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# Opportunities to enhance conservation success for sharks



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Sharks, rays, and chimaeras are among the most threatened vertebrate lineages. Despite considerable conservation efforts, the extinction risk of sharks continues to rise. We present a quantitative analysis of the shark conservation literature, exploring trends and interconnectivities in key topics using a machine learning approach. We show that shark conservation research is a well interconnected, coherently structured, and rapidly expanding field centred around a conservation nexus linking human-wildlife interactions to species use and management. Shark conservation research is increasingly interdisciplinary and is well prioritised toward key threats that drive the decline of shark populations, both of which are key to effective management. However, we also identify opportunities to further strengthen research and management. These include improved integration of key research topics, enhancing the understanding of combined threats, and greater consideration for the role of sub-lethal impacts. Lastly, we stress that meaningful integration of research topics, rather than simple contextualisation, is essential to building the comprehensive and nuanced understanding necessary to inform effective conservation actions. By leveraging the strengths of the field and addressing its remaining weaknesses, there is hope for a future where sharks thrive and contribute to healthy, resilient marine ecosystems.

The late Professor Dame Georgina Mace put it simply, we must bend the biodiversity-loss curve by 2030 or face an Anthropocene mass extinction. Sharks, rays, and chimaeras (class: Chondrichthyes, hereon "sharks") are among the most threatened taxa. Over one-third of all shark species are threatened with extinction, according to the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species[1]. All threatened species are recognised as imperilled by overfishing, solely, or in combination with habitat degradation, and climate change[1]. One species (the Java stingaree *Urolophus javanicus*) is considered Extinct[2], two are considered Possibly Extinct[1], and other so-called 'lost sharks' have not been observed for decades. The direct drivers of shark decline and emerging threats for the future are well established and widely accepted, having been analysed, reviewed, and discussed at length[1,3,4]. As the status of sharks and the drivers of their decline have come increasingly into focus, governments and intergovernmental organisations have created, implemented, revised, and re-implemented conservation plans and actions. Nonetheless, the overall global exploitation mortality of these species continues to rise[5].

Self-reflection is a critical step in guiding the future of any research field. Several papers have done just that, reviewing historic and ongoing research in shark science and charting a path forward toward improved conservation outcomes[3,4,6–8]. These papers reveal weaknesses in the research landscape, such as heavy biases toward charismatic species and large geographic disparities in research efforts, often poorly aligned with the taxonomy and distribution of the most threatened species[7,8]. While these

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reviews have provided valuable insights into the field, they are often selective in scope; being shaped by the geographic, taxonomic, methodological, and discipline specialities of the authorship team[3,4,6,7]; and may impose a priori the authors' beliefs on the themes and topics which comprise the research field[7,8]. This can lead to a natural focus on research topics or themes which correspond to the authors' areas of experience and interest. There has been little in the way of objective content analyses, but those available suggest a limited focus on conservation[8]. Additionally, there is a common tendency to avoid explicitly prioritising research and exploring how different research topics interconnect and interact.

Conservationists widely acknowledge that interdisciplinary work is essential to achieving conservation goals for species[9,10]. Exploring and understanding the linkages, or lack thereof, between different aspects of shark conservation research is critical in identifying opportunities to strengthen this research field. Addressing these opportunities could contribute greatly to halting or even reversing the biodiversity-loss curve for this taxa. Within this context, we present a quantitative analysis of the shark conservation literature using a machine learning approach that seeks to minimise the influence of our a priori beliefs about the current body of work. Through this research, we aim to:

(1) Identify the research topics composing the shark conservation literature and how they relate to priority threats for these species;
(2) Assess interdisciplinarity and examine the interconnectivity of research topics within the shark conservation field;
(3) Explore strengths and weaknesses inherent in current patterns of interconnectivity between different research topics; and
(4) Highlight research opportunities that could help bend the biodiversity-loss curve for sharks.

By providing a comprehensive and interconnected overview of shark conservation research, we hope not only to guide future research directions but also to inform effective conservation strategies and policy decisions for sharks, ultimately contributing to more sustainable management practices and enhancing global biodiversity conservation efforts.

## Results and discussion

### High topic diversity and a critical nexus within the interconnected field of shark conservation

We quantitatively analysed the abstracts of 4401 peer-reviewed scientific papers and identified 29 topics in the shark conservation literature (Fig. 1a, Table S1). Some topics, specifically *Geography & Species*, *Habitats*, *Monitoring & Methodology*, and *Research Type* were deemed to be purely contextual topics and were therefore excluded from further analyses. The number of topics identified here is generally much greater than seen in previous studies that have quantitatively examined trends and priorities within shark research[4,7,8]. This disparity demonstrates the complexity that may be lost when topics are selected a priori by the authors, rather than being identified directly from the data. The network of identified topics shows the field of shark conservation to be well interconnected with coherent structuring (Fig. 1a).

Four primary clusters of topics were quantitatively identified, each loosely corresponding to a different aspect of shark research:

(1) Life history – Growth, Reproduction, Sexual Dimorphism;
(2) Ecology and biology – Early Life, Ecosystem Role, Ecotoxicology, Movement Ecology, Spatial Distribution & Environmental Change, Spatial Management, Stress & Physiology, Trophic Ecology;
(3) Conservation science – Extinction Risk & Protections, Fisheries & Bycatch, Genetics, Markets & Fisheries Management, Population Structure, Taxonomy & Phylogeny; and
(4) Human-wildlife interaction - Behaviour & Deterrence, Public Perceptions, Shark Attack & Stingray Envenomation, Tourism.

A fifth evolutionary cluster was also identified but was largely not pertinent to shark conservation, and so was not considered further – *Anatomy & Central Nervous System*, *Evolution*, *Immunology*, and *Proteomics*. The cluster arises largely from the use of sharks as an evolutionary model system through which to understand key innovations in vertebrate evolution such as the development of the jaw, the appearance of the segmented organised brain, and the evolution of live-bearing young and maternal investment[11,12]. Although considered an out-group for the purposes of our conservation-focused analysis, the evolutionary innovations and novelty of sharks has been used as a driver of conservation actions, such as through the EDGE (Evolutionary Distinct and Globally Endangered) paradigm[13]. The evolutionary cluster is connected to the shark conservation literature through the topics of *Stress & Physiology*, *Taxonomy & Phylogeny*, and *Genetics*. Additionally, the evolutionary cluster forms a bridge between shark conservation and broader biological inquiries, enriching our comprehension of shark biology and conservation while also contributing to the wider field of evolutionary biology, offering perspectives that are crucial for understanding the past, present, and future of vertebrates on Earth.

Central to the network are three topics that form the key nexus of shark conservation as a field of study: *Public Perception*, *Markets & Fisheries Management*, and *Extinction Risk & Protections* (Fig. 1a). This nexus bridges the gap between human-wildlife interactions and conservation, encapsulating what could be considered the most critical relationships in conservation science. This connection highlights how human interactions with nature shape the utilisation and management of natural resources, ultimately influencing their degradation and recovery[14,15]. The nexus can also be thought of in economic terms. The market for sharks sits at the centre, being controlled through the balance of supply (*Management* and *Extinction Risk & Protections*) and demand (*Public Perceptions, Shark Attack & Stingray Envenomation*), where the goal of conservation is to adjust supply and demand in such a way as to improve conservation outcomes. Regardless, it is around this nexus that much of the shark conservation literature appears to revolve and to which most other topics can be traced.

The first set of key connections is apparent in two fully interconnected groups of topics associated with *Public Perceptions* and *Extinction Risk & Protections*, respectively. *Public Perceptions* of sharks, as a topic, is closely tied to fear in many areas of the world, particularly in the "west" (i.e. USA, Europe, South Africa and Australia), which dominates the research landscape[8]. This fear of sharks largely stems from deeply rooted cultural attitudes and is exacerbated in popular media[16,17]. However, negative perceptions are slowly shifting through awareness campaigns and by positive exposures to sharks via ecotourism and recreational activities[18,19]. This dynamic is reflected in the network by complete interconnectivity among *Shark Attack & Stingray Envenomation*, *Tourism*, *Behaviour & Deterrence*, and *Public Perceptions*, which also serve to link the ecology and human-wildlife interaction clusters (Fig. 1a). *Public Perceptions* also influence pro-conservation attitudes and norms[3,19] and have the potential to influence behaviour regarding consumptive use of sharks.

Similarly, full interconnectivity of *Extinction Risk & Protections*, *Genetics*, *Taxonomy & Phylogeny*, and *Population Structure* is observed within the network. An example of this connectivity is the control of international trade of shark products through the Convention on International Trade in Species (CITES). To-date more than 150 shark and ray species are listed on the appendices of CITES. CITES listings are a trade-focused measure which do not directly reduce the demand or supply of shark products but do attempt to ensure that international trade does not threaten the survival of species in the wild. One of the major challenges in enforcing trade restrictions and management efforts has been reliable species identification of shark products. Indeed, cases exist where improper species identification has led to entire fisheries statistics and subsequent trade records being rendered useless[20]. Identification tasks rely on the development of dependable taxonomic keys, and genetic barcoding has become increasingly valuable for identifying cryptic species, fins, and body parts that have otherwise been difficult to monitor in global trade and markets[21,22]. Similarly, with the advent of affordable and high-resolution genetic markers in the early 2000s, molecular tools have been increasingly used to reveal population structure and connectivity, as well as to address

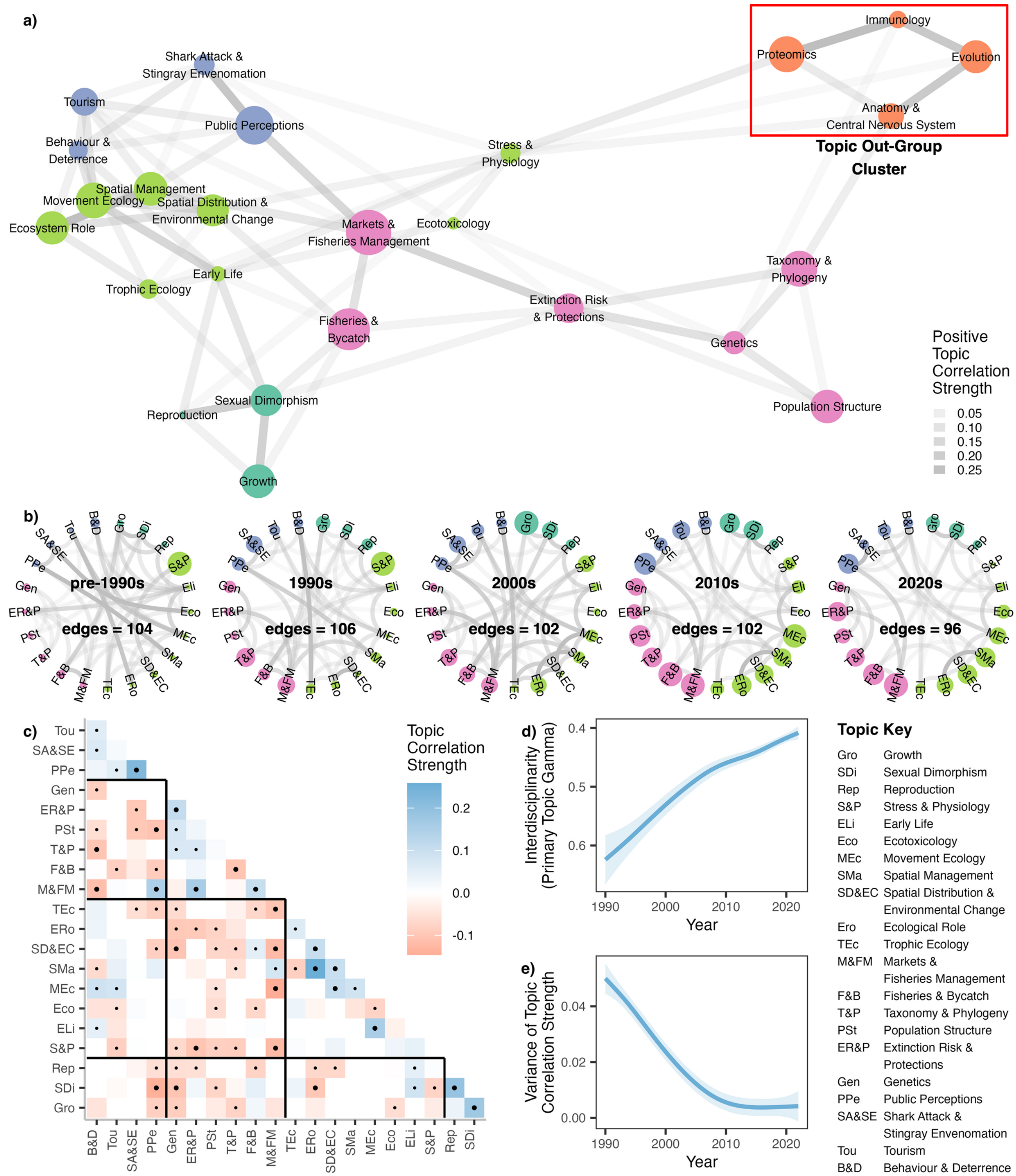


**Fig. 1 | The structure and evolution of shark conservation science through time.** **a** Structural network of shark conservation and its constituent topics based on the strength of positive correlations in the scientific literature. **b** Change in the structural network of shark conservation topics over time. **c** Overall topic correlation, topic clusters are delineated by black lines, small points indicate correlations greater than 0.05 or less than −0.05, large points indicate correlations greater than 0.1 or less than −0.1. **d** Interdisciplinarity (± SE), proxied by change in mean primary topic gamma value over time (note inverted y-axis). **e** Variance of topic correlation strengths (± SE) within the network over time. Node diameter indicates relative topic frequency, node colour indicates topic clusters.

evolutionary, taxonomic, and phylogenetic issues in sharks[23–25]. Both the *Public Perceptions* and *Extinction Risk & Protections* groups of topics are isolated from other topics in the conservation nexus, but are not disconnected from the wider network, where we also find groups of topics that share links between multiple components of the topic nexus.

The second set of connections can be seen in those groups of topics that associate with more than one part of the topic nexus. *Fisheries & Bycatch* forms a secondary link between *Markets & Fisheries Management* and *Extinction Risk & Protections*, with fisheries being the largest source of shark mortality and primary driver of shark extinction risk[1,5]. *Fisheries & Bycatch* is subsequently linked closely with the key life-history topics, including *Growth*, *Reproduction*, *Early Life*, and *Sexual Dimorphism*, which are the underpinnings of fisheries stock assessments and management[26,27]. *Fisheries & Bycatch* also links to *Spatial Distribution & Environmental Change*, which is key in defining the spatial risk to sharks posed by fisheries[28–30] and mortality due to ship strikes[31], as well as the future of fisheries and sharks in a changing climate[1]. Similarly, *Spatial Management* forms a secondary link between *Markets & Fisheries Management* and *Public Perceptions* and likely reflects the role that public attitudes and engagement play in both the establishment and ongoing effectiveness of management strategies for sharks[32,33]. Like *Fisheries & Bycatch*, *Spatial Management* also acts as a link between other topics and the conservation nexus, specifically ecological topics like *Movement Ecology*, *Spatial Distribution & Environmental Change*, *Ecosystem Role*, and *Trophic Ecology*, topics that are critical to justifying and designing marine protected areas and other spatial protections[34].

The remaining topics, *Ecotoxicology* and *Stress & Physiology*, appear to be more peripheral to the conservation nexus, with *Ecotoxicology* only sharing a very weak link to *Extinction Risk & Protections* and *Stress & Physiology* sharing no link at all (Fig. 1). This indicates that both topics are not well integrated into the conservation literature, yet their inclusion is crucial for a comprehensive understanding of conservation science and future threats[35–37]. Physiological research in sharks generally lags behind their teleost counterparts. Firstly, these types of research are typically carried out on only a handful of well-studied, small species that are amenable to captivity, which limits knowledge to certain taxa (e.g., Squalidae, Rajidae, Hemiscylliidae, Scyliorhinidae). Additionally, sharks have unique respiratory, osmoregulatory, and energy mobilisation pathways that are still being untangled, and these limit the current understanding of ecotoxicological and stressor impacts[38,39]. Whether effects seen in well studied species can be directly extrapolated to other taxonomic groups is still uncertain. *Ecotoxicology* plays a pivotal role in identifying the impacts of pollutants on marine life, offering insights into lethal and sub-lethal stressors, including reproductive success, which may impact species survival[40]. Similarly, *Stress & Physiology* provides critical insights into how environmental stressors, both natural and anthropogenic, affect the health and viability of individuals and potentially of populations[41].

### Negative associations expose existing weaknesses in shark conservation research

Despite the encouragingly strong interconnectivity generally found within the shark conservation literature, the analysis also reveals clear gaps that highlight potential opportunities and under-explored areas of study. Negative correlations observed between topics often simply reflect fundamental incompatibilities (Fig. 1c). For instance, it is unsurprising that *Ecotoxicology* and *Shark Tourism* rarely intersect. More concerning are those cases where clearly related topics, sometimes even those within the same topic cluster, appear to be disconnected. Here we discuss some of the prominent examples of negative correlations revealing what we consider to be key weaknesses and research gaps.

*Spatial Management* was negatively correlated with *Trophic Ecology*, despite being in the same topic cluster, and *Behaviour & Deterrence*. Spatial management approaches are commonly cited as potentially key conservation tools in the protection of sharks, particularly for species with relatively small movement ranges and/or where critical habitats such as foraging grounds can be identified for protection[34,42]. The effect of protected areas on the behaviour and trophic interactions of sharks within them will likely be key to the success of conservation measures and the effects sharks might have within protected areas. The decoupling of these topics could, therefore, weaken prospective designs and assessments of success of spatial management measures for sharks. Similarly, both *Stress & Physiology* and *Ecotoxicology* were negatively correlated with *Growth*, and *Stress & Physiology* was also negatively correlated with *Sexual Dimorphism*. This decoupling was found despite the known potential for toxins and other stressors to negatively affect growth and developmental patterns, which may result in impacts on individual fitness, reproduction, population dynamics, and species' recovery potential[35,36,43].

Arguably the most prominent example of decoupling between topics was observed for *Movement Ecology* and *Population Structure*. Our analysis suggests that papers addressing these two topics were least commonly contextualised by or within other topics (Fig. 2c). This apparent weakness is exacerbated by negative correlations, both between these two topics and with other topics that would be expected to be closely related. For example, demographics of species sub-populations are often related to ontogenetic or sexual segregation of habitat preferences[44], genetic connectivity is often a reflection of a species' dispersal behaviour[45], and spatial management is less effective for species that can migrate beyond the borders of a protected area[46]. Despite these clear ecological connections, *Population Structure*, *Genetics*, and *Markets and Management* were all negatively correlated with *Movement Ecology*. Similarly, *Population Structure* was negatively correlated with *Spatial Distribution & Climate Change* and *Reproduction*, regardless of the demographic differences in spatial distribution of many species[44,47] and the clear link between sexual demographics and reproductive ecology.

It is important to be clear that negative correlations between topics do not mean that they are never discussed together within the shark conservation literature. Rather, it indicates where topics have rarely been brought together specifically for targeted analyses. A more comprehensive overview of potential weaknesses can be found in Table 1. Addressing these key weaknesses would represent progress toward a more comprehensive understanding of sharks as it relates to their conservation, presenting opportunities for researchers to specifically target key gaps and design their research accordingly.

### An increasingly interdisciplinary science

There is broad consensus that interdisciplinary conservation research is critical in achieving conservation success across marine and terrestrial environments because human dimensions are critical to the design and implementation of effective management[9,10]. This is no different for shark conservation. While the call for interdisciplinarity is often explicitly associated with bridging the gaps between the biological, social, and economic sciences, the sentiment also applies to the integration of topics within each of these disciplines. The number of positive correlations (edges) remained relatively stable over time (Fig. 1b) but variance in the strength of these correlations did not ($F = 93.0$, $p < 0.001$). Variance in topic correlation strength has declined (Fig. 1e) because of reductions in the extreme correlation strengths seen between some topic pairs in earlier works (Fig. 1b). At first glance, this decline in extreme correlation strengths might appear as a weakening of the network structure but, when paired with the simultaneous declines seen in *gamma* values for primary topics ($F = 46.2$, $p < 0.001$, Fig. 1d), it instead suggests that shark conservation research has become increasingly interdisciplinary (Fig. 1d). Further, there are several popular research topics closely associated with the boundary between the social and economic sciences and the biological sciences, including *Markets & Fisheries Management*, *Public Perceptions*, and *Tourism* (Fig. 1a, Fig. 2a). This trend of increasing interdisciplinarity in shark conservation must be considered a success for the field, reflecting an acknowledgement of its importance for effective conservation. Researchers should continue to strive for and promote interdisciplinary approaches going forward, helping to build meaningful linkages between research topics.

### Key threats receive highest scientific effort, but combined threats are rarely considered

Examination of topic frequency metrics shows some divergence, but several topics rank consistently high and low across measures (Fig. 2a, b). Specifically, the topics of *Markets & Fisheries Management*, *Fisheries & Bycatch*, *Movement Ecology*, *Taxonomy & Phylogeny*, and *Public Perceptions* are popular in the scientific literature. It is also notable that specific components of *Fisheries & Bycatch*, such as species stock assessments, exist largely outside of the peer-reviewed literature in scientific journals. Instead, such work

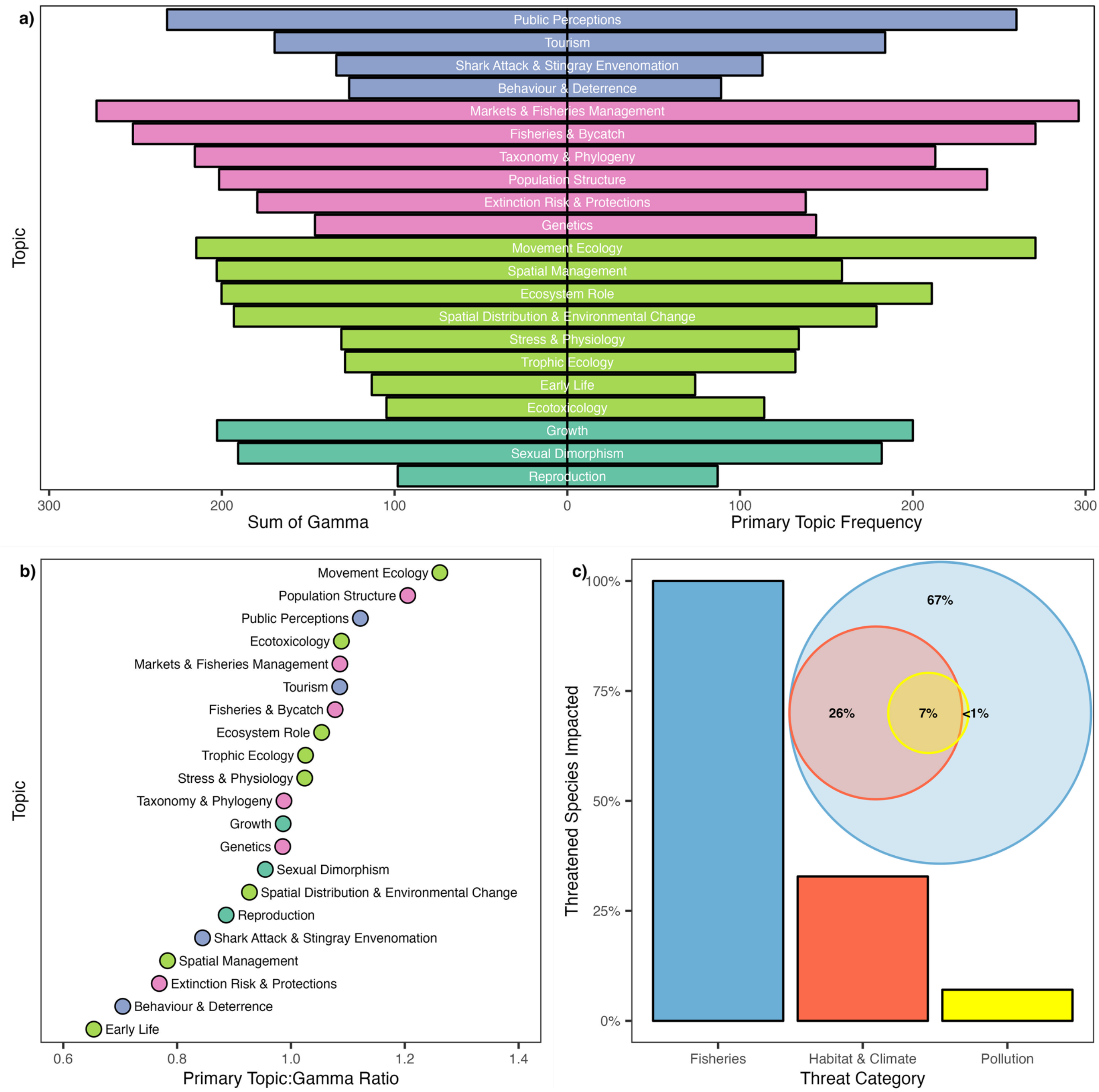


**Fig. 2 | The popularity of topics in the shark conservation literature and how this compares with conservation threats.** **a** Topic frequency based on gamma (the modelled proportional contribution of each topic to a given paper) and primary topic, grouped by topic cluster. **b** Primary topic to gamma ratio, higher values indicate topics more likely to be the primary topic within the papers in which they occur. **c** Percentage of threatened species by threat category and percentage of species impacted by overlapping threats according to the IUCN Red List.

is typically published as peer-reviewed reports or grey literature, and so the relative popularity of this research topic is likely much greater than represented here. Conversely, *Reproduction*, *Early Life*, and *Ecotoxicology* receive relatively little attention, as do *Behaviour & Deterrence* and *Shark Attack & Stingray Envenomation* when considering only the primary topic of papers. *Behaviour & Deterrence* and *Shark Attack & Stingray Envenomation* are both closely linked to and discussed within the context of *Public Perceptions*, which likely explains their lower occurrence as primary topics relative to their overall contribution to the literature.

The primary direct threats to sharks are from exploitation in fisheries, habitat loss and degradation, and climate change, with pollution contributing relatively little to the overall extinction risk of species[1]. The limited importance of pollution as a threat may result from of the relative underdevelopment of *Ecotoxicology* as a research field in shark conservation, its primary focus on individual organism survival, and as-yet limited evidence for population level effects. The current prioritisation of threats is reflected in the relative popularity of topics, with *Fisheries & Bycatch* and *Markets & Fisheries Management* being among the most popular topics, *Spatial Distribution & Environmental Change* a topic of moderate popularity, and *Ecotoxicology* being among the least common topics (Fig. 2a, b). Approximately 33% of threatened species are impacted by combinations of these threats (Fig. 2c); yet, we found only a weak positive correlation between the topics *Fisheries & Bycatch* and *Spatial Distribution & Environmental Change* and there was no correlation between *Ecotoxicology* and any other key threat related topic. Further, there was evidence for a negative correlation between *Markets & Fisheries Management* and *Spatial Distribution & Environmental Change* (Fig. 1c). Taken together this suggests that there is relatively little research that integrates the combined effects of multiple and

**Table 1 | Summary of key weaknesses of connectivity within the shark conservation literature**

| Topic | Key Weaknesses | Weakness justification |
|---|---|---|
| Behaviour & Deterrence | - Not applicable | No key weaknesses. |
| Early Life | - Extinction Risk & Protections | Juvenile survival and exposure to threats influences extinction risk and informs management[26,42]. |
| Ecosystem Role | - Extinction Risk & Protections | Ecosystem role often used to justify protections but data supporting this is limited to a few taxa and ecosystems[48]. |
| | - Taxonomy & Phylogeny | Evolutionary history predicts ecosystem role[62,63]. |
| Ecotoxicology | - Growth | Pollutants have the potential to impact growth and development[35,64]. |
| Extinction Risk & Protections | - Stress & Physiology | Sub-lethal stressors may exacerbate the impacts of direct threats on extinction risk[35,36]. |
| | - Ecosystem Role | Ecosystem role often used to justify protections but data supporting this is limited to a few taxa and ecosystems[48]. |
| | - Spatial Management | Protected areas are often suggested for sharks but may only be suitable for certain species or life stages[46,65]. |
| | - Early Life | Juvenile survival and exposure to threats influences extinction risk and informs management[26,42]. |
| Fisheries & Bycatch | - Public Perceptions | Improving attitudes and norms can drive changes in pro-conservation behaviour[66,67]. |
| | - Tourism | Livelihood-based interventions or conservation financing mechanisms linked to tourism can be used to offset fishing pressure[18,68]. |
| | - Reproduction | Reproduction is a key in understanding species' resilience and managing fisheries[27]. |
| Genetics | - Spatial Distribution & Environmental Change | eDNA can help identify species presence and monitor distribution patterns[69]. |
| | - Movement Ecology | Movement patterns play a key role in gene dispersal[45]. |
| Growth | - Ecotoxicology | Pollutants have the potential to impact growth and development[35,64]. |
| | - Markets & Fisheries Management | Growth is key in understanding species' resilience and subsequent management[27]. |
| | - Stress & Physiology | Stressors may inhibit growth and development[35,36]. |
| | - Spatial Distribution & Environmental Change | Environmental change may alter growth and development[35,36]. |
| Markets & Fisheries Management | - Spatial Distribution & Environmental Change | Management strategies should be spatially explicit and account for the possible impacts of ongoing environmental change[1,43]. |
| | - Growth | Growth is key in understanding species' resilience and subsequent management[27]. |
| | - Taxonomy & Phylogeny | Correct identification of species is critical to management, unresolved species complexes have been found even in well-studied and actively managed species[20,70]. |
| | - Movement Ecology | Understanding of movement ecology can inform fisheries management[71]. |
| Movement Ecology | - Markets & Fisheries Management | Understanding of movement ecology can inform fisheries management[71]. |
| | - Genetics | Movement patterns play a key role in gene dispersal[45]. |
| | - Population Structure | Movement patterns play a key role in population connectivity and structuring[72]. |
| Population Structure | - Spatial Distribution & Environmental Change | Population structuring and connectivity can help identify environmental barriers[73,74]. |
| | - Movement Ecology | Movement patterns play a key role in population connectivity and structuring[72]. |
| Public Perceptions | - Fisheries & Bycatch | Improving attitudes and norms can drive changes in pro-conservation behaviour[66,67]. |
| Reproduction | - Fisheries & Bycatch | Reproduction is a key in understanding species' resilience and managing fisheries[27]. |
| | - Spatial & Environmental Change | Environmental change may inhibit or alter reproduction[35,36]. |
| Sexual Dimorphism | - Stress & Physiology | There is evidence of sex-specific differences in shark stress responses[37]. |
| Shark Attack & Stingray Envenomation | - Not applicable | No key weaknesses. |
| Spatial Distribution & Environmental Change | - Markets & Fisheries Management | Management strategies should be spatially explicit and account for the possible impacts of ongoing environmental change[1,43]. |
| | - Genetics | eDNA can help identify species presence and monitor distribution patterns[69]. |
| | - Taxonomy & Phylogeny | Distribution and environmental barriers play key a role in genetic connectivity which underlies speciation processes[73,74]. |
| | - Population Structure | Population structuring and connectivity can help identify environmental barriers[73,74]. |
| | - Reproduction | Environmental change may inhibit or alter reproduction[35,36]. |
| | - Growth | Environmental change may alter growth and development[35,36]. |
| Spatial Management | - Extinction Risk & Protections | Protected areas are often suggested for sharks but may only be suitable for certain species or life stages[46,65]. |
| | - Trophic Ecology | Understanding foraging activities may be important in defining key spatial areas[34,42]. |
| Stress & Physiology | - Extinction Risk & Protections | Sub-lethal stressors may exacerbate the impacts of direct threats on extinction risk[35,36]. |

**Table 1 (continued) | Summary of key weaknesses of connectivity within the shark conservation literature**

| Topic | Key Weaknesses | Weakness justification |
|---|---|---|
| | - Sexual Dimorphism | There is evidence of sex-specific differences in shark stress responses[37]. |
| | - Growth | Stressors may inhibit growth and development[35,36]. |
| Taxonomy & Phylogeny | - Spatial Distribution & Environmental Change | Distribution and environmental barriers play key a role in genetic connectivity which underlies speciation processes[73,74]. |
| | - Trophic Ecology | Evolutionary history predicts trophic ecology and functionality[62,63]. |
| | - Ecosystem Role | Evolutionary history predicts ecosystem role[62,63]. |
| | - Markets & Fisheries Management | Correct identification of species is critical to management, unresolved species complexes have been found even in well-studied and actively managed species[20,70]. |
| Tourism | - Fisheries & Bycatch | Livelihood-based interventions or conservation financing mechanisms linked to tourism can be used to offset fishing pressure[18,68]. |
| Trophic Ecology | - Taxonomy & Phylogeny | Evolutionary history predicts trophic ecology and functionality[62,63]. |
| | - Spatial Management | Understanding foraging activities may be important in defining key spatial areas[34,42]. |

Key weaknesses are based on the identification and subsequent interpretation of negative correlations among topics.

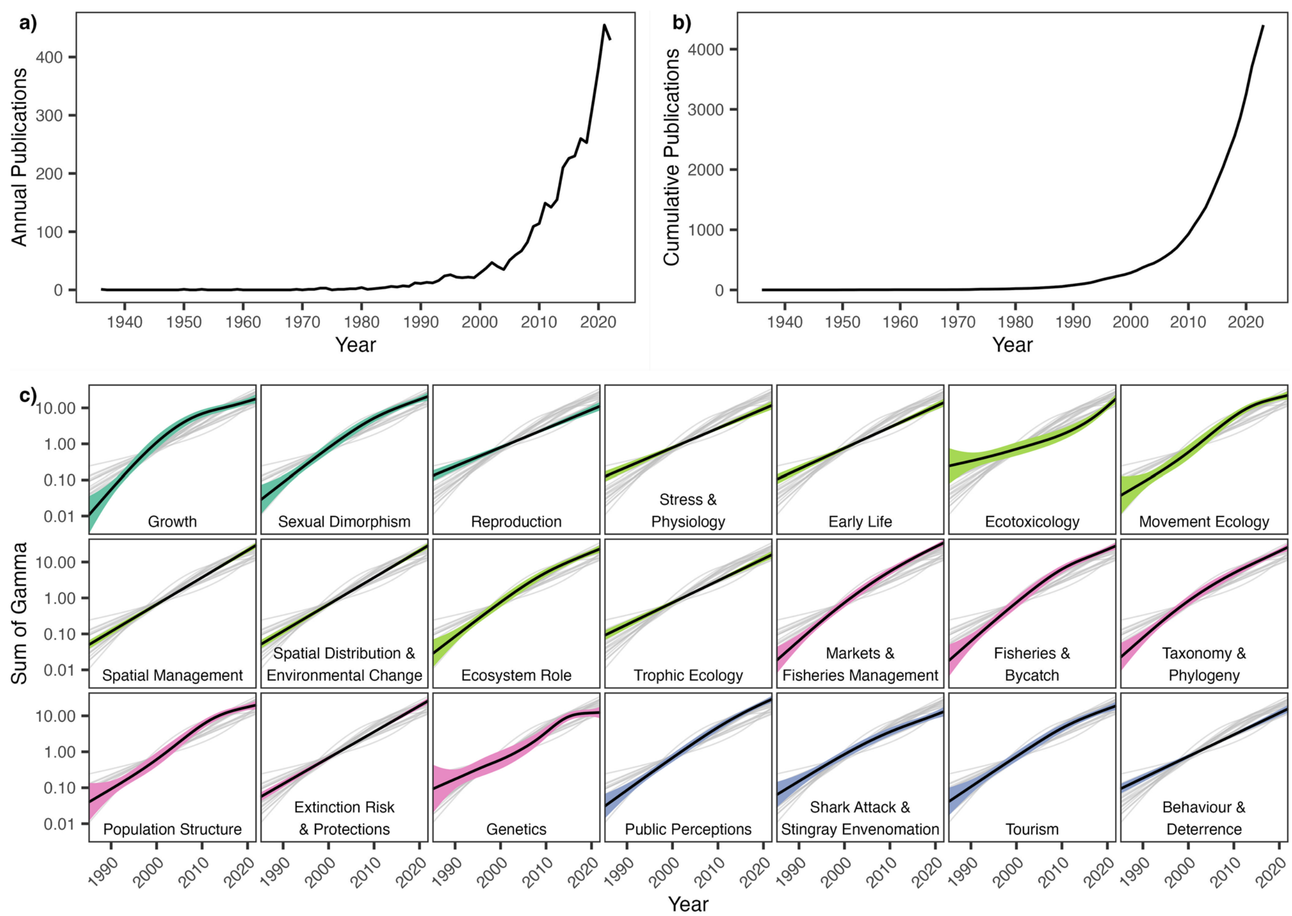


**Fig. 3 | Growth and thematic composition of the shark conservation field.** **a** Annual number of publications in shark conservation by year. **b** Cumulative number of publications in shark conservation by year. **c** Trends in shark conservation topics by year, note logarithmic scale on the y-axis.

potentially synergistic threats, highlighting this as a clear priority for future shark conservation research.

### A rapidly growing field with some emergent topics but others falling by the wayside

The shark conservation literature has existed since at least the 1930s but its growth rapidly increased in the 1990s (Fig. 3a, b). The cumulative number of publications grew by 258% between 1990 and 2000, by a further 225% between 2000 and 2010, and by another 250% between 2010 and 2020, reflecting rapid exponential growth in the field. This rapid growth is reflected in the continuous exponential growth of almost all topics within the shark conservation scientific literature (Fig. 3c).

While all topics have shown rapid ($p < 0.001$) and often exponential growth, some have experienced a “boom and bust” cycle with specific periods of rapid growth followed by a relative deceleration (Fig. 3c). The most prominent example is the topic *Growth*, which expanded particularly quickly between the late 1990s and early to mid-2000s, due to pioneering work in this time by a core group of researchers publishing *Growth* studies for numerous shark species. As a result, *Growth* became a core research topic in shark science, leading to a relative stabilisation in the topic's growth rate. To a lesser extent, *Sexual Dimorphism*, *Ecosystem Role*, *Tourism*, *Markets & Fisheries Managements*, *Fisheries & Bycatch*, and *Taxonomy & Phylogeny* showed similar patterns, with particularly high relative growth during the 2000s and *Fisheries & Bycatch* sustaining this into the 2010s. These trends are likely driven by a combination of factors, including heightened global conservation awareness, the implementation of international agreements and national regulations aimed at protecting marine biodiversity, increased ocean exploration, and significant scientific discoveries that underscored the ecological importance of sharks[48,49]. The sustained growth rate of *Fisheries & Bycatch* into the 2010s can be attributed to ongoing concerns over the impacts of commercial fishing practices on shark populations and the broader marine ecosystem, as well as improvements in monitoring technologies[50]. Indeed, the rate of change for *Fisheries & Bycatch* may be even greater than it appears here, given that much of technical work in this area exists outside of the peer-reviewed literature published in scientific journals.

*Movement Ecology*, *Population Structure* and *Genetics* all showed the greatest relative increases in growth rates during the early 2010s. Advancements in, and accessibility of, biotelemetry and genetic sequencing technologies are likely a major driver of this change, dramatically enhancing our ability to study the movement patterns, population genetics, and genomic diversity of sharks[23,50]. These technological breakthroughs have provided unprecedented insights into shark behaviour, migration, and population connectivity, informing conservation strategies and management practices. Additionally, the early 2010s saw an increased emphasis on the role of genetic diversity and ecosystem dynamics in the resilience of shark populations to environmental changes and human pressures[51,52]. Since then, the growth rate of publications in *Genetics* has slowed substantially, suggesting the field has reached a phase of maturation where initial rapid advancements and discoveries (e.g., genetic barcoding, eDNA, genome sequencing etc.) have given way to a phase of consolidation and deeper exploration, and findings for new molecular markers have become more difficult to publish on their own. Additionally, the high costs and technical expertise required for genomic research may limit the initiation and success rate of new studies. As the field of *Genetics* becomes more integrated with other areas of shark research, such as ecology and conservation strategies, the focus may shift from pure genetics to interdisciplinary studies that incorporate genomic data and more deeply explore its implications for shark conservation and management.

The one exception to these general patterns is *Ecotoxicology*, which is a recent emergent topic in the shark and ray conservation literature. Since the late 2010s, *Ecotoxicology* has shown rapid growth, reflecting increased awareness of the potential impacts on human health from the consumption of shark meat and the realisation that pollutants may contribute to elevated extinction risk[53–55].

## Conclusions

Our analysis reveals shark conservation to be a complex but generally well interconnected, coherently structured, increasingly interdisciplinary, rapidly expanding, and well-prioritised field of study. The field largely revolves around the critical conservation nexus of human perceptions and interactions with sharks, and their use and management[14,15]. This same dynamic will ultimately define the success or failure of biodiversity conservation for all species in the Anthropocene. The shark conservation literature is well integrated with this nexus, with most research topics connected to it either directly or indirectly. This connectivity suggests that research is generally well contextualised in the conservation nexus and appears to be increasingly designed with it in mind. There is clear evidence of increasing interdisciplinary research over the last three decades, reflecting the widespread recognition of this approach as critical to conservation success[9,10]. Furthermore, research is generally well prioritised in relation to the key threats faced by sharks[1], with fisheries and fisheries associated research growing rapidly in response to the identification of fisheries as the key threat to these species, the continued growth of research relating to environmental change, and the relatively recent emergence of research addressing the potentially overlooked threat of pollution. Overall, our findings are a testament to the efforts of the shark research community and a source of optimism for the future of these species.

While we find many strengths in shark conservation research, our analysis also highlights probable weaknesses that present opportunities to further strengthen the field. For example, both *Movement Ecology* and *Population Structure* were poorly connected to one another and to a range of other key topics, with limited inclusion in interdisciplinary research. Both topics have the potential to benefit directed fisheries management and spatial management approaches, which, when combined, may have powerful synergistic effects for the conservation of some shark species[46]. Our analysis also reveals a notable gap in studies exploring the synergistic impacts of multiple threats, such as overfishing and climate change, despite at least 33% of threatened shark species being impacted by multiple direct threats. Moreover, the decoupling of *Stress & Physiology* and *Ecotoxicology* from core conservation topics suggests a limited integration of sub-lethal endpoints, such as reduced reproductive success and physiological stress responses, into broader conservation frameworks. Our identification of key weaknesses in the interconnectivity of shark conservation literature does not mean that no studies exist in these spaces. However, these gaps highlight potentially missed and/or underexplored opportunities to understand the nuanced ways in which sharks interact with their changing environments and the complex threats they face.

Lastly, although we present evidence for increasing interdisciplinary research, it is critical to ensure that research is moving beyond merely contextualising results within the broader conservation discourse and instead works toward a more integrated approach that builds truly meaningful linkages between research topics. Shifting from contextualisation to integration can enhance our understanding of the complex interplay between different conservation threats, help identify and address the ultimate indirect social and economic drivers, and lead to more appropriate, holistic, and effective management. Addressing these and the other opportunities outlined in this analysis holds the potential to effect positive change for shark species around the globe.

Looking forward, the future of shark conservation research in the Anthropocene will continue to present new challenges and opportunities. To truly bend the biodiversity-loss curve for sharks, researchers, conservationists, and policymakers must embrace an increasingly holistic view of shark conservation. This includes recognising the interconnectedness of various threats and the importance of addressing them through integrated research and management strategies. Addressing the challenges of the Anthropocene will therefore demand innovative, interdisciplinary approaches that can tackle the complex, multifaceted threats facing sharks. This will require concerted efforts to foster interdisciplinary collaborations that bridge the current divides between research domains. By leveraging the strengths of the field and addressing its remaining weaknesses, there is hope for a future where sharks thrive and contribute to healthy, resilient marine ecosystems. While the field of shark conservation has made significant strides, the journey is far from over, but we are heading in the right direction.

## Methods

### Literature compilation

We conducted a systematic search of the shark conservation literature based on established methods, and reported our results in line with the ROSES *pro forma*[56] (Fig. S1). Literature searches were conducted on the 24th of August 2023 using both Web of Science (www.webofscience.com) and Scopus (www.scopus.com). Results were restricted to articles written in or translated into English. An optimised search string was developed using Boolean logic to combine terms relating to sharks and their conservation to maximise the number of relevant search returns while minimising the inclusion of extraneous results. Searches were conducted for article titles and abstracts only. The final search string used was: *("shark*" OR "elasmobranch*" OR "batoid*" OR "guitarfish*" OR "wedgefish*" OR "sawfish*" OR "manta*"*

*OR "mobulid*" OR "skate*" OR "chondrichthyan*" OR "stingray*") AND ("threat*" OR "conserv*").* Terms like *"ray"*, *"chimaera"*, *"management"*, and *"protections"* were not included as these led to the incorporation of very high volumes of irrelevant search returns. The title, abstract, and year of publication were extracted for all search returns. Search returns from Web of Science ($n = 3669$) and Scopus ($n = 5053$) were combined, retaining unique results ($n = 5140$). These initial returns were then filtered to only include peer-reviewed scientific publications while excluding editorials, meeting abstracts, conference reviews, news items, and book reviews. Retracted publications and/or corrected or erratum versions of publications were also removed. Technical reports are not available in Web of Science or Scopus and so were not considered. A manual title and abstract sift was then conducted to remove spurious results that did not relate to shark and ray research. A final list of 4401 publications was taken forward for analysis, the list of publications can be found in the Supplemental Materials. All analyses were carried out in R v4.1.0 using RStudio[57,58], a full list of packages used can be found in the Supplemental Materials.

## Topic modelling

Topic modelling is an unsupervised machine learning approach for the analysis of text data, categorising text into a user-defined number of topics based on word co-occurrence. Here we used Structured Topic Models to analyse the abstracts of the identified publications. Unlike other popular topic models, Structured Topic Models allow for both correlation among topics identified in the data and the incorporation of metadata into the model[59]. We included the year as a smoothed variable in the model because topic prevalence and composition are likely to vary with time. The model was built using the *stm* package.

Before submission to the Structured Topic Model, the abstracts were cleaned using the package *tm*. All punctuation and non-alphabetic characters were removed, as was a list of pre-defined English stop-words. All remaining words were transformed into lower case and all excess whitespace (i.e., any double-or-more spaces) was removed. Next, we removed a series of terms, including some of the key search terms used, which appeared commonly in the literature but were adjudged to be uninformative: *shark*, *sharks*, *elasmobranch*, *elasmobranchs*, *batoid*, *batoids*, *guitarfish*, *guitarfishes*, *wedgefish*, *wedgefishes*, *sawfish*, *sawfishes*, *manta*, *skate*, *skates*, *stingray*, *stingrays*, *ray*, *rays*, *chondrichthyan*, *chondrichthyans*, *threat*, *conservation*, *species*, and *data*. Copyright statements were manually removed. Lastly, to remove extraneous terms, we set a minimum threshold requirement of 22 or more (i.e. ≥0.5%) publications for a word to be retained for analysis. The final dataset contained a vocabulary of 3052 words (Fig. 4).

The dataset was then queried with a series of Structured Topic Models with user-defined topic numbers ranging from 10 to 50. This range was chosen with the understanding that 10 topics represents the minimum number of expected to be present in the literature, while 50 topics were considered a reasonable maximum manageable number for effective interpretation. Models were estimated with spectral initialisation. Measures of fit were extracted and compared, including Held-Out Likelihood, Residuals, Lower Bound, Semantic Coherence and Exclusivity (Fig. S2). Emphasis was placed on selecting the number of topics that balanced Semantic Coherence, which closely corresponds to topic interpretability, and Exclusivity, which acts as a measure of topic specificity. Topic numbers that provided an apparent balance between Semantic Coherence and Exclusivity were 28, 29, 30, and 35 (Fig. S2). These models were taken forward as candidates for model selection.

Candidate models were subsequently re-run and their outputs compared. For each of the four candidate models, we inspected the 10 highest weighted words for each topic as identified by four separate measures: (1) *Highest Prob*: the words with the highest probability of association with each given topic, (2) *FREX*: a weighted harmonic mean of each word's exclusivity and frequency, (3) *Lift*: which gives higher weights

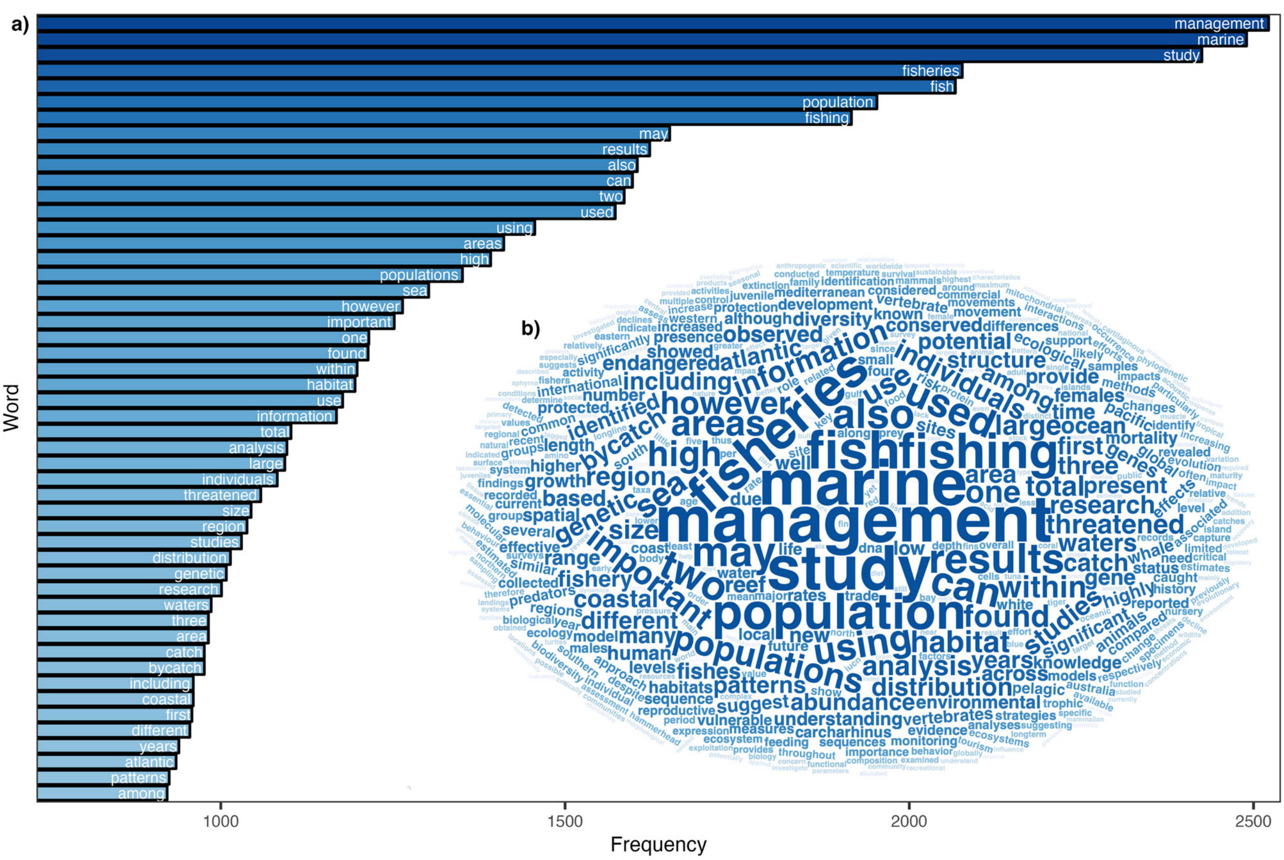


**Fig. 4 | Composition of the shark conservation literature after data cleaning.** **a** Frequency plot of the most frequent 50 words. **b** Word cloud of the most frequent 500 words. Note shortened x-axis.

to words that are less frequent in other topics, and (4) *Score*: which is the division of the log frequency of a word in the topic by the log frequency of words in other topics. Additionally, the 10 abstracts with highest associated probability scores for each topic were manually inspected. Topics were evaluated and named based on highly weighted words and associated abstracts. The candidate model with the highest number of interpretable topics was selected and taken forward for further analysis. It should be noted that, while we seek to minimise the potential impact of a priori beliefs, there remains some potential for these to factor into the interpretation of identified topics.

### Topic networks, trends, and weaknesses

After the final model was selected and topics were identified, we estimated *gamma* values, the modelled proportional contribution of each topic to each abstract. Some topics identified were deemed contextual, meaning they pertained not to a research discipline but instead to aspects such as the geographical scope of the work. While these topics were identified and are presented, they were not considered relevant to the aim of this paper and so were excluded from further analysis. The *gamma* values of all other topics were rescaled to account for removal of contextual topics.

Correlations among topics were assessed after first conducting a non-paranormal transformation of *gamma* values[60]. Topic networks were built based on positive correlations for all data combined and for five distinct time periods (pre-1990, 1990s, 2000s, 2010s, and 2020s). Topic clusters within the complete topic network were identified using the Multilevel clustering algorithm[61]. Key weaknesses within the shark conservation literature were based on the identification and subsequent interpretation of negative correlations among topics. Correlation and network analyses were carried out using packages *igraph* and *huge*.

The interdisciplinarity of shark research was calculated using the maximum *gamma* value for each abstract and the variance in correlation strengths between topics, was calculated yearly between 1990 and 2022. Interannual trends in interdisciplinarity and variance in correlation strength were analysed using Generalised Additive Models. Models were fitted using Restricted Maximum Likelihood with gaussian assumptions. Year was fitted as a thin plate regression spline. Patterns were relatively simple, and so iterative knot selection was not required. Generalised Additive Models were carried out using packages *mgcv* and *nlme*.

### Topic frequency, trends, and species conservation threats

We used cumulative *gamma* values to identify topic frequency. However, *gamma* may overweight the contribution of secondary topics to a publication because abstracts often discuss findings within the context of other topics (e.g., often contextualising results for their use in management), though the paper itself may place very little, if any, focus on research in these secondary topics. Therefore, a primary topic was also assigned to each article based on the topic that received the highest *gamma* value, and the frequencies of primary topics were also compared. Topic frequency was considered in the context of known threats to species, which were quantified based on threats listed for threatened sharks (Critically Endangered, Endangered, or Vulnerable) in the IUCN Red List of Threatened Species (www.iucnredlist.org). Trends in topic popularity through time were also explored using Generalised Additive Models, fitted using Restricted Maximum Likelihood and using the negative binomial family. Year was fitted as a thin plate regression spline by topic to create factor smooth interactions. Patterns were relatively simple, and so iterative knot selection was not required.

## Data availability

All publications used in the analyses presented here are available in the supplementary materials, all associated code will be made available upon reasonable request.

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## Author contributions
A.J.T.: Conceptualisation, Methodology, Formal analysis, Investigation, Data Curation, Writing - Original Draft, Writing - Review & Editing, Visualisation, and Funding acquisition. J.E.M.C., A.P., N.K.D., E.C., S.W., H.B., C.R.W., B.F., A.B.H., M.R.H., I.S., J.L.R.: Investigation, Writing - Original Draft, and Writing - Review & Editing. M.L.B.: Writing - Review & Editing and Funding acquisition.

## Competing interests
The authors declare no competing interests.

## Additional information
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