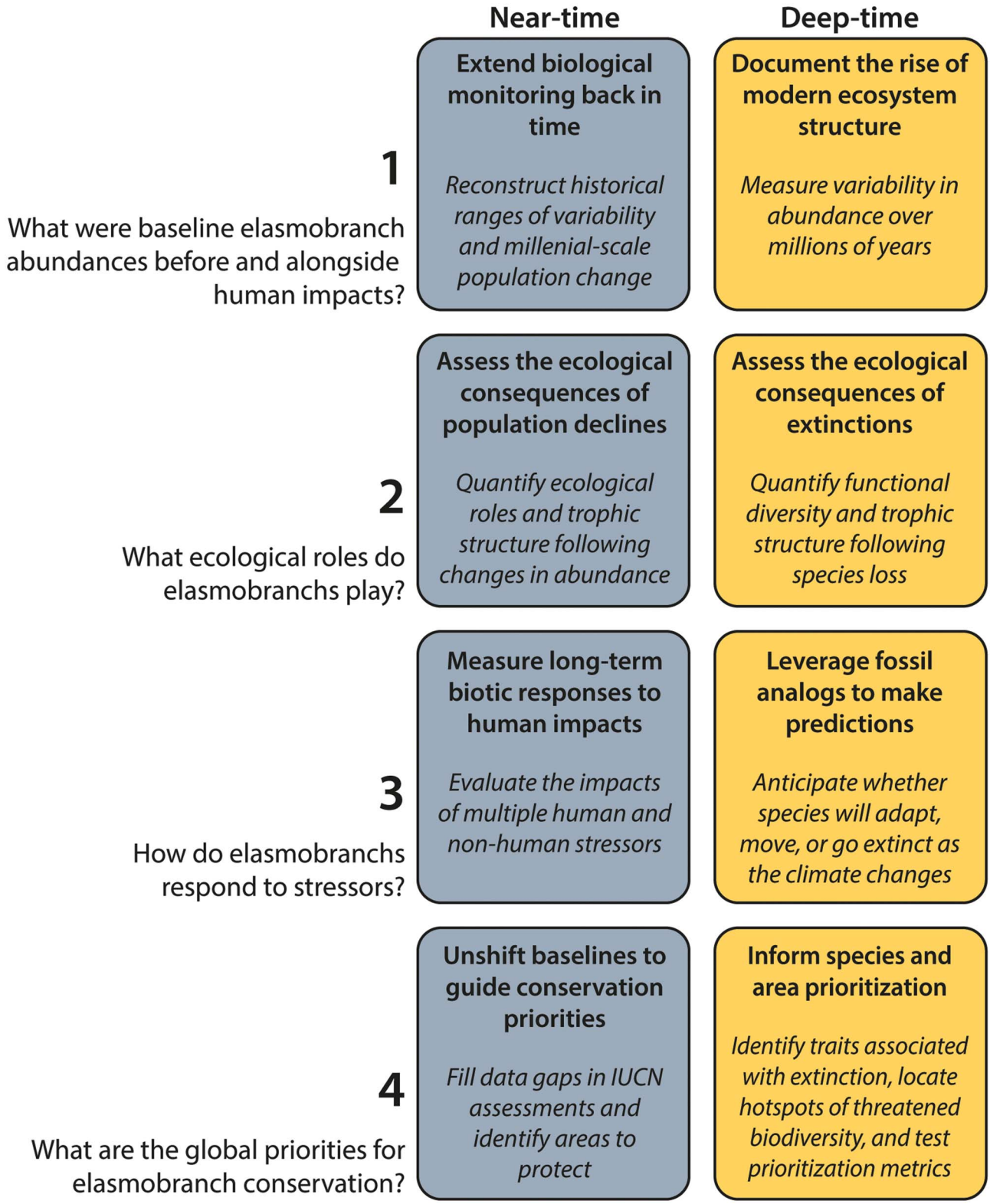


Figure 3. The elasmobranch fossil record offers a model to align conservation paleobiology research agendas with conservation. Research topics for which near- and deep-time geohistorical records have potential to address knowledge gaps in elasmobranch science and conservation include: (1) baselines, (2) ecological roles, (3) threats, and (4) conservation priorities. IUCN, International Union for Conservation of Nature.

1997; Jackson et al. 2001). These baselines define ranges of natural variability that provide benchmarks to measure the timing, magnitude, and drivers of ecological change over human timescales (Willis and Birks 2006; Lotze and Worm 2009; Fig. 1C–G). Without accurate baselines, our understanding of elasmobranch ecology and conservation status can become skewed, leading to

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unrealistic or unambitious conservation targets (Lotze and Worm 2009; McClenachan et al. 2012).

Elasmobranch biologists recognize the value of baselines (Heupel et al. 2019; Jorgensen et al. 2022; Table 1) and have employed creative approximations to compensate for the lack of historical data. Elasmobranch baselines have been inferred using space-for-time comparisons on remote islands (Sandin et al. 2008; Bradley et al. 2017), population models (Ferretti et al. 2018), model-estimated regional averages (MacNeil et al. 2020; Simpfendorfer et al. 2023), and predictions based on environmental variables like primary productivity (Nadon et al. 2012; Valdivia et al. 2017; Fig. 4A). Available time-series data have also been collated in databases (e.g., Mull et al. 2022). Collectively, these studies have mapped spatial variation in modern elasmobranch abundance to quantify depletion and understand the ecology of less disturbed systems.

However, relying on modern survey data alone to shape expectations of elasmobranch baselines might be misleading given the ubiquity of human activities, which can overwrite the environmental drivers of elasmobranch abundance (MacNeil et al. 2020; Clementi et al. 2021). Discrepancies also exist across survey methods, because elasmobranchs are challenging to count (McCauley et al. 2012a). Geohistorical records can therefore complement ecological and fisheries surveys to track long-term population change. In deep time, fossils track the rise of modern ecosystem structure, whereas near-time records reconstruct historical variability over shorter time periods to contextualize modern elasmobranch communities (Fig. 3).

Over millions of years, fossils chronicle how elasmobranch abundances have shifted alongside their prey base, marking transitions between ecosystem states (Fig. 3). Relating these biological changes to major events in Earth's history can, in turn, evidence the environmental, climatic, and ecological factors that have shaped the emergence of ecosystems that we study and manage today (see Topics 3 and 4). For example, Sibert et al. (2016) used fossil dermal denticles and fish teeth accumulating in deep-sea sediment cores to demonstrate that open-ocean ecosystems have been restructured multiple times over the last 85 Myr. Importantly, they observed a geologically abrupt disappearance of elasmobranchs at 19 Ma, which might offer insight into the eco-evolutionary implications of recent declines (Sibert and Rubin 2021). Baseline carrying capacities of elasmobranchs today are the legacy of these past events, underscoring the value of measuring variability in deep time.

The near-time fossil record, alongside archaeological and historical records, can extend biological monitoring back in time to reconstruct elasmobranch baselines throughout human history and before extensive human impact (Fig. 3). For example, fossil dermal denticles accumulating in coral reef sediments have been used as a proxy for relative shark abundance to reconstruct pre-exploitation baselines and millennial-scale change along Panama's Caribbean coast (Dillon et al. 2021; Fig. 4A). When compared with monitoring data (Chevis and Graham 2022), these fossil assemblages suggest that the current dominance of demersal species like nurse sharks (*Ginglymostoma cirratum*) deviates from the historical state of shark communities in the area (Fig. 4B). Likewise, archaeological records (Fossile et al. 2023) and cultural artifacts (Drew et al. 2013) have revealed shifts in shark community composition through the lens of harvesting as well as demonstrated their socioeconomic significance as a food resource and cultural symbol (López de la Lama et al. 2021). Over more recent timescales, historical records—including photographs, archival landings data, and local ecological knowledge—have documented elasmobranch population vulnerability and trajectories before industrial fishing (e.g., Ferretti et al.

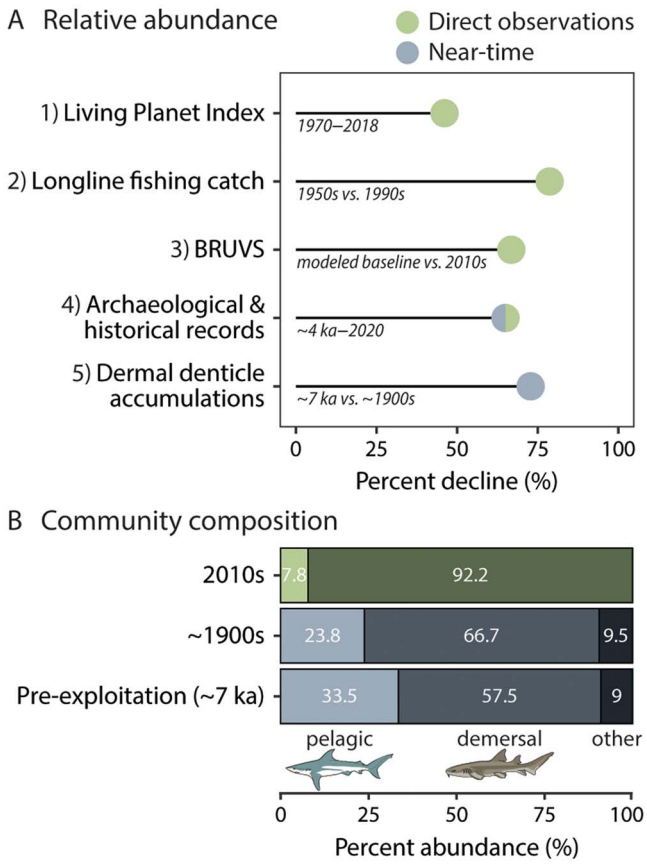


Figure 4. Geohistorical and historical data can contextualize the extent of ongoing elasmobranch declines. **A,** Elasmobranch population trends are estimated using a variety of methods, including fisheries and monitoring data, historical and archaeological records, and near-time fossil records. A collection of available data from the Atlantic Ocean, including the Caribbean Sea—a region in which dramatic declines in shark abundance in the late twentieth century portended their dire conservation status—are compared here. These include: (1) the Living Planet Index calculated from abundance time-series data for 14 oceanic shark and ray species (Pacoureau et al. 2021); (2) a comparison of longline fisheries catch rates for four oceanic shark species in the Gulf of Mexico from the 1950s and 1990s (Baum and Myers 2004); (3) relative abundances of two resident shark species on Caribbean reefs recorded from Baited Remote Underwater Video Stations (BRUVS) compared with a model-predicted regional baseline (Simpfendorfer et al. 2023); (4) perceived abundances of sharks inferred from archaeological, historical, ecological, and fisheries records in Caribbean Panama (Dillon et al. 2021); and 5) a comparison of shark dermal denticle accumulations from mid-Holocene and modern reefs in Caribbean Panama and the Dominican Republic (Dillon et al. 2021). These methods have different biases and temporal spans, with fishing impacts preceding most observational records. Baselines are either inferred from time-series data (1) or historical observations (2 and 4) when available, predicted using a model where all parameters are set those expected with no human impacts (3), or measured from fossil accumulations before major human impact (5). Each method reports large declines ranging from 46% to 79%, with some of the higher estimates produced when the baseline is extended farther back in time (although note that the data span multiple species and areas). **B,** In Caribbean Panama, BRUVS deployed from 2016 to 2019 overwhelmingly recorded nurse sharks (*Ginglymostoma cirratum*), a demersal reef-associated species (upper green bar; Chevis and Graham 2022). Dermal denticle accumulations sampled from modern (middle blue bar) and mid-Holocene (lower blue bar) reefs in the same area suggest that the current dominance of nurse sharks likely does not reflect the historical state of shark communities (Dillon et al. 2021). The shading indicates the relative abundances of pelagic (light), demersal (darker), and other (darkest) sharks in each record. Illustrations by Ashley Diedenhofen.

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2008; McClenachan 2009; Bom et al. 2020; Martínez-Candelas et al. 2020; Herbst et al. 2023). These examples demonstrate how historical elasmobranch baselines can be pieced together using a variety of methods to fill an established knowledge gap. However, this information is not yet commonly applied in elasmobranch conservation.

What makes a baseline actionable? We see at least three avenues for increasing the salience of historical baselines in elasmobranch conservation. First, because baselines vary with environmental context (Valdivia et al. 2017), geohistorical records could be collected from additional regions, habitats, and time points to inform local conservation targets and model the biophysical drivers of natural variability. Additionally, elasmobranch populations could be reconstructed during cultural periods with different fishing intensities or management strategies to track their responses to human activities over millennia (see Topic 3). This work is being facilitated by the development of new methods, such as lab protocols to access lesser-known dermal denticle records (Dillon et al. 2017; Sibert et al. 2017), machine learning to classify fossil material (Mimura et al. 2023), paleoecological time-series analyses (Simpson 2018; Mottl et al. 2020), and time-series databases (Smith et al. 2023). As data accumulate, a next step could include developing data synthesis workflows akin to those for other fossil assemblages (e.g., fossil pollen; Flantua et al. 2023).

Second, baselines derived from geohistorical records could be reported using formats compatible with modern data to create a common currency for translating changes in elasmobranch populations across timescales. For example, Rodrigues et al. (2019) proposed a framework for comparing modern species' abundances to historical reference points to quantify long-term human impacts. Their classification system consisted of categories defined by percentage change intervals relative to a baseline before major human impact, enabling standardized comparisons despite patchy data. To deal with uncertainty when mobilizing diverse datasets, they specified the likelihood of each category and provided conservative estimates of the magnitude of change (Rodrigues et al. 2019). Communicating uncertainty around baseline estimates is critical to build trust in the methods, clarify their biases, and propagate the effects of that uncertainty into downstream conservation decisions (Dietl 2019; Cooke et al. 2020; White et al. 2023).

Series of paleobiological data measured in the same units are more readily compared. The magnitude of change from a baseline could be calculated as a percentage or effect size along with confidence intervals, sample ages and chronological uncertainty, and either sensitivity analyses or models that account for the loss of skeletal material through taphonomic and depositional processes (e.g., Tomašových and Kidwell 2017; Kiessling et al. 2023; Tomašových et al. 2023). For example, Dillon et al. (2021) compared both absolute and relative dermal denticle abundances across time points and sampling locations to characterize elasmobranch community change. Denticle accumulations can also be compared with contemporaneous records (e.g., fish teeth or otoliths) after accounting for differences in taphonomy and production rates (Sibert et al. 2016, 2017). Converting denticle accumulations into absolute shark densities poses a greater challenge, as denticle abundances are affected by depositional, taphonomic, and biological processes. At a minimum, information about denticle densities and shedding rates, shark body sizes, sedimentation rates, and taphonomic alteration would be needed to produce such estimates (Sibert et al. 2017; Dillon et al. 2021, 2022a). In the absence of this information, ground-truthing studies have attempted to correlate elasmobranch fossil accumulations (e.g., dermal denticles) with modern surveys (e.g., shark densities) in wild (Dillon et al. 2020) and aquarium (Dillon et al. 2022a) settings to evaluate their ecological fidelity.

Finally, baselines should be framed in terms of conservation needs. This process begins with investing in partnerships with conservation practitioners to ensure that the end goal, users, and timeline of a conservation need inform data collection strategies (Beier et al. 2017; Cooke et al. 2020; Dietl et al. 2023). When building collaborations, partners could discuss how a baseline is selected and what success might look like in relation to that baseline (Campbell et al. 2009; Redford et al. 2011; MacKeracher et al. 2019; Cooke et al. 2020), consider the interplay between baselines and human cultural practices (Simpfendorfer et al. 2021; Hoel et al. 2022), and design multiple anticipatory recovery goals that situate a baseline in its current sociopolitical context (Dietl 2019; Ingeman et al. 2019). These conversations are important given the ecological and political challenges of recovering large predators (Marshall et al. 2016; Stier et al. 2016; Ingeman et al. 2022) and the potential for human–wildlife conflict if recovery is successful (Carlson et al. 2019). In addition to sourcing research questions from practitioners, historical baselines could help iteratively shape elasmobranch conservation priorities by flagging populations that are either vulnerable or have high recovery potential (see Topic 4). Baselines might also uncover elasmobranch populations that have resisted decline, thus creating opportunities to learn from these "bright spots" (Lotze et al. 2011; O'Dea et al. 2017; Ingeman et al. 2022). In sum, geohistorical records offer an exciting research avenue to contextualize recent elasmobranch population change and retroactively fill monitoring gaps, especially when integrated with modern datasets in conservation assessments.

Topic 2: What Ecological Roles Do Elasmobranchs Play?

When organisms are lost from an ecosystem—either through population declines, extirpations, or extinctions—their ecological functions can also be lost. Conservation efforts have traditionally focused on species diversity, but there is a growing interest in preserving species' contributions to ecosystem processes (Soulé et al. 2003; Sanderson 2006; Akçakaya et al. 2020). One way to measure these contributions is through species' ecological traits, such as body size, diet, and mobility (Petchey and Gaston 2002; Villéger et al. 2008; Gagic et al. 2015). Ecological traits reflect how energy or other resources are assimilated and moved across ecosystems (Done et al. 1996; Bellwood et al. 2019). These traits, in turn, constitute the functional diversity of a community or assemblage, apart from its taxonomic composition. Functional diversity has been measured in both modern and fossil assemblages to quantify their responses to disturbances (Mouillot et al. 2013), identify functions that disappear or emerge when species' configurations shift (Graham et al. 2014; Pimiento et al. 2017; Bellwood et al. 2019; Fig. 1D), and predict future ecosystem states using traits as proxies (Streit and Bellwood 2022).

Elasmobranchs are at greater risk of losing functional diversity than any other marine megafauna group under simulated extinction scenarios, likely as a result of their threatened status and because species with extreme trait combinations are selectively fished (Pimiento et al. 2020). Indeed, sharks are already thought to be "functionally extinct" in some areas where their numbers

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are too low to maintain their ecological functions (Jackson et al. 2001; MacNeil et al. 2020). However, the ecological consequences of elasmobranch declines are still being unraveled (Stevens 2000; Heithaus et al. 2008, 2022; Ferretti et al. 2010; Roff et al. 2016), and their functional diversity is often overlooked in current conservation priorities (Pimiento et al. 2023).

These knowledge gaps arise because we are still learning about elasmobranchs' ecological roles as they are concurrently being eliminated or modified by human activities (Table 1). For example, we know that great sharks (i.e., large apex predators) structure food webs through direct predation (Ferretti et al. 2010; Heupel et al. 2014; Fig. 2A). However, whether these top-down effects cascade to lower trophic levels is still debated, particularly in complex ecosystems like coral reefs (Bascompte et al. 2005; Estes et al. 2011; Frisch et al. 2016; Roff et al. 2016; Casey et al. 2017; Desbiens et al. 2021). Because historical overfishing depleted large apex sharks (Jackson et al. 2001), it is unclear whether the lack of robust evidence stems from food web properties (e.g., omnivory, functional redundancy, or diffuse predation), buffering by bottom-up processes (e.g., environmental variation controlling prey availability), or potential confounds (e.g., simultaneous fishing of predators and prey), or alternatively, whether trophic cascades occurred before biological monitoring (Roff et al. 2016). Modern ecological studies are typically limited to testing these hypotheses after apex predators have already been removed from food webs, and they sometimes arrive at different conclusions (Heithaus et al. 2022).

Elasmobranchs are more than just predators. They alter prey behavior (Heithaus et al. 2008; Sherman et al. 2020), compete with or create feeding opportunities for other species (Papastamatiou et al. 2006; Oliver et al. 2011), energetically connect resource pools across habitats (McCauley et al. 2012b), transport nutrients (Williams et al. 2018), and are prey themselves (Ford et al. 2011; Mourier et al. 2013). These lesser-studied functions are presumed to promote ecosystem health, yet the mechanistic linkages remain untested or are similarly predicated on a shifted baseline (Roff et al. 2016; Jorgensen et al. 2022).

For each of these cases, recent methodological developments have improved our ability to extract relevant ecological information from the elasmobranch fossil record. We discuss three approaches here: (1) traits inferred from morphology, (2) biomechanical reconstructions, and (3) geochemistry. These approaches can be used in conjunction with occurrence data to reconstruct elasmobranchs' ecological roles, biotic interactions, and functional diversity in both near and deep time. Near-time studies typically apply these methods to detect the ecological consequences of elasmobranch population change following fishing, whereas deep-time studies aim to infer the trophic ecology of extinct species and assess how disturbances like past extinction events alter food web structure and functional diversity (Fig. 3).

Traits Inferred from Morphology

Some ecological traits can be inferred from shark tooth morphology (e.g., body size, prey preference, and feeding mechanism; Fig. 2G), although the associations between tooth measurements and functional traits are not always one to one (Frazzetta 1988; Ciampaglio et al. 2005; Cooper et al. 2023). Because shark teeth can be identified to species (Naylor and Marcus 1994; Cappetta 2012; Paillard et al. 2021), biological processes related to these traits can be explored over microevolutionary scales. Shark dermal denticles also encode biological information (e.g., body size, mobility, position in the water column, schooling behavior, and bioluminescence), although they are less taxonomically resolved than teeth (Reif 1985; Raschi and Tabit 1992; Dillon et al. 2017; Ferrón and Botella 2017; Ferrón and Palacios-Abella 2022). Additionally, elasmobranch vertebral rings preserve life-history traits such as growth rates and age (Daiber 1960; Shimada 2008). Together, these traits reflect functional ecology, as they relate to how species use resources (Tavares et al. 2019). For example, analyses of fossil shark tooth morphology across the Cretaceous/Paleogene (K/Pg) mass extinction documented a reduction in the body size and ecological diversity of Lamniformes (Belben et al. 2017) and a proliferation of similar tooth morphologies within Carcharhiniformes (Bazzi et al. 2018), suggesting morphological turnover. Other studies use traits to constrain inferences from food web networks. A. Shipley et al. (2023) incorporated traits into a metacommunity web to model how trophic dynamics shifted after *Otodus megalodon* went extinct at the end of the Pliocene, foreshadowing the potential ecological consequences of losing extant apex predators like white sharks (*Carcharodon carcharias*). Beyond measuring individual traits, shark teeth and dermal denticles can be ascribed to functional groups based on their morphologies, which correspond with ecological life modes (Reif 1985; Cappetta 1986; Dillon et al. 2017; Ferrón and Botella 2017) and can be used to infer the ecological structure of shark communities (Dillon et al. 2021; Fig. 4B).

Biomechanical Reconstructions

When interpreting traits based on morphology, it is important to establish the relationship between each trait and its ecological function (Streit and Bellwood 2022; Brown et al. 2023). One way to test hypothesized relationships between form and function is through biomechanical reconstructions. Much of this work for elasmobranchs has focused on locomotion and feeding kinematics (Motta and Wilga 2001; Dean and Bhushan 2010). Dermal denticles' hydrodynamic properties have been experimentally tested using pieces of shark skin (Oeffner and Lauder 2012; Afroz et al. 2016), 3D printed biomimetic foils (Wen et al. 2014; Lauder et al. 2016; Domel et al. 2018), or simplified replicas (Bechert et al. 2000; Lang et al. 2008). Computational fluid dynamics models have also been applied to simulate water flow over denticles (Díez et al. 2015). These biomechanical studies support the placement of denticles into functional groups. In contrast, biomechanical tests of shark tooth performance show that some tooth morphotypes used to infer diet are hazy (Whitenack and Motta 2010; Corn et al. 2016; Ballell and Ferrón 2021), motivating reassessments of their value as ecological proxies to determine which tooth measurements are most informative (Cooper et al. 2023). Collectively, this work has refined our understanding of the functional significance of shark tooth and dermal denticle morphology, allowing insights to be extended back in time. Additional promise lies in applying these methods to fossil morphologies that lack extant analogues.

Geochemistry

Geochemical approaches such as stable isotope analysis augment what we can learn from fossil morphology. Notably, they have revolutionized studies of elasmobranch diet and habitat use (Vennemann et al. 2001; Boecklen et al. 2011; Hussey et al. 2012; Kim and Koch 2012). Elasmobranch diet in the fossil record

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was traditionally deduced from either tooth morphology (e.g., Cappetta 1986) or from infrequent bite marks, coprolites, or preserved stomach contents (e.g., Aguilera and de Aguilera 2004; Benites-Palomino et al. 2022). Minute signatures of enameloid-bound nitrogen isotopes ($\delta^{15}N$) can now be measured in fossil shark teeth using the oxidation–denitrifer method (Kast et al. 2022), which has begun to reveal the diet, trophic position, and energetic requirements of ancient sharks. In parallel, bulk nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotopes have been extracted from collagen in teeth sampled from living sharks (Polo-Silva et al. 2012; O. N. Shipley et al. 2021, 2023) and zooarchaeological remains (Burg Mayer and de Freitas 2023) to document resource use and connectivity—highlighting conceptual overlap across timescales. Other promising trophic indicators include zinc isotopes ($\delta^{66}Zn$; McCormack et al. 2022, 2023) and calcium isotopes ($\delta^{44/42}Ca$; Martin et al. 2015; Assemat et al. 2022). Nitrogen and zinc isotope analyses have provided new insights into the trophic evolution of apex predators, suggesting that large Cenozoic megatooth sharks (genus *Otodus*) reached higher trophic positions than any extant marine species (Kast et al. 2022) and/or potentially competed for resources with *C. carcharias* (McCormack et al. 2022). Additionally, stable isotopes can trace elasmobranch movement across isotopically distinct waterbodies (i.e., $\delta^{18}O$ and $^{87}Sr/^{86}Sr$; Fischer et al. 2013). As these isotope systems are applied to ever-smaller fossils with increasing precision, it could be fruitful to characterize trophic niches using multiple complementary isotopes (Cybulski et al. 2022; Lüdecke et al. 2022) and to track changes in trophic niches across disturbance events.

How can we better leverage ecological data preserved in the elasmobranch fossil record to anticipate and manage their future functional ecology? As we have shown, ecological traits convey information about ecosystem functioning that can be translated across timescales (Fig. 3). Consequently, opportunity lies in combining fossil and modern trait datasets (Brown et al. 2023). One path forward could be to develop a conceptual framework that unites elasmobranch functional ecology through time. Such a framework could establish best practices for data collection, archiving in online trait databases, and reporting. To encourage collaboration across potential users, this framework could be codeveloped by paleobiologists, biologists, and conservationists asking similar trait-based questions over varying temporal and spatial scales. Ultimately, if conservation success is framed as restoring functionally viable populations (Akçakaya et al. 2020), then information about past ecosystem processes could play a role in setting and measuring progress toward recovery goals.

Topic 3: How Do Elasmobranchs Respond to Stressors?

Understanding how species respond to threats is important for guiding conservation strategies. Elasmobranchs provide a useful case study for gleaning conservation lessons from a lineage's past failures and successes. Elasmobranchs and their relatives have endured major extinction events and weathered episodes of global cooling and warming in the geological past (Kriwet et al. 2008; Whitenack et al. 2022), marking millions of years of stability punctuated by pronounced change (Sibert et al. 2016). Elasmobranchs now face a new threat. Over mere decades, overfishing has pushed their populations to the brink of collapse (Ward and Myers 2005; Dulvy et al. 2021; Pacoureau et al. 2021), and its effects are compounded by habitat degradation, pollution, and climate change (Dulvy et al. 2014; Sherman et al. 2023).

However, key questions remain about how these anthropogenic and environmental stressors affect elasmobranchs (Table 1). We have more to learn about how climate change will interact with other stressors to impact elasmobranch populations (Chin et al. 2010; Rummer et al. 2022), where to focus management efforts as their ranges shift (Dulvy et al. 2017; Tanaka et al. 2021; Diaz-Carballido et al. 2022), and which species are most sensitive (Jorgensen et al. 2022). Because elasmobranchs are large and mobile, it is generally not feasible to manipulate them in real time, hindering mechanistic insight into how stressors control their populations. Instead, the fossil record spans a range of scenarios that can be leveraged to study how elasmobranchs responded to combinations of stressors in the past and, in turn, assess their susceptibility to future change. Because threats to elasmobranch populations operate over different timescales, both near- and deep-time records are pertinent.

Geohistorical records spanning centuries to millennia demonstrate elasmobranchs' responses to long-term anthropogenic stressors such as fishing and habitat loss. These records can help evaluate the relative impacts of multiple human and nonhuman stressors and identify conservation actions with the biggest potential to mitigate their effects (Fig. 3). For example, Dillon et al. (2021) documented a 71% decline in shark dermal denticle accumulation since the mid-Holocene in Caribbean Panama, suggesting a significant drop in shark abundance (Fig. 4A; see Topic 1). To better understand the mechanisms, they examined differences in the amount of decline across denticle functional groups and found that commercially valuable sharks were preferentially affected, implicating fishing as the dominant cause (Fig. 4B). Yet they also observed declines in sharks that are infrequently fished, evidencing the additional contribution of indirect human pressures such as habitat degradation (Dillon et al. 2021). Other examples come from historical ecology, where studies have aligned time series of elasmobranch abundance derived from archival sources with putative stressors in locations such as Hawai'i (Kittinger et al. 2011) and the Adriatic Sea (Fortibuoni et al. 2010). By comparing the timing, direction, and magnitude of ecological change with cultural events in each location, these studies disentangled the relative contributions of different human stressors (e.g., fishing vs. habitat degradation vs. climate change) and often showed a progression of impacts starting with historical small-scale harvesting (a pattern documented more broadly by Jackson et al. [2001], Pandolfi et al. [2003], and Lotze et al. [2006]). Additional insight could be gained from pairing these studies with modern surveys to sharpen their temporal resolution given the fast pace of elasmobranch population declines and conservation action.

Deep-time geohistorical records are well suited to addressing elasmobranchs' responses to climate change. Over millions of years, the fossil record offers valuable parallels for future projected environmental conditions that have not yet been experienced in human history (Fig. 3). Earth is heading toward a climate similar to the Paleocene–Eocene thermal maximum (56 Ma) (Burke et al. 2018; Fig. 1A) and an extinction crisis not seen since the K/Pg mass extinction (66 Ma) (Barnosky et al. 2011; Ceballos et al. 2015). Although these protracted time frames might appear juxtaposed with conservation's forward-facing gaze (Dietl et al. 2019), they foreshadow how species might respond to future climate change based on how they fared during past episodes of rapid global warming. Natural experiments in the fossil record could anticipate elasmobranch range shifts in response to climate perturbations or describe refugia to guide adaptive spatial

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management (see Topic 4). For example, Villafaña and Rivadeneira (2018) tested how ecological and life-history traits modulated elasmobranch distributions following environmental change during the Neogene. The fossil record could also reveal the drivers of elasmobranch diversity dynamics. For example, Condamine et al. (2019) found that Lamniformes experienced a significant decline in diversity over the last 20 Myr due to climatic cooling and competition with other clades. Although the climatic stressors faced by elasmobranchs today differ (i.e., a warming, acidified, and deoxygenating ocean), this study illustrates how diversity covaries with abiotic and biotic factors through deep time. These examples demonstrate how deep-time analogues can be leveraged to anticipate vulnerability in extant species and plan for resilience under future climatic conditions.

Topic 4: What Are the Global Priorities for Elasmobranch Conservation?

Current efforts to halt extinction typically use prioritization tools that identify species and areas that are in most need of protection (Arponen 2012; Butchart et al. 2012). These priorities exist because extinctions do not occur randomly on the tree of life (Wang and Bush 2008) and because resources to protect biodiversity are limited (Murdoch et al. 2007). The International Union for Conservation of Nature (IUCN) Red List of Threatened Species provides a robust framework to categorize species according to their extinction risk and is widely used for conservation prioritization (Mace and Lande 1991; Rodrigues et al. 2006; Hoffmann et al. 2008; Mace et al. 2008; Betts et al. 2020). IUCN statuses have also been combined with various dimensions of biodiversity (e.g., phylogenetic and functional) in prioritization metrics to identify endangered species for which extinction will result in irreplaceable losses of evolutionary history or ecological functions. These metrics include EDGE (Evolutionarily Distinct and Globally Endangered; Isaac et al. 2007) and FUSE (Functionally Unique, Specialized, and Endangered; Pimiento et al. 2020) (for a complete list, see Pimiento and Antonelli 2022). The EDGE metric prioritizes evolutionary history by combining species' IUCN statuses with a phylogeny-based calculation of their evolutionary distinctiveness (Isaac et al. 2007), whereas the FUSE metric prioritizes species' contributions to functional diversity by combining their IUCN statuses with a trait-based calculation of their functional uniqueness and specialization (Pimiento et al. 2020). These data-driven prioritizations can then be fed into policy and management decisions such as the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES).

According to the IUCN, 37% of elasmobranch species are at risk of extinction (Fig. 5A), making them the most threatened marine vertebrate group today (Dulvy et al. 2014, 2021). Threatened elasmobranch species are both evolutionarily (Stein et al. 2018) and functionally (Pimiento et al. 2023) distinct. However, the EDGE and FUSE metrics highlight different elasmobranch species, demonstrating the value of considering multiple metrics (Pimiento et al. 2023). Additionally, prioritization tools have been used to identify hotspots of threatened elasmobranch biodiversity (Fig. 5B) as well as to assess the spatial congruence between different dimensions of their biodiversity (Lucifora et al. 2011; Stein et al. 2018; Derrick et al. 2020; Pimiento et al. 2023). Although some hotspots overlap, functional diversity appears to have a distinct spatial fingerprint (Pimiento et al. 2023). Importantly, many biodiversity hotspots coincide with industrial fishing, and most fall outside

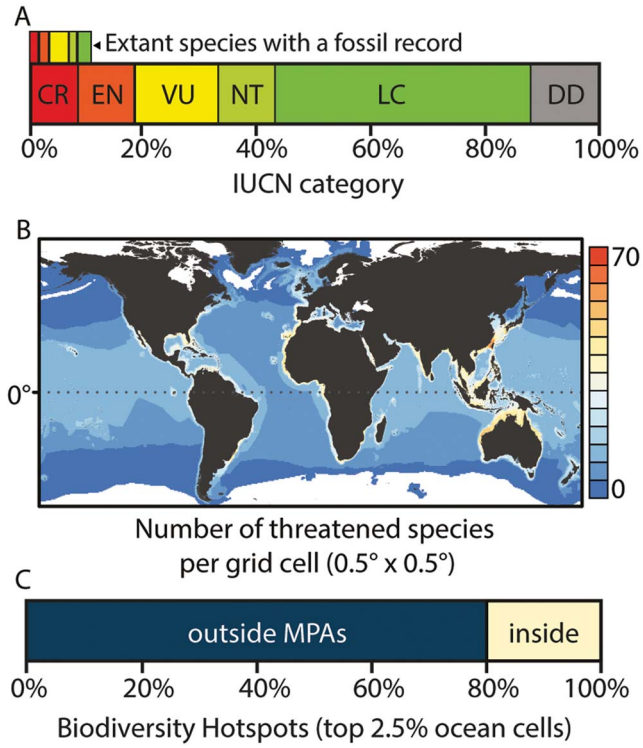


Figure 5. Elasmobranch threats and conservation status. **A,** Percentage of elasmobranch species across the International Union for Conservation of Nature (IUCN) statuses: CR, Critically Endangered; EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern; DD, and Data Deficient. Data downloaded from the IUCN Red List of Threatened Species (http://www.iucnredlist.org, last accessed November 2023). Adapted from Dulvy et al. (2021). The top panel shows the same information for just extant species with a fossil record (Paillard et al. 2021). **B,** Global distribution of threatened species (represented by number of species categorized by the IUCN as CR, EN, VU) per grid cell. Adapted from Pimiento et al. (2023). **C,** Mean percentage of hotspot cells (top 2.5%) defined using various dimensions of biodiversity (i.e., species richness, functional richness, phylogenetic diversity, threatened species (see B), EDGE (Evolutionarily Distinct and Globally Endangered), FUSE (Functionally Unique, Specialized, and Endangered), evolutionary distinctiveness, functional specialization, and functional uniqueness) falling inside or outside existing marine protected areas (MPAs). Adapted from Pimiento et al. (2023).

the existing marine protected area network (Davidson and Dulvy 2017; Pimiento et al. 2023; Fig. 5C). Together, these studies underscore the urgency to protect elasmobranchs (Fig. 2D) but suggest that no single metric epitomizes the global priorities for elasmobranch conservation.

Elasmobranch conservation has benefited from new information about their biology and threats (e.g., Dulvy et al. 2014, 2021; Osgood and Baum 2015; Mull et al. 2022), resulting in additional species protections (Fordham et al. 2022) and priority area designations (Hyde et al. 2022). However, many species remain poorly understood, leaving taxonomic and geographic gaps in our knowledge of their extinction risk (Dulvy et al. 2017; Guy et al. 2021) and the biological outcomes of management efforts (Ferraro and Pressey 2015; Daly et al. 2018; Pacoureau et al. 2023; Table 1). Furthermore, elasmobranch conservation priorities primarily react to ongoing losses rather than anticipate future vulnerabilities. A longer-term perspective is needed to ground current conservation priorities in an understanding of past extinctions. Here, we discuss how near- and deep-time geohistorical records can optimize elasmobranch conservation priorities by: (1) contextualizing IUCN assessments, (2) identifying correlates

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of extinction risk, (3) evaluating prioritization metrics, and (4) mapping spatial distributions of threatened elasmobranch biodiversity (Fig. 3).

Contextualizing IUCN Assessments

Near-time fossil and historical records spanning the last century can contextualize IUCN assessments (McClenachan et al. 2012; Leonetti et al. 2020; Kowalewski et al. 2023). These data are especially informative for elasmobranchs, because the IUCN measures population changes over a period of 10 years or three generations (up to 100 years; Mace and Lande 1991), which for long-lived species usually exceeds modern survey data. For example, Ferretti et al. (2008) used historical records to reconstruct population trends of five shark species in the Mediterranean Sea since the early nineteenth century. They found that these species had declined >96–99.9% from their historical abundances, suggesting an ~2.5-fold larger decline than estimates based solely on available fisheries data spanning the last two decades (Cavanagh and Gibson 2007; Ferretti et al. 2008). Equally large declines went undetected in oceanic whitetip sharks (*Carcharhinus longimanus*) between the 1950s and 1990s in the Gulf of Mexico (Baum and Myers 2004; Fig. 4A). By extending the time window over which extinction risk was evaluated, historical records contributed to the oceanic whitetip shark's classification as Critically Endangered on the IUCN Red List (Rigby et al. 2019) and a bycatch ban (PEW Environment Group 2012). Finally, historical records are now considered in IUCN Green List assessments, which measure species' recoveries against historical baselines (Akçakaya et al. 2018; Grace et al. 2019; see Topic 1). These examples show that by documenting changes in species' abundances or geographic ranges over multiple decades, historical records in particular can unshift the baselines used in IUCN assessments and flag species that might be poorly monitored or not thought to be at risk (Fig. 3).

Identifying Correlates of Extinction Risk

Over deeper timescales, the fossil record can reveal ecological and life-history traits that make species prone to extinction. In turn, these correlates of extinction risk can be used to test the accuracy of IUCN assessments (Raja et al. 2021; Fig. 1B), predict the extinction risk of Data Deficient species (Dulvy et al. 2014; Walls and Dulvy 2020), and identify intrinsically vulnerable species before they start to decline (McKinney 1997; Pimiento and Antonelli 2022). Although correlations between traits and extinction risk can be inferred from extant taxa (e.g., Ripple et al. 2017; Dulvy et al. 2021), this information is often restricted to short ecological timescales and is not available for all regions or species. The fossil record offers a wealth of complementary insight into extinction selectivity patterns over long evolutionary timescales. For example, intrinsic traits such as geographic range, body size, diet, and thermoregulation have been associated with extinction risk across different clades and extinction events (Harnik et al. 2012; Finnegan et al. 2015; Payne et al. 2016; Pimiento et al. 2017; Reddin et al. 2021). In some clades, intrinsic traits predict extinctions better than abiotic factors alone (Boyer 2010). Consequently, the fossil record could facilitate more proactive conservation by applying lessons from past extinctions to better understand which species might be most vulnerable—or resilient—in the current biodiversity crisis (Pimiento and Antonelli 2022).

Elasmobranchs have suffered at least two major extinction events over the last 150 Myr. Tracing the traits that influence extinction selectivity across these events could help contextualize their current vulnerabilities and corroborate extinction risk correlates inferred from extant species (i.e., body size and depth; Dulvy et al. 2014, 2021). During the K/Pg mass extinction, at least 62% of elasmobranch species went extinct, with diet, habitat, and geographic range determining extinction selectivity (Kriwet and Benton 2004; Guinot and Condamine 2023). Another important extinction event occurred during the early Miocene Epoch, when oceanic elasmobranchs declined in abundance by >90% and morphological diversity by >70% (Sibert and Rubin 2021; see Topic 1). During this event, habitat again predicted extinction, with elasmobranchs restricted to deep-sea habitats being most affected. Although ecological specialization appears to be a common correlate of extinction risk across these two events, it is difficult to compare them, because they were studied using different analytical approaches and taxonomic resolutions.

Analytical advances have improved efforts to model extinction rates and their correlates more consistently. For example, macroevolutionary dynamics can be estimated using R packages like DivDyn (Kocsis et al. 2019; used by Villafaña et al. 2023), capture–mark–recapture approaches (Liow and Nichols 2010; used by Sibert et al. 2018), and Bayesian process-based birth–death models (Silvestro et al. 2014; used by Guinot and Condamine 2023), some of which combine fossil occurrences with phylogenetic information (Heath et al. 2014; used by Brée et al. 2022). Machine learning algorithms are increasingly used to model relationships between extinction risk and traits, allowing the vulnerability of extant taxa to be predicted based on their traits (e.g., Finnegan et al. 2015; Raja et al. 2021). New methods have also facilitated measurements of traits like trophic position, which are hypothesized to predict extinction risk but are challenging to infer from fossils (see Topic 2). With these tools in hand, it has become more possible to analyze deep-time fossil trait and occurrence data to identify which intrinsic traits are shared across extinction events with different magnitudes and causes (Pimiento and Antonelli 2022) or where discrepancies emerge (i.e., mismatches between trait-based predictions of extinction risk and IUCN statuses; Raja et al. 2021).

Evaluating Prioritization Metrics

Geohistorical records can also be incorporated into species-based conservation prioritization metrics like EDGE and FUSE to test their performance. For example, Cavin and Kemp (2011) showed that when fossils are included in the lungfish (Sarcopterygii: Dipnoi) phylogeny, the rankings of top EDGE species change. The fossil record has also been used to evaluate the evolutionary implications of conservation actions guided by the EDGE metric—namely whether it prioritizes species representing the "seeds" of future radiations or whether it preserves the tail ends of depauperate clades now "doomed" to extinction. Bennett et al. (2019) found that, when applied to mammals, the EDGE metric does not prioritize seeds or doomed clades but rather slow-evolving "living fossils" that disproportionately contribute to their clade's evolutionary history. This approach could be applied to elasmobranchs to simulate how phylogenetic diversity and EDGE prioritizations might change after hypothetically losing or saving threatened species with unique evolutionary histories (Pimiento and Antonelli 2022). Additionally, the fossil record could test the extent to which implementing the FUSE metric would preserve

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ecosystem functioning over time. Such tests could show whether certain components of elasmobranchs' ecological distinctiveness (uniqueness vs. specialization) are more vulnerable to extinction or important for maintaining functional diversity (Pimiento and Antonelli 2022). At least 10% of extant elasmobranch species (~100 species) have a fossil record (Paillard et al. 2021; Fig. 5A), making them a good testing ground for evaluating these prioritization metrics and predicting the evolutionary and functional legacies if they are used to guide conservation decisions (Fig. 3).

Mapping Spatial Distributions of Threatened Elasmobranch Diversity

Fossil occurrences archive spatially explicit relationships between biodiversity and environmental conditions through geological time, which could help guide area-based conservation. For example, Carrillo-Briceño et al. (2018) used the Neogene elasmobranch fossil record to catalog geographic patterns of paleodiversity in Tropical America, a study that has since contextualized regional conservation priorities (Ehemann et al. 2019; Becerril-García et al. 2022). Similarly, macroevolutionary analyses could demonstrate whether diversity hotspots are conserved and might represent resilient areas worth protecting (Pimiento and Antonelli 2022). Another example comes from Finnegan et al. (2015), in which the geographic distribution of extinction risk predicted from the Neogene–Pleistocene fossil record was overlaid with maps of human impacts and climate velocity to locate present-day hotspots of extinction vulnerability. Although fossil-informed maps of extinction vulnerability have yet to be incorporated into decision-making processes (Kiessling et al. 2019), there is a precedent for similar maps of current anthropogenic impacts to prioritize areas for protection (e.g., Queiroz et al. 2019).

Fossil and historical occurrences are also increasingly used in conjunction with modern occurrences in species distribution models. These models have been implemented to hindcast ecological niches (Nogués-Bravo 2009; Myers et al. 2015; Monsarrat et al. 2019; Skroblin et al. 2021), evaluate area-based prioritization strategies (Williams et al. 2013), and identify potential refugia or range shifts under future projected climate scenarios for a variety of taxa (Maguire et al. 2015; Lima-Ribeiro et al. 2017; Jones et al. 2019; see Topic 3). There is great potential to apply these methods to elasmobranch occurrence data (e.g., Klippel et al. 2016; Birkmanis et al. 2020; Sabadin et al. 2020; Diaz-Carballido et al. 2022), especially for large migratory species, to describe their spatial distributions and protect areas that harbor threatened diversity (Fig. 3). At the same time, because elasmobranch distributions do not fall neatly within the geopolitical boundaries in which conservation policies are implemented (Dulvy et al. 2017; Fordham et al. 2022), incorporating fossils into area-based conservation begins with investing in collaborative international science that is coproduced by researchers and decision makers.

Limitations

Conservation paleobiology can contribute valuable temporal perspective to current elasmobranch conservation priorities (Fig. 3, Table 1), although certain attributes of geohistorical records limit their application (Kidwell 2013, 2015; Kidwell and Tomašových 2013; Kowalewski et al. 2023). The fossil record is inherently incomplete due to a combination of geological, sampling, and taphonomic biases that influence what is preserved, when, and where (Raup 1972, 1976; Sepkoski et al. 1981; Benson et al. 2021). Furthermore, although elasmobranch teeth are diagnostic, other components of their fossil record (e.g., vertebrae) cannot be identified to species or even genera, limiting taxonomic insight (Reif 1985; Cappetta 2012). Paleobiological work on elasmobranchs also appears to be biased toward sharks, leaving rays, a highly threatened clade (Dulvy et al. 2021), less studied. Some limitations can be addressed by investing in taxonomic expertise, specimen and data digitization, and additional field or collections work, which could expand available datasets and improve our understanding of elasmobranch systematics and traits. Additionally, future work could assess whether sharks could serve as taxonomic surrogates for rays. At the same time, striking differences in the pace and scale of human impacts on elasmobranch populations today relative to the time-averaged eco-evolutionary dynamics captured by the fossil record remain an impasse. This often manifests as misalignment between the spatiotemporal scale of a conservation problem and available geohistorical records (Dietl et al. 2019; Kiessling et al. 2019). Although no silver bullet, pairing one record's limitations with another's strengths could help improve data coverage and resolution (Buma et al. 2019).

Other elasmobranch conservation needs fall outside the scope of conservation paleobiology. For example, Jorgensen et al. (2022) identified several priorities that are not answerable using information preserved in geohistorical records, such as those involving tourism, vessel tracking, trade laws, and bycatch mitigation policies (Table 1). Effective governance and community buy-in are critical for achieving conservation successes but cannot be tackled with fossils alone. Other priorities identified by the authors would require creative reframing for geohistorical records to be relevant (e.g., tagging technologies, which track species' movement), highlighting the value of jointly developing these priority questions. To increase the conservation relevance of paleobiological data, conservation paleobiologists could collaborate across disciplinary boundaries, such that geohistorical records are matched with conservation problems that they are well suited to address in complement with approaches from other fields. Doing so could help ensure that paleobiological research, when applicable, considers the multidimensional nature of conservation problems and provides actionable results targeted to specific conservation needs that are voiced by practitioners or other decision makers (Savarese 2018; Dietl et al. 2023). This collaborative approach could ultimately help cement geohistorical records' place in conservation problem-solving toolboxes.

Coda

Throughout this article, we have highlighted research directions in conservation paleobiology that have potential to address emergent priorities in elasmobranch science and conservation. These priorities were broadly assembled from expert opinions (Jorgensen et al. 2022), whereas on-the-ground conservation problems may be more context specific and evolve as needs change. Nonetheless, this exercise could serve as a model for understanding which geohistorical records are most useful for conservation practice. Evaluating alignment between conservation needs and geohistorical records could lead to more tangible conservation paleobiology research goals that are designed with implementation in mind, for elasmobranchs as well as other clades. We find that these areas of overlap are often best addressed with information spanning many timescales and branches of paleontology and biology, creating opportunities for interdisciplinary

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collaboration and synthesis. For conservation paleobiologists seeking to increase the practical applications of their work, we encourage finding similar horizon-scanning lists of priority questions (or similar venues where such priorities are exchanged) as a potential starting point for initiating conversations with practitioners working in their study systems. These two-way interactions could define shared questions that conservation paleobiology could help answer and, in doing so, coproduce more actionable science.

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