Received: 25 May 2023 | Revised: 15 September 2023 | Accepted: 22 October 2023
DOI: 10.1002/aqc.4039

RESEARCH ARTICLE

WILEY

Murky waters: Assessing the vulnerabilities of Indo-West Pacific non-marine elasmobranchs to inform future conservation planning priorities

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Abstract

1. Globally, freshwater environments are imperilled, with freshwater vertebrate species declining at twice the rate of marine and terrestrial populations. Non-marine elasmobranchs (freshwater obligates and euryhaline generalists) remain understudied and overlooked by conservation efforts.
2. This study aimed to adapt and apply a vulnerability assessment framework to understand the conservation priorities of Indo-West Pacific non-marine elasmobranch species. An exposure sensitivity adaptability (ESA) framework was used to assess vulnerability to environmental threats, and an exposure susceptibility productivity (ESP) framework was used to assess vulnerability to fisheries.
3. Resulting species vulnerabilities were categorized into three conservation priority tiers. The general patterns of conservation priority tiering were as follows: (i) large-bodied euryhaline species occurring in densely populated nations had the highest ESA and ESP vulnerabilities; (ii) freshwater obligates also had high ESA vulnerability rankings, although ESP vulnerability rankings were lower as their smaller body sizes suggest increased population productivity and higher potential for resilience; and (iii) euryhaline species with large range proportions in northern Australia had moderate to low vulnerability rankings across ESA and ESP assessments, as these species benefit from reduced fisheries mortality compared with species occurring in other regions.
4. The outcomes from the vulnerability assessment framework for the conservation priority rankings of species corresponded with their respective International Union for Conservation of Nature (IUCN) Red List status, whereby priority 1 and 2 species also have elevated extinction risks. Environmental threats were at high or moderate levels in all nations assessed, while Cambodia, China, Malaysia, and Myanmar face the highest pressure from inland fisheries.
5. The major knowledge gaps identified included species-specific productivity estimates, population dynamics (population movements and habitat requirements), and information on mortality from the threats considered. The

present ESA–ESP framework was effective for the broad and data-poor context of Indo-West Pacific non-marine elasmobranchs, and the results will be useful for guiding future conservation planning for high-priority species and nations.

KEYWORDS
adaptive capacity, ecological risk assessment, freshwater, productivity analysis, susceptibility analysis, vulnerability assessment

1 | INTRODUCTION

Freshwater environments are some of the most biodiverse on the planet, harbouring one-third of all vertebrate species, and almost half of all fish species, despite covering only approximately 1% of the Earth's surface (Tickner et al., 2020; Su et al., 2021). However, this diversity is in rapid decline, and freshwater species are increasingly under threat of extinction. Almost one-third (27%) of freshwater fish species assessed are listed as threatened (Extinct in the Wild, Critically Endangered, Endangered, or Vulnerable; IUCN, 2022a) in the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (hereafter 'IUCN Red List'; IUCN, 2022b). Freshwater megafauna (body mass > 30 kg) declined by 88% between 1970 and 2012 (He et al., 2019), and more than half of the world's rivers have shown marked decreases in the diversity of their fish assemblages (Su et al., 2021). At present, freshwater vertebrate populations are considered to be declining at twice the rate of marine and terrestrial populations (McRae, Deinet & Freeman, 2017).

These severe declines in freshwater biodiversity are driven by a range of human threats (Dudgeon et al., 2006; Reid et al., 2019). Coastlines, and the banks of lakes and rivers, provide ideal places for human development, with ready access to a source of food, water, building materials, and transport (Compagno & Cook, 1995). Land clearing for urbanization and agricultural purposes has led to increased sedimentation, and pollution from fertilizers, pesticides, and heavy metals, reducing habitat quality and affecting primary production within ecosystems (Acero Triana, Chu & Stein, 2021). The widespread construction of dams has further reduced habitat quality through altering flow and sediment regimes, resulting in population fragmentation (Grill et al., 2019). In addition, the overexploitation of fisheries (Allan et al., 2005; He et al., 2019) and the introduction of invasive species (Havel et al., 2015) have increased the strain on freshwater populations.

There is global concern for elasmobranchs (sharks and rays) that inhabit non-marine environments (freshwater and estuaries) (Grant et al., 2019). Confined predominantly to tropical latitudes where human population density is highest, it is likely that non-marine elasmobranchs are exposed to severe human pressures and are suffering similar declines to the declines observed in other riverine megafauna (Grant, Mizrahi & Mather, 2022). Furthermore, elasmobranchs typically display 'slow' life-history traits, including late maturation, long generation lengths, and low fecundity (Cortés, 2000), making them particularly susceptible to population declines compared with other freshwater teleosts. Grant et al. (2019) found that of the non-marine elasmobranch species with sufficient information for population assessment (34/72 species), 74% are threatened with extinction on the IUCN Red List (version 2018-2). This highlights both the high extinction risks that these species are facing and the general lack of species-specific information available for many non-marine elasmobranchs.

Given the numerous challenges non-marine elasmobranchs are likely to be facing, greater research efforts are required to assess how they are affected by human pressures, particularly in areas of dense and rapidly growing human populations that rely on riverine fisheries resources (Dudgeon, 2002). One such area is the Indo-West Pacific, where there are 13 non-marine elasmobranch species, 11 of which are listed as threatened with extinction on the IUCN Red List. These species include five freshwater obligates, which spend their entire life history in fresh water, and eight euryhaline generalists, capable of withstanding prolonged exposure to both marine and freshwater environments (Grant et al., 2019). An issue in understanding population status and developing conservation initiatives for these species is a lack of species-specific and nation-specific information on how human activities are affecting populations. There is an urgent need to identify which species may be facing the greatest risks of extinction, and in which nations they are exposed to the greatest population pressures. Such information is needed to direct conservation efforts and facilitate the collection of additional information for the highest priority species and nations within the Indo-West Pacific.

Environmental vulnerability assessments are an increasingly used tool for evaluating the status of data-poor species. These assessments identify which species are expected to be at greatest risk from particular threats (Walker et al., 2021) and can also identify knowledge gaps, directing future research. For example, in the absence of direct information, Chin et al. (2010) evaluated the vulnerability of elasmobranch species to climate change by considering three factors: their exposure to climate change impacts, their innate sensitivity, and their ability to adapt. Meanwhile, the use of productivity susceptibility assessments (PSAs) to evaluate the vulnerability of multiple species to fisheries has been found to be robust when applied to elasmobranchs caught incidentally in the northern prawn fishery of Australia (Stobutzki et al., 2002; Griffiths et al., 2006; Hobday et al., 2011). Incorporating both approaches, Walker et al. (2021) lay out an exposure sensitivity adaptability (ESA) and exposure susceptibility productivity (ESP) framework to evaluate semi-quantitatively the impacts of both anthropogenic climate change and fisheries pressures on chondrichthyan fauna (sharks, rays, and chimaeras) in southern Australia. The ESA–ESP framework determines the risk of decline of a species as a product of its 'exposure vulnerability' and its 'resilience vulnerability'. Exposure vulnerability is external and varies through space and time. It is possible to alter exposure vulnerability, and this can help to identify activities that can be managed to reduce the risk of declines in a species. Resilience vulnerability refers to the intrinsic biological and ecological characteristics of the species, with sensitivity and adaptability used to assess vulnerability to environmental impacts (within the ESA), and with susceptibility and productivity (within the ESP) used to assess the impacts of mortality associated with fisheries.

The conservation and management value of the ESA–ESP framework is that it can be adapted to a range of species and is able accommodate considerable uncertainty or lack of data. It is therefore a promising method for assessing the vulnerability of data-poor non-marine elasmobranchs in river environments of the Indo-West Pacific. In addition, such tailored population assessment approaches provide a more comprehensive and in-depth accounting of threats and vulnerabilities than the existing IUCN Red List assessments (which focus on extinction risk only; Collen et al., 2016), as they consider a wider range of attributes and interactions, and can be conducted at flexible spatial scales. As such, this study had two aims: (i) to develop a vulnerability assessment framework applicable to non-marine elasmobranch populations in the Indo-West Pacific; and (ii) to apply the framework to determine the vulnerability to population decline for selected species caused by environmental degradation and fisheries pressures within their non-marine habitat.

The results are intended to identify species and nations with the highest relative conservation priorities, and to identify knowledge gaps that will benefit future population assessments of these species.

2 | METHODS

2.1 | Study species and geographical extent

This study focused on non-marine elasmobranch species distributed across the Indo-West Pacific, including river basins where they are known to occur (Table 1). Non-marine elasmobranchs include euryhaline species that also occur in marine environments in sub-adult and adult life history phases; however, the purpose of this study was to improve our understanding of the vulnerabilities of non-marine elasmobranchs to riverine pressures, so marine ranges and pressures were not considered in this study. Species ranges followed those considered in recent IUCN Red List assessments (IUCN, 2022b) (Table 1). Species distributions encompassed the nations of Pakistan, India, Bangladesh, Myanmar, Indonesia (Sumatra, Kalimantan and Java only), Malaysia (Peninsular and Borneo), Thailand, Lao People's Democratic Republic (herein, Laos), Cambodia, Vietnam, China, Brunei, Papua New Guinea, and northern Australia (Western Australia, Northern Territory, and Queensland). In China, only the Pearl River was considered, including the Yu River Tributary at its confluence with the Xunjiang/Qianjiang River, moving upstream to Nanning, then following the Xuo/Lijiang/Ping'er River south west through Longzhou to the Vietnamese border (based on the freshwater range of Bennett's stingray, *Hemitrygon bennetti*).

The largetooth sawfish *Pristis pristis* and bull shark *Carcharhinus leucas* were the only two species with ranges that extend beyond the study area (both are more globally distributed, including ranges

TABLE 1 List of study species, their common names, IUCN Red List categories, and range nations (from west to south east) where species are known to have extant freshwater or estuarine populations.

Species	Common name	IUCN Red List status	Range (nations)
Freshwater obligates			
Fluvitrygon kittipongi	Roughback whipray	EN	Indonesia, Malaysia, Thailand
Fluvitrygon oxyrhynchus	Marbled whipray	EN	Indonesia, Malaysia, Thailand, Cambodia
Fluvitrygon signifer	White-edge whipray	EN	Indonesia, Malaysia, Thailand
Hemitrygon bennetti[a]	Bennett's stingray	VU	China
Hemitrygon laosensis	Mekong stingray	EN	Thailand, Laos, Cambodia
Makararaja chindwinensis	Chindwin cowtail ray	DD	Myanmar
Euryhaline generalists			
Carcharhinus leucas	Bull shark	VU	Pakistan, India, Bangladesh, Myanmar, Indonesia, Malaysia, Thailand, Vietnam, Brunei, Papua New Guinea and Australia
Glyphis gangeticus	Ganges river shark	CR	Pakistan, India, Bangladesh, Myanmar, Malaysia
Glyphis garricki	Northern river shark	VU	Papua New Guinea, Australia
Glyphis glyphis	Speartooth shark	VU	Papua New Guinea, Australia
Pristis pristis	Largetooth Sawfish	CR	Pakistan, India, Bangladesh, Indonesia, Papua New Guinea, Australia
Urogymnus dalyensis	Freshwater whipray	LC	Papua New Guinea, Australia
Urogymnus polylepis	Giant freshwater whipray	EN	India, Bangladesh, Myanmar, Indonesia, Malaysia, Thailand, Laos, Cambodia, Vietnam, Brunei

Abbreviations: CR, Critically Endangered; DD, Data Deficient; EN, Endangered; LC, Least Concern; VU, Vulnerable.
[a]Note, although *H. bennetti* has a much broader marine distribution, this assessment considers only the freshwater population, which is limited to China.

throughout much of the Americas). These species were only considered where their range overlaps with other study species, as both *C. leucas* and *P. pristis* are relatively well studied, and their inclusion provides a useful basis for comparison with the other more poorly studied species. In addition, as this study focused on the river conservation context, only the isolated freshwater population of *H. bennetti* was considered, which is located in the Pearl River, southern China (Zhang et al., 2010). This *H. bennetti* population is considered to be isolated from the marine conspecific populations (which are not known from non-marine environments in other parts of its Indo-Pacific range; Rigby et al., 2020) and it is treated as an independent freshwater obligate population.

TABLE 2 Exposure attributes and factors, the rationale for including them in the exposure sensitivity adaptability (ESA), and the data used for assessment.

Attributes	Description	Rationale	Data and source
Water quality (WQ)	This attribute refers to the physical, chemical, and biological characteristics of a water body. In this study, this is broken down into three factors (WQ1–WQ3)	Poor water quality (e.g. turbidity, eutrophication, and pollution with pesticides or heavy metals) results in reduced habitat suitability or availability.	Three factors represent the main drivers of water quality decline (see WQ1–WQ3)
WQ1: Human population density	This factor indicates the level of urban and industrial development, and the overall human pressure on natural systems in a nation	Densely populated areas impose greater pressures on natural systems through residential and industrial waste, land clearing, and extractive resource use.	Number of people per square kilometre (2021 data) (CIA World Factbook, 2021)
WQ2: Agricultural land use	This factor indicates the level of deforestation and run-off of sediment, fertilizers, and pesticides into freshwater environments	Run-off of sediment into rivers can alter physical habitat through deposition and increased turbidity. Run-off of fertilizers and pesticide may result in trophic impacts and physiological stress	Percentage of land converted for agricultural use (2021 data) (CIA World Factbook, 2021)
WQ3: Mining intensity	This factor indicates the level of habitat modification and potential chemical pollution linked to mining activity	Causes declines in water quality through land clearing, habitat modification, extractive water use, and chemical pollutants, such as heavy metals	Number of mining features per square kilometre (dataset of mining sites with reported activity between 2000 and 2017) (Maus et al., 2020)
Damming	The damming intensity in river basins is represented by one factor	Dams influence flow regimes of water and sediment. Altered depth or flow rate can affect physical parameters such as temperature and turbidity. Dams may also prohibit migration up and down the river, restricting seasonal or ontogenetic migrations to vital spawning or nursery grounds. This also limits gene flow and supplementation among fragmented populations	Average number of dams per river basin, based on the visual counts of dams published on the Global Dam Watch database (https://www.globaldamwatch.org) (Grill et al., 2019), together with additional dam structures visible on the satellite image. Counts commenced at the river mouth or confluence at which the river is defined and moved upstream. Dams were counted in the main stream first, followed by those in the tributaries of the basin
Climate change	This indicates how severely each nation is affected by extreme weather events driven by climate change, and is represented by one factor	Climate change is expected to produce both chronic and acute pressures on freshwater environments globally, through rising temperatures, changing rainfall patterns, and more frequent and severe weather events (Lennox et al., 2019). The global climate risk index (CRI) is based on fatalities and economic losses as a result of extreme weather events, rather than environmental degradation. However, it provides a suitable proxy for the severity of climate change impacts in a given nation	National CRI values for 2019. Note that given the global nature of climate change, the rankings are based on the global range of values, rather than just the range of nations in the study area (Eckstein & Kreft, 2020)

Owing to the data-poor nature of river environments in the Indo-West Pacific (Dudgeon, 2011), in most instances exposure data were not available at the scale of individual river basins, and national-level data were therefore used. Where exposure data were available at a sub-national scale (e.g. damming intensity is available at the scale of individual river basins, and population density is available for each state in Australia), the average was taken for all river basins, states, or islands (relevant to Indonesia) where the study species are known to occur, and used to represent the nation (this allowed the exclusion of river basins where the study species do not occur in these nations).

2.2 | ESA

The ESA is the first of two concurrent assessments used in this vulnerability framework. The ESA assesses the vulnerability of a species to population declines resulting from environmental threats. The first component of the ESA, exposure, considers the intensity of environmental pressures in the river environment and their spatial overlap with the distribution of the species under study (Table 2). Non-marine elasmobranchs are exposed to a wide range of environmental pressures, including eutrophication, pollution (of various sorts), altered water and sediment flows by damming rivers, and increasingly severe fluctuations in temperature and rainfall as a result of climate change (Grant et al., 2019; Grant, Mizrahi & Mather, 2022; Kyne & Lucifora, 2022). Given the broad study area, finding consistent, reliable data for each of these pressures was not feasible. Instead, a conceptual model was devised to link the identified threats, their immediate causes, the activities producing them, and, ultimately, three overarching drivers for these threats (Figure 1). In this framework, exposure is derived from three attributes, with each representing one of the three drivers (water quality, damming, and climate change) (Figure 1; Table 2). The attribute 'water quality' was further broken down into three factors: human population density, agricultural land use, and mining.

A key assumption of this assessment is that the primary impact of environmental threats on the study species is indirect, through changes in habitat suitability or extent, rather than direct,

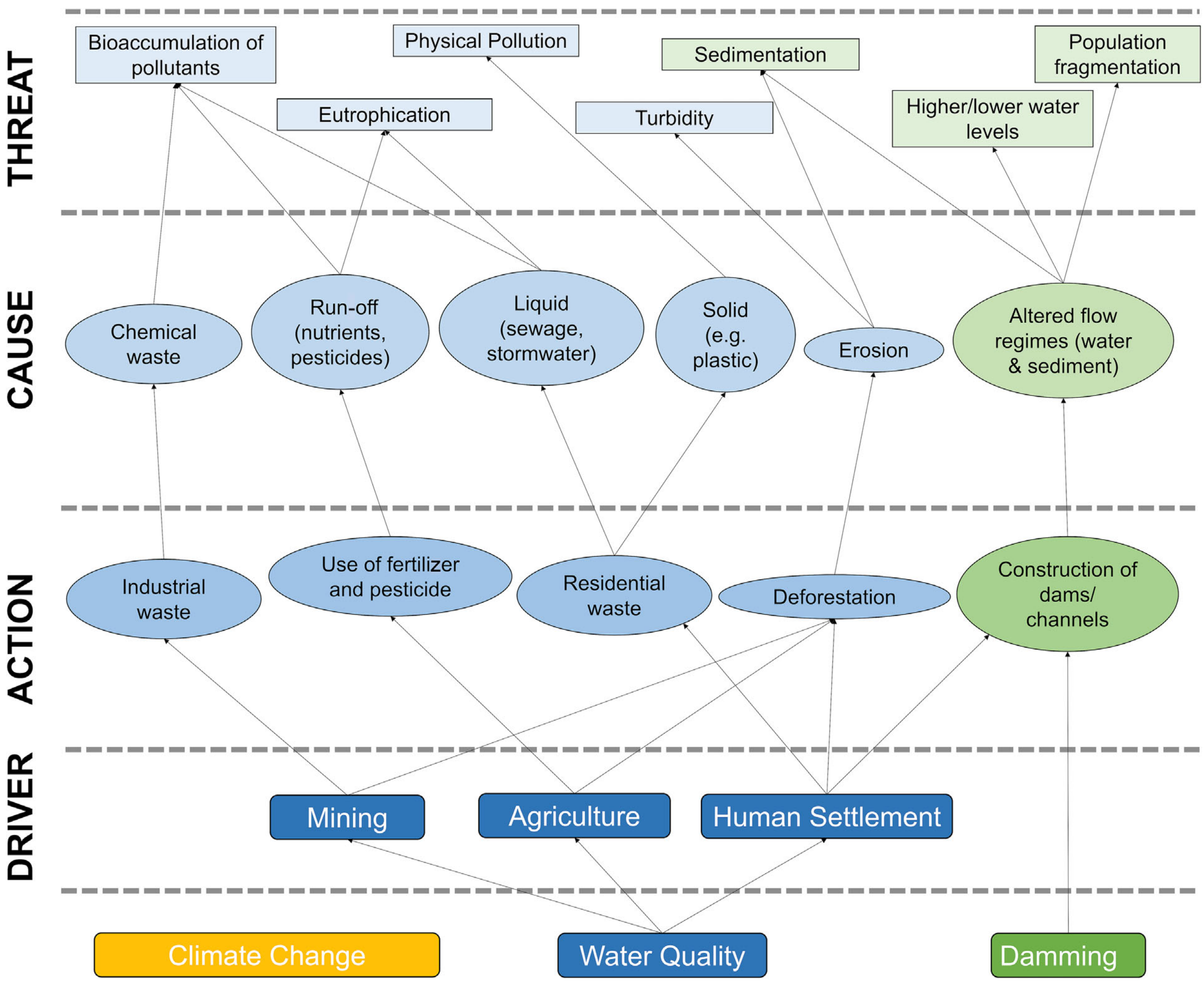

FIGURE 1 Conceptual model depicting an assortment of environmental threats facing freshwater environments, their immediate causes, the actions producing them, and the overarching drivers of these actions. This formed the basis for identifying climate change (yellow), water quality (blue), and damming (green) as the three attributes within the exposure component of the Exposure Sensitivity Adaptability (ESA) assessment.

through changes in mortality or reproductive rates (Walker et al., 2021). As such, the assessment is focused on attributes relating to the ecology of the species, including rarity, habitat specificity, distributional flexibility, trophic specificity, and mobility. These attributes fall into the second and third components: sensitivity (Table 3) and adaptability (Table 4).

2.3 | ESP

The second assessment in the vulnerability framework is the ESP assessment, which assesses vulnerability to population decline from fisheries threats. The exposure component considers the intensity of inland fishing effort and its overlap with the distribution of the study species. Over 100 types of fishing gear are used across the Indo-West Pacific, by commercial, artisanal, subsistence, and recreational fishers (Ainsworth, Cowx & Funge-Smith, 2021). To capture the intensity of freshwater fisheries effort throughout the Indo-West Pacific, exposure is considered through the attributes of national inland fisheries production and demand for aquatic protein (Table 5).

A key assumption of this assessment is that the primary impact of fisheries on the study species is direct, affecting their mortality and population productivity. As such, the assessment considers attributes relating to the susceptibility of the species to fisheries mortality (i.e. susceptibility component, Table 6), and species productivity, as a measure of tolerance to additional fisheries mortality at the population level (i.e. productivity component, Table 7).

The second component of the ESP analysis considers the susceptibility of a species to fishing-related mortality (Table 6). Following Walker et al. (2021), this component comprises four nested attributes (Table 6), expressed as:

$$\textit{Susceptibility} = \textit{Availability} \times \textit{Encounterability} \times \textit{Selectivity} \times \textit{Post} - \textit{encounter mortality}.$$

2.4 | Assessment and integration

Where quantitative data were available, the full range of values for the attribute (or factors comprising the attribute) was divided into equal thirds, which were then assigned as high, moderate, or least vulnerability (Tables 8 and 9). Where reliable and consistent quantitative data were not available, descriptive criteria were devised to assign high, moderate, or least vulnerability (Tables 8

TABLE 3 Sensitivity attributes and factors, the rationale for including them in the exposure sensitivity adaptability (ESA) assessment and the data used .

Attributes	Description	Rationale	Data and source
Rarity	Represents the population size and associated intrinsic vulnerability of the species. Owing to the absence of population size estimates for the study species, rarity is assessed based on a combination of its abundance and range (i.e. how widespread it is). Although IUCN Red List status is not a proxy for abundance or 'rareness', it has been used as a measure of how depleted a species is relative to the last 10 years or past three generation lengths, whichever is greater (i.e. CR species are depleted by at least 80%). In addition, all species considered have been assessed under Criterion A2 on the IUCN Red List. Therefore, our measure of rarity is relative to each species individually, and not to the other species being considered. We retain the use of the term 'rarity' for this study to be consistent with previous ESA literature	The impact of mortality events is greater on small, restricted, or fragmented populations, making rare or depleted species more sensitive to environmental threats (Chin et al., 2010)	IUCN Red List and number of nations occupied by range (IUCN, 2022b)
Habitat specificity	The range of habitats that a species can occupy within the river basin. This study focuses on two ecological groups: freshwater obligates and euryhaline generalists (Grant et al., 2019). The euryhaline generalists are further divided into two subgroups: those that require access to fresh water (e.g. *Pristis pristis*) and those that do not (e.g. *Glyphis* spp.)	If a species is highly dependent on particular habitat types, it is likely to be highly sensitive to environmental threats that degrade those habitats or restrict their accessibility	Ecological group (Grant et al., 2019)

TABLE 4 Adaptability attributes and factors, the rationale for including them in exposure sensitivity adaptability (ESA) assessment, and the data used.

Attributes (factors)	Description	Rationale	Data and source
Distributional flexibility (DF)	Refers to the physical and chemical tolerance of a species, and the potential to adjust its distribution both within and between individual river basins, as well as across the Indo-West Pacific. In this study, this is represented by three factors (DF1–DF3)	If a species has a broad distribution and is able to shift to a new location as a result of localized threats, it will be less vulnerable to population decline	Three factors (see DF1–DF3 below)
DF1: Number of regions	Represents the overall spatial extent of the known extant range of the species. In this study, a 'region' is defined as a country, a land mass (in the case of Malaysia and Indonesia), or a state/territory (in the case of Australia)	A species with a broad range is less likely to be affected by localized mortality events at the population level. Malaysia, Indonesia, and Australia have been divided into multiple regions to allow consideration for land mass or state/territory-specific data	Proportion of the total number of regions within the study area, where the species occurs (Table S14, and 'range' section of Tables S1–S13, Supporting information)
DF2: Latitudinal range	Represents the range of climates a species can withstand and is measured from their latitudinal range. For species that occur in both hemispheres, the latitudinal range is measured from the equator to the highest latitude within their range	Species with wide latitudinal ranges can withstand a broader range of climates, and are thus considered more adaptable	Species known extant range. Occurring in one hemisphere: latitudinal range. Occurring in both hemispheres: latitude at point of range furthest from equator (Tables S1–S13, Supporting information)
DF3: Salinity tolerance	Represents the distributional flexibility of a species within a river basin. Other physical and chemical tolerances may also be considered in place of this factor, such as thermal tolerance or depth range (e.g. Walker et al., 2021); however, little data were available on the thermal tolerance of the study species and, given the focus on shallow river environments, depth was not deemed relevant	A narrow window of salinity tolerance would indicate the limited potential of a species to adapt its distribution in response to environmental pressures, and therefore elevated resilience vulnerability	Inferred based on ecological categorizations of non-marine elasmobranchs, as quantitative data were not available for all study species (Grant et al., 2019)
Trophic specificity	Refers to the diversity of possible prey taxa a species can exploit. This attribute is typically measured using the proportions of taxa in the diet of a species; however, the proxies of body size and mouth gape were used in this study, as detailed information on the diets was not available for most of the study species. Represented by one factor	Species that feed high in the trophic web have higher trophic specificity and reduced ability to adapt their diet in response to changing prey availability, and thus have greater resilience vulnerability. This is based on differences in biomass and biodiversity along the trophic spectrum	Body size (Tables S1–S13, Supporting information)
Mobility	Refers to the ability of an individual within a species to travel within, or between, river basins. Represented by one factor	Highly mobile species, capable of moving up and down or between rivers, have a greater potential to adapt to environmental threats by relocating, thereby reducing their resilience vulnerability	Inferred from migratory patterns and ecological categorizations of non-marine elasmobranchs (Tables S1–S13, Supporting information)

and 9). Where neither quantitative nor qualitative information were available for a particular species, the attribute was ranked as high, consistent with the precautionary principle used in other ESA and ESP studies (Stobutzki et al., 2002; Chin et al., 2010; Hobday et al., 2011).

The components representing the vulnerability of a species (ESA, sensitivity and adaptability; ESP, susceptibility and productivity) were assessed for each species. Exposure components were first assessed for each nation, and the ranking of each species was then based on the average ranking from all nations within its range. Once all factors

TABLE 5 Exposure attributes, the rationale for including them in the exposure susceptibility productivity (ESP) assessment, and the data and source used.

Attributes	Description	Rationale	Data and source
Inland fisheries production	Provides a direct measure of the level of fishing pressure experienced in rivers and lakes in each nation	Fisheries-specific catch and effort data were not available, given the number of different fisheries operating in the study area (Ainsworth, Cowx & Funge-Smith, 2021)	Average inland fisheries production per capita (2007–2011) (Funge-Smith, 2018)
Aquatic protein demand	Represents the demand for aquatic protein, as an additional indicator of likely fishing pressure in each nation	Many of the study species are not targeted and sold, but instead caught incidentally and consumed locally, and may therefore go unreported. Including a measure of demand for fisheries products accounts for undocumented fisheries pressure	Average aquatic protein consumption per capita (2015) (Table S16, Supporting information)

TABLE 6 Susceptibility attributes, the rationale for including them in the exposure susceptibility productivity (ESP) assessment, and the data used.

Attributes	Description	Rationale	Data and source
Availability	Refers to the proportion of the spatial distribution of a species that overlaps with the spatial distribution of fishing gear deployment (Walker et al., 2021). This attribute does not consider the fishing intensity or type, only the parts of the distribution of the species where fishing occurs	Species that are highly available to fisheries are more vulnerable, as they are more likely to interact with fishers and fishing gear	Extent of fishing activity across the range of a species, informed by the 'Threat and Scope' classification and text within the 'Threats' section of the IUCN Red List Assessment for each species (IUCN, 2022b)
Encounterability	Refers to the proportion of the available population that may encounter the fishing gear (Walker et al., 2021). This relates to the mobility of a species and position in the water column, relative to fishing gear	Species that swim at depths where they are likely to encounter fishing gear are more vulnerable than species that swim under or above the locations where fishing gear is set. Given the shallow depth range available in most rivers compared with marine environments, together with the diversity of gears used, all study species are considered highly vulnerable to encountering fishing gear. The attribute was included to maintain consistency with other ESP studies	Species habitat preferences, and distribution of fishing gears in water column, informed by the text within the 'Threats', 'Use and Trade', and 'Habitat and Ecology' sections of the IUCN Red List Assessment for each species (IUCN, 2022b)
Selectivity	Refers to the proportion of the population encountering fishing gears, which are then caught by those gears	Fish that encounter fishing gear may or may not be captured by the fishing gear. Species that have high selectivity to fishing gear are more vulnerable as every time they encounter that gear, they are more likely to be captured by it	Variety of fishing gears and types (e.g. commercial, artisanal, subsistence) species are exposed to. Informed by the text within the 'Threats' and 'Use and Trade' sections of the IUCN Red List Assessment for each species (IUCN, 2022b)
Post-encounter mortality	Refers to the proportion of the population caught by fishing gear that die as a result of the encounter	Fishes that are always retained or that have high post-capture mortality are more vulnerable than species that may be released because they are less desirable, or species that are more likely to survive after being released	Frequency with which species are retained for sale, local consumption, or cultural reasons, informed by the text within the 'Threats' and 'Use and Trade' sections of the IUCN Red List Assessment for each species (IUCN, 2022b)

TABLE 7 Productivity attributes, the rationale for including them in the exposure susceptibility productivity (ESP) assessment, and the data used.

Attribute	Description	Rationale	Data and source
Body size	Represents the intrinsic growth rate of a population, based on body size as a proxy for the natural mortality and reproductive rate of a species. This component typically considers attributes such as fecundity, longevity, growth rate, and natural mortality (e.g. Walker et al., 2021). However, this information is not available for most of the species considered in this study	The productivity of a species determines the rate at which it can recover from depletion through fishing pressure. Body size was identified as a suitable proxy, based on an established relationship between increasing body size and decreasing potential growth rates in chondrichthyan species (Dulvy et al., 2014)	These categories refer to the body size categories developed and applied consistently by the IUCN SSC Shark Specialist Group for IUCN Red List assessments of all chondrichthyans since 2015

TABLE 8 Criteria used to define the conservation priority of species for all exposure sensitivity adaptability (ESA) attributes and their factors.

Exposure				
Attributes	**Factors of attribute**	**High vulnerability**	**Moderate vulnerability**	**Low vulnerability**
Water quality	Human population density (people/km^2)	>840.49	420.33–840.49	<420.33
	Agricultural land use (%)	>47.56	25.03–47.56	<25.03
	Mining intensity (mining features/100,000 km^2)	>40.18	20.78–40.18	<20.78
Damming (average number of dams/river)		>20.66	10.33–20.66	<10.33
Climate change (climate risk index)		<62.67	62.67–118.17	>118.17

Sensitivity			
Attributes	**High vulnerability**	**Moderate vulnerability**	**Low vulnerability**
Rarity	Listed as Critically Endangered or Data Deficient on the IUCN Red List (inclusion of Data Deficient is precautionary), and/or only occurs in one river basin	Listed as Endangered or Vulnerable on the IUCN Red List, and found in multiple river basins and nations across the Indo-West Pacific	Listed as Near Threatened or Least Concern on the IUCN Red List, and found in multiple river basins and nations across the Indo-West Pacific
Habitat specificity	Freshwater obligate species	Euryhaline generalist species that directly use freshwater environments for prolonged periods in their life history	Euryhaline generalist species that do not directly use freshwater environments in their life history

Adaptability				
Attributes	**Factors of attribute**	**High vulnerability**	**Moderate vulnerability**	**Low vulnerability**
Distributional flexibility	Number of regions	<4.66	4.66–8.33	>8.33
	Latitudinal range(degrees)	<11.28	11.28–21.88	>21.88
	Salinity tolerance	Freshwater obligate species that are not known to use estuarine or marine salinities in the wild	Species with a moderate window of salinity tolerance but a tendency to avoid either very low or very high salinities. Do not occur far into freshwater reaches of rivers	Euryhaline generalist species, capable of tolerating both marine and freshwater conditions for an extended period of time. Can occur far into freshwater reaches of rivers
Trophic specificity		Large-bodied (>2 m total length), large-mouthed sharks	Large-bodied (>1 m disc width), large-mouthed rays	Small-bodied (<1 m disc width), small-mouthed rays
Mobility		Sedentary and demersal species, restricted distribution within river basin(s), or freshwater obligates with unknown movement patterns	Euryhaline species capable of wide movements, although tend to require a particular river environment for prolonged periods	Euryhaline species that travel freely within rivers, and do not appear to require a particular river environment

TABLE 9 Criteria used to define conservation priority of species for all exposure, susceptibility, and productivity attributes.

Attributes	High vulnerability	Moderate vulnerability	Low vulnerability
Exposure			
Inland fisheries production (kg/capita/year)	>23.27	11.66–23.37	<11.66
Aquatic protein demand (kg/capita/year)	>39.8	20.86–39.8	<20.86
Susceptibility			
Availability	Species where fishing (of any kind or intensity) occurs in 100% of its riverine range	Species where fishing (of any kind or intensity) occurs in 50%–100% of its riverine range	Species where fishing (of any kind or intensity) is known only to occur in <50% of its riverine range
Encounterability	Species that always occur in the same part of the water column as relevant fishing gears	Species that occasionally occur in the same part of the water column as relevant fishing gears	Species that do not occur in the same part of the water column as relevant fishing gears
Selectivity	Species that are exposed to a large variety of gears within commercial and small-scale fisheries, across their entire riverine range	Species that are exposed to a large variety of gears within commercial and small-scale fisheries, across the majority of their riverine range. May also be exposed to recreational or cultural fisheries with limited variety of gear types, within their riverine range	Species that are only exposed to a large variety of gears within commercial or small-scale fisheries in the minority of their range or are only exposed to recreational or cultural fisheries with limited variety of gear types within their riverine range
Post-encounter mortality	Species are known to be almost always retained for consumption and sale (sale may include food or aquarium trade)	Species that are usually retained for sale, consumption, or for cultural reasons	Species that are not commonly retained for sale, consumption, or for cultural reasons
Productivity			
Body size (maximum DW or TL)	Rays (DW): >150 cm Sharks, sawfish (TL): >300 cm	Rays (DW): 50–150 cm Sharks, sawfish (TL): 150–300 cm	Rays (DW): <50 cm Sharks, sawfish (TL): <150 cm

and attributes were ranked for all species, these results were integrated to determine the three component rankings and, in turn, an overall ESA and ESP ranking for each species. It is important to note that these rankings are relative to the species considered in the study only, and that a low ranking should not imply a lack of vulnerability.

Although most attributes considered only one factor, for attributes composed of several factors (e.g. water quality and distributional flexibility), the most precautionary ranking of those factors was taken as the ranking for that attribute. Once each attribute was scored for each species, the component ranking was taken as the most conservative ranking of the attributes within it. The only exception to this was the integration of the four susceptibility components (availability, encounterability, selectivity, and post-encounter mortality) in the ESP assessment. As these attributes are nested, they were assigned a numerical value (high = 1, moderate = 0.67, and low = 0.33) and then multiplied. The product was then used to rank the susceptibility of the species, with values ranging from 0 to 0.33 ranked as least vulnerability, values ranging from >0.33 to 0.67 ranked as moderate vulnerability, and values ranging from >0.67 to 1.00 ranked as high vulnerability, following the methodology of Chin et al. (2010) and Walker et al. (2021).

Once all three components had been ranked for each of the study species, environmental exposure, sensitivity, and adaptability were assigned numerical values as described above (high = 1, moderate = 0.67, and low = 0.33) and then multiplied using a multiplication matrix to obtain an overall ESA ranking (Figure 2). The same process was used to combine fisheries exposure, susceptibility, and productivity to obtain an overall ESP ranking, following the methodology of Walker et al. (2021).

Once each species was assigned a vulnerability ranking for both assessments, these were combined to obtain the overall conservation priority, relative to the other species considered:

- Priority 1: HxH or MxH
- Priority 2: LxH or MxM
- Priority 3: LxM or LxL

Note that all study species are threatened with extinction, but species categorized as priority 3 are considered less vulnerable compared with the other species considered within the study. It should be stressed that this does not imply low vulnerability compared with other freshwater species, or with marine chondrichthyans. These results are relative to the study species.

FIGURE 2 Diagram of component integration matrix, adapted from Chin et al. (2010), showing how exposure and sensitivity and adaptability (ESA), or susceptibility and productivity (ESP) components are combined to rank species as either high, moderate, or low vulnerability. H, high; L, low; M, moderate. *A mathematical idiosyncrasy of this approach is that when all components are ranked as moderate, the calculated vulnerability is low (i.e. M × M = L). In this case, vulnerability is set as moderate.

Sensitivity × Adaptability
or
Susceptibility × Productivity

Exposure	L × L	L × M	L × H	M × M	M × H	H × H
H	0.11 (L)	0.22 (L)	0.33 (L)	0.44 (M)	0.66 (M)	1.00 (H)
M	0.07 (L)	0.14 (L)	0.22 (L)	0.29* (M)	0.44 (M)	0.66 (M)
L	0.03 (L)	0.07 (L)	0.11 (L)	0.14 (L)	0.22 (L)	0.33 (L)

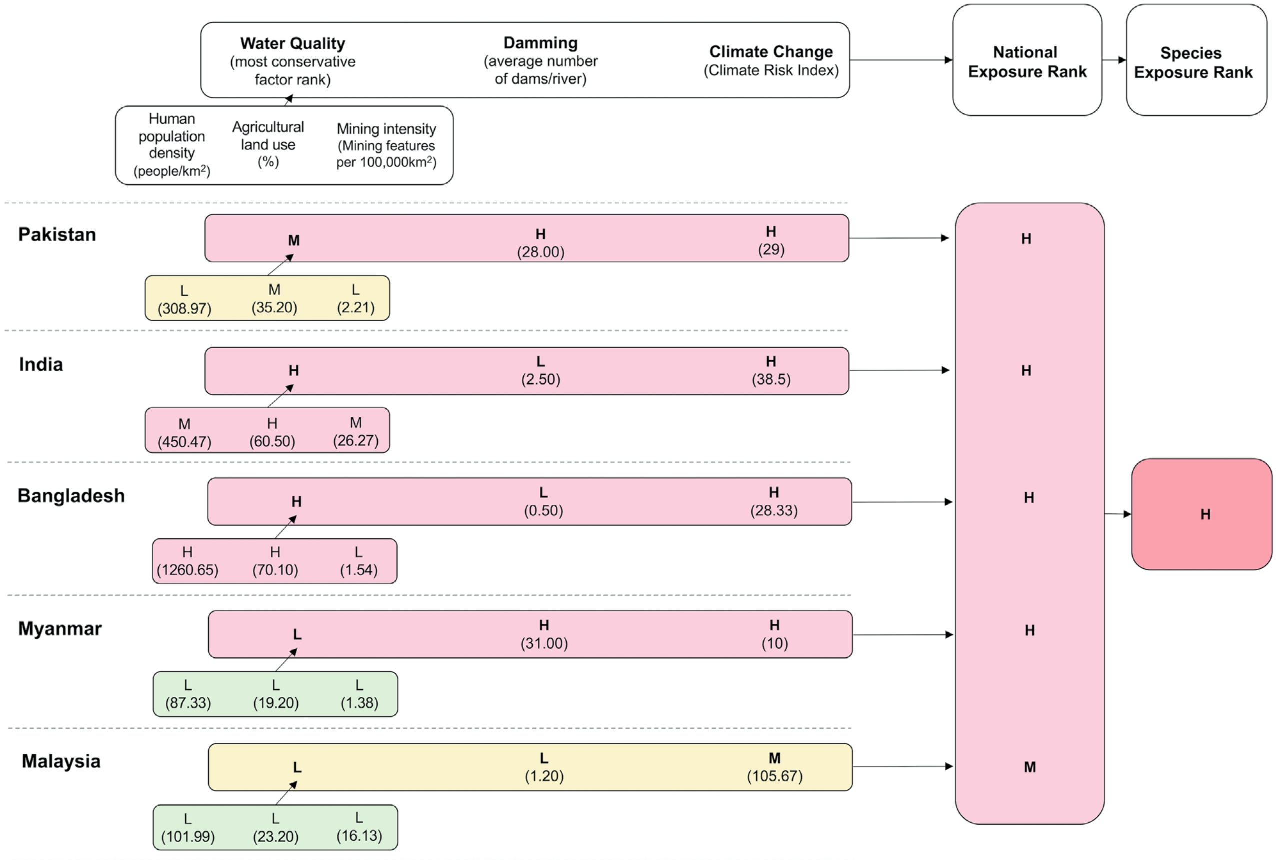

FIGURE 3 Diagram demonstrating how the ranking for the exposure component for *Glyphis gangeticus* was obtained. The diagram contains raw data and rankings from the three attributes (including the three factors considered within water quality) used to determine the exposure ranking for each of the nations within the range of *G. gangeticus*, and their average score was taken as the overall exposure ranking for the species. For data sources, see Table S15 of Supporting information. H, high vulnerability; L, low vulnerability (within study scope); M, moderate vulnerability.

2.5 | Worked example: *Glyphis gangeticus*

The process of applying ESA and ESP assessments is demonstrated here using *G. gangeticus*. The first step of the ESA was to evaluate the vulnerability of the species to the exposure to environmental threats. The three water quality factors (Figure 3) were first ranked using the criteria outlined in Table 8. The most precautionary of the three ranks was then taken as the water quality attribute ranking for each nation

(Figure 3): for example, Pakistan yielded a low ranking for human population density and mining intensity, and a moderate ranking for agricultural land use, and is therefore deemed to be at moderate vulnerability to threats associated with water quality. The remaining attributes (damming and climate change) were then ranked, and the most conservative ranking of all three attributes was used to determine the exposure ranking for that nation (Figure 3): for example, Pakistan is ranked with high vulnerability for damming and climate change, and thus Pakistan is given a high exposure vulnerability overall.

To rank exposure for *G. gangeticus*, the average of the five nations within its range was calculated based on numerical values assigned to the high, moderate, and low vulnerability rankings (high = 1, moderate = 0.67, and low = 0.33), as follows:

$$\textit{Exposure vulnerability} = \frac{1+1+1+1+0.67}{5};$$

$$\textit{Exposure vulnerability} = 0.93.$$

This yields a score of 0.93 and an overall ranking of high for the exposure component.

The next stage in the ESA was evaluating the sensitivity and adaptability components. The two attributes for sensitivity (rarity and habitat specificity) were ranked according to the descriptive criteria laid out in Table 8, yielding rankings of high and low, respectively (Figure 3). Using the most conservative ranking of the two, this gave *G. gangeticus* a ranking of high for the sensitivity component.

To assess the first attribute of the adaptability component, distributional flexibility, three factors were considered: the number of regions (ranked high), latitudinal range (ranked moderate), and salinity tolerance (ranked low) (Figure 4). Using the most conservative ranking for these factors, the vulnerability associated with adaptability was deemed to be high for *G. gangeticus*.

The three component rankings were then integrated (Figure 2), yielding an overall ESA ranking of high, categorizing *G. gangeticus* as a top priority for conservation against environmental threats.

The ESP assessment was then carried out, beginning with evaluating exposure to fisheries threats. Two attributes were considered and, as in the ESA, were ranked for each of the nations where *G. gangeticus* occurs. Once again, the most conservative ranking of the two attributes was used to determine each nation's ranking for the exposure component, with India and Pakistan deemed to be at low vulnerability among the study nations, Bangladesh ranked as moderate vulnerability, and with Malaysia and Myanmar ranked as high vulnerability (Figure 5). To obtain a single fisheries exposure vulnerability ranking for *G. gangeticus*, the average of the five nations within its range was calculated based on numerical values assigned to the high, moderate, and low vulnerability rankings (high = 1, moderate = 0.67, and low = 0.33), as follows:

$$\textit{Exposure vulnerability} = \frac{0.33+0.33+0.67+1+1}{5};$$

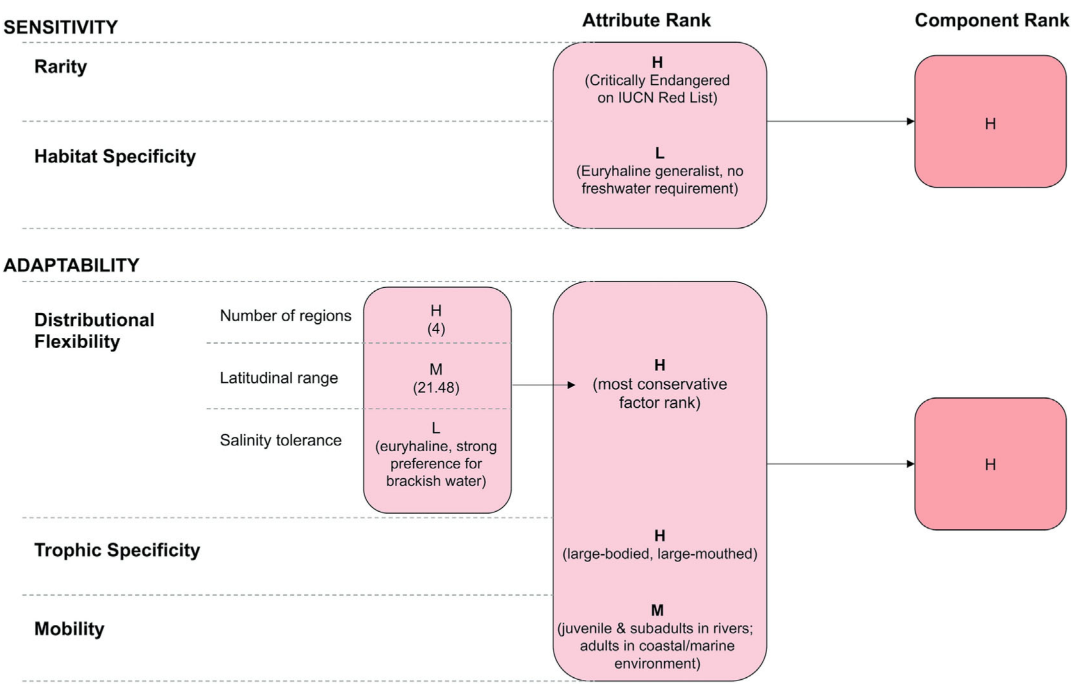

FIGURE 4 Diagram demonstrating how the rankings for sensitivity and adaptability components were obtained for *Glyphis gangeticus*. The diagram contains raw data and rankings from each attribute (including three factors considered within distributional flexibility) used to determine the two component ranks. For data sources, see Table S5 in Supporting information. H, high vulnerability; L, low vulnerability, within study scope; M, moderate vulnerability.

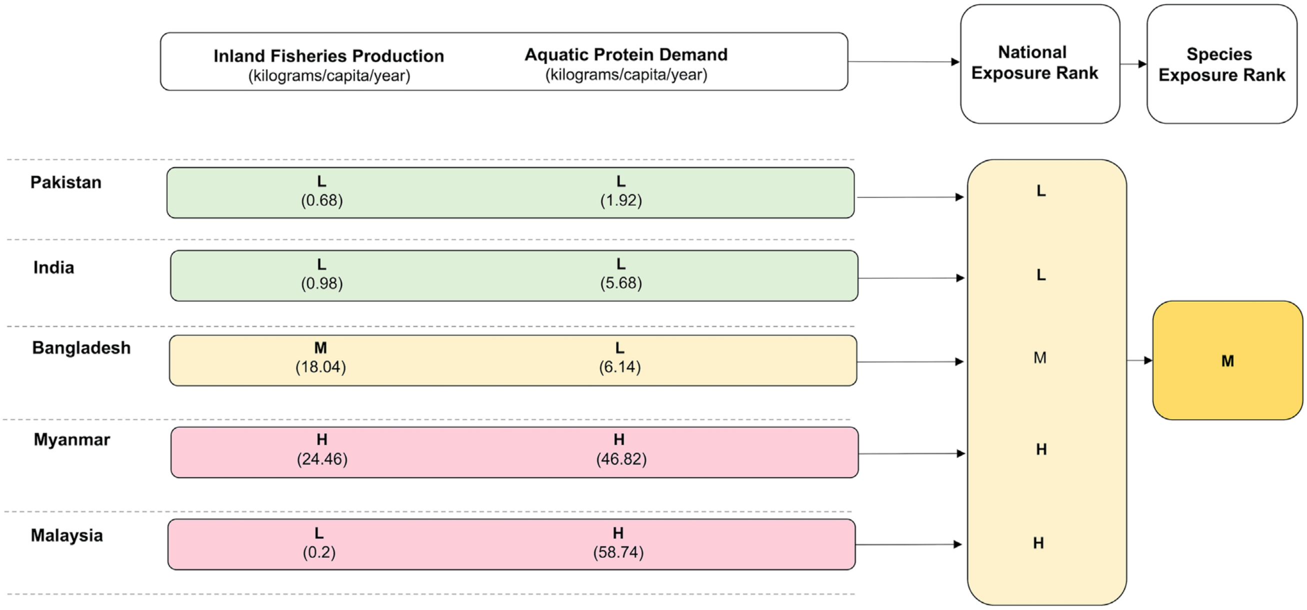

FIGURE 5 Fisheries threat exposure component data and rankings for the three attributes (including the three factors considered within water quality), informing the overall component ranking for each of the nations within the range of *Glyphis gangeticus*. For data sources, see Table S16 in Supporting information. H, high vulnerability; L, low vulnerability, within study scope; M, moderate vulnerability.

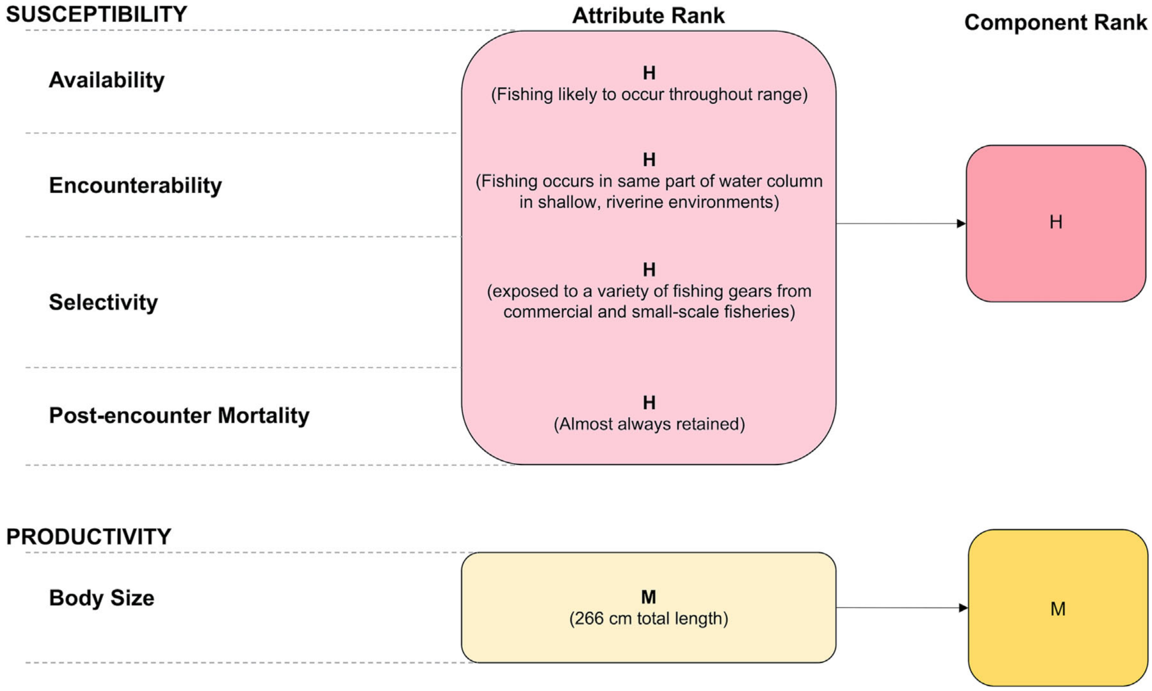

FIGURE 6 Susceptibility and productivity component data and rankings for all attributes and factors, informing the overall component rankings for *Glyphis gangeticus*. H, high vulnerability; L, low, within study scope; M, moderate vulnerability.

$$\textit{Exposure vulnerability} = 0.67.$$

This yields a score of 0.67 and an overall ranking of moderate for the fisheries exposure component.

The four attributes of the second ESP component, susceptibility, were all ranked 'high' (Figure 6). Given their nested nature, the rankings for these attributes were assigned numerical values (high = 1, moderate = 0.67, and low = 0.33) and multiplied to give the component ranking of 'high' (1 × 1 × 1 × 1 = 1). The final component, productivity, was based on just one attribute, body size, with *G. gangeticus* ranked at moderate vulnerability.

TABLE 10 Results of the environmental susceptibility analysis, including ranking for all attributes (*italics*) considered in each component (**bold**), and overall rank for each freshwater obligate and euryhaline generalist species.

			Sensitivity			Adaptability				
	Species	Exposure	Rarity	Habitat specificity	Sensitivity vulnerability	Distributional flexibility	Trophic specificity	Mobility	Adaptability vulnerability	ESA ranking
Freshwater obligates	*Fluvitrygon kittipongi*	**H**	*M*	*H*	**H**	*H*	*L*	*H*	**H**	**H**
	Fluvitrygon oxyrhynchus	**H**	*M*	*H*	**H**	*H*	*L*	*H*	**H**	**H**
	Fluvitrygon signifer	**H**	*M*	*H*	**H**	*H*	*L*	*H*	**H**	**H**
	Hemitrygon bennetti	**H**	*H*	*H*	**H**	*H*	*L*	*H*	**H**	**H**
	Hemitrygon laosensis	**H**	*H*	*H*	**H**	*H*	*L*	*H*	**H**	**H**
	Makararaja chindwinensis	**H**	*H*	*H*	**H**	*H*	*L*	*H*	**H**	**H**
Euryhaline generalists	*Carcharhinus leucas*	**H**	*M*	*L*	**M**	*L*	*H*	*L*	**H**	**M**
	Glyphis gangeticus	**H**	*H*	*L*	**H**	*H*	*H*	*M*	**H**	**H**
	Glyphis garricki	**H**	*M*	*L*	**M**	*H*	*H*	*M*	**H**	**M**
	Glyphis glyphis	**H**	*M*	*L*	**M**	*H*	*H*	*M*	**H**	**M**
	Pristis pristis	**H**	*H*	*M*	**H**	*M*	*H*	*M*	**H**	**H**
	Urogymnus dalyensis	**H**	*L*	*M*	**M**	*H*	*M*	*M*	**H**	**M**
	Urogymnus polylepis	**H**	*M*	*M*	**M**	*L*	*M*	*L*	**M**	**M**

Note: For details of raw data used in calculations for each species, see Tables S1–S15 in Supporting information.

Abbreviations: ESA, exposure sensitivity adaptability; H, high vulnerability (red); L, low vulnerability, relative to other species considered in the present study (green); M, moderate vulnerability (yellow).

As with ESA, the scores of the three ESP components were integrated (Figure 2), producing an overall ranking of moderate and categorizing *G. gangeticus* as priority 1 for conservation against fisheries threats.

3 | RESULTS

3.1 | ESA

All freshwater obligate species were found to be highly vulnerable owing to environmental threats, with high levels of exposure, high sensitivity because of a high degree of habitat specificity, and poor adaptability because of their limited mobility (Table 10). *Fluvitrygon kittipongi*, *Fluvitrygon oxyrhynchus*, and *Fluvitrygon signifer* yielded the same results across all attributes, reflecting their similar biology and range. The remaining freshwater obligate species (*H. bennetti*, *Hemitrygon laosensis*, and *Makararaja chindwinensis*) also exhibit high vulnerability, with similar patterns of habitat specificity, distributional flexibility, and mobility (Table 10). Although these species exhibit slightly larger body sizes than *Fluvitrygon* spp., they maintain low trophic specificity. *Hemitrygon bennetti*, *H. laosensis*, and *M. chindwinensis* are highly sensitive owing to their rarity, with the native freshwater distributions of all three species restricted to a single river basin.

Vulnerability to environmental threats was more variable among euryhaline generalist species than among freshwater obligates, with high exposure but generally reduced sensitivity, and with greater variability among the attributes of adaptability (Table 10). The euryhaline generalist species considered in this study are larger bodied than the freshwater obligates, suggesting a greater degree of trophic specificity through increased high trophic level piscivory and reduced taxonomic diversity in their diets, compared with obligate freshwater rays feeding primarily on invertebrates. The ability of euryhaline generalists to travel between fresh and marine waters reduces their sensitivity linked with habitat specificity, and their greater mobility improves their adaptability.

Glyphis gangeticus was ranked as highly vulnerable to environmental threats and deemed highly sensitive because of its rarity. Despite having the same level of habitat specificity to *G. gangeticus*, *C. leucas*, *Glyphis glyphis*, and *Glyphis garricki* were ranked as moderately vulnerable to environmental threats, owing to their moderate rarity. *Urogymnus dalyensis* and *Urogymnus polylepis* were found to be moderately vulnerable to environmental threats, with high exposure and moderate sensitivity. The difference between these species was their adaptability, with *U. dalyensis* exhibiting less distributional flexibility and mobility than the more widely distributed *U. polylepis*. *Pristis pristis* was deemed to be highly vulnerable to environmental threats, attributed to its high exposure and rarity, and being a large-bodied elasmobranch with high trophic specificity.

3.2 | ESP

The freshwater obligate species considered in this study were predominantly found to have low vulnerability to fisheries threats (Table 11). All freshwater obligate species except *H. laosensis* are exposed to high levels of fishing pressure (based on Funge-Smith, 2018), and all are highly susceptible to all factors influencing fisheries mortality. However, owing to the small body size of all freshwater obligate species (excluding *H. bennetti*), these species are considered to have higher productivity compared with other species, and thus their overall ESP ranking was lower than the euryhaline generalist species.

The euryhaline generalist species considered in this study are generally exposed to greater fishing pressure than the freshwater obligates, and are less productive owing to their larger body size (Table 11). The three *Glyphis* species share similar biological traits; however, *G. glyphis* and *G. garricki* were both rated as having lower vulnerability to fisheries pressures, whereas *G. gangeticus* was found to be at moderate vulnerability owing to greater susceptibility. This species is exposed to a greater variety of fishing gear, and is more likely to be retained than *G. glyphis* or *G. garricki*, considering the respective ranges of these species. *Urogymnus dalyensis* is less susceptible to fisheries mortality because of low selectivity and low post-encounter mortality. Conversely, the closely related *U. polylepis* was ranked as highly vulnerable across all attributes and components. *Urogymnus polylepis* is exposed to high fishing pressure across a range of fishing gear, with a high likelihood of being retained and with low productivity, as suggested by its large body size. *Pristis pristis* and *C. leucas* were both found to be moderately vulnerable to fishery pressures, relative to other species considered, as despite having low productivity these species are exposed to moderate fishing pressure in the study area and are sometimes retained. *Pristis pristis*, although often retained for its valuable fins and rostra in parts of its range, is well protected in its extensive Australian range, and is not considered to be commonly retained there.

3.3 | Geographical trends

Non-marine elasmobranchs in Myanmar and Cambodia were found to be most vulnerable, as they are exposed to high rates of damming, climate change, and inland fisheries production. The least vulnerable nation was Papua New Guinea, with seemingly better water quality, lower rates of damming, low inland fisheries production and consumption, and moderate vulnerability to extreme weather events owing to climate change impacts.

The majority of Indo-West Pacific nations where non-marine elasmobranchs occur are exposed to a high degree of environmental pressure, with the most widespread threat being climate change (Table 12). Of the 14 nations considered, 11 were ranked with high vulnerability and three were ranked with moderate vulnerability for extreme weather events owing to climate change. Damming was

TABLE 11 Results of exposure susceptibility productivity (ESP) analysis, including the ranking for all attributes (*italics*) considered in each component (**bold**), and overall rank for each freshwater obligate and euryhaline generalist species.

			Susceptibility						
	Species	Exposure	Availability	Encounterability	Selectivity	Post-encounter mortality	Susceptibility vulnerability	Productivity	Overall ESP ranking
Freshwater obligates	*Fluvitrygon kittipongi*	**H**	*H*	*H*	*H*	*H*	**H**	**L**	**L**
	Fluvitrygon oxyrhynchus	**H**	*H*	*H*	*H*	*H*	**H**	**L**	**L**
	Fluvitrygon signifer	**H**	*H*	*H*	*H*	*H*	**H**	**L**	**L**
	Hemitrygon bennetti	**H**	*H*	*H*	*H*	*H*	**H**	**M**	**M**
	Hemitrygon laosensis	**M**	*H*	*H*	*H*	*H*	**H**	**L**	**L**
	Makararaja chindwinensis	**H**	*H*	*H*	*H*	*H*	**H**	**L**	**L**
Euryhaline generalists	*Carcharhinus leucas*	**M**	*H*	*H*	*H*	*M*	**M**	**H**	**M**
	Glyphis gangeticus	**M**	*H*	*H*	*H*	*H*	**H**	**M**	**M**
	Glyphis garricki	**M**	*H*	*H*	*L*	*L*	**L**	**M**	**L**
	Glyphis glyphis	**M**	*H*	*H*	*L*	*L*	**L**	**M**	**L**
	Pristis pristis	**M**	*H*	*H*	*M*	*M*	**M**	**H**	**M**
	Urogymnus dalyensis	**M**	*H*	*H*	*L*	*L*	**L**	**M**	**L**
	Urogymnus polylepis	**H**	*H*	*H*	*H*	*H*	**H**	**H**	**H**

Note: For details of raw data used in calculations for each species, see Tables S1–S14 and S16 in Supporting information.
Abbreviations: H, high vulnerability (red); L, low vulnerability, relative to other species considered in the present study (green); M, moderate vulnerability (yellow).

TABLE 12 Exposure of each nation (from west to south east) considered in the study to environmental and fishing pressures, including rankings for individual attributes (*italics*) and overall rankings (**bold**) for both threat types.

Nation	Water quality	Damming	Climate change	Environmental threats	Per capita aquatic protein consumption	Inland fisheries production	Fisheries threats
Pakistan	*M*	*H*	*H*	**H**	*L*	*L*	**L**
India	*H*	*L*	*H*	**H**	*L*	*L*	**L**
Bangladesh	*H*	*L*	*H*	**H**	*L*	*L*	**L**
Myanmar	*L*	*H*	*H*	**H**	*H*	*H*	**H**
Indonesia	*H*	*L*	*M*	**H**	*M*	*L*	**M**
Malaysia	*L*	*L*	*M*	**M**	*H*	*L*	**H**
Thailand	*M*	*M*	*H*	**H**	*M*	*L*	**M**
Laos	*L*	*H*	*H*	**H**	*L*	*L*	**L**
Cambodia	*H*	*H*	*H*	**H**	*M*	*H*	**H**
Vietnam	*M*	*H*	*H*	**H**	*M*	*L*	**M**
China	*H*	*H*	*H*	**H**	*M*	*L*	**H**
Brunei	*H*	*L*	*L*	**H**	*M*	*H*	**H**
Papua New Guinea	*L*	*L*	*M*	**M**	*L*	*L*	**L**
Australia	*H*	*L*	*H*	**H**	*M*	*L*	**M**

Note: For details of raw data used in calculations for each species, see Tables S15 and S16 in Supporting information.
Abbreviations: H, high vulnerability (red); L, low vulnerability, relative to other nations considered in the present study, with the exception of 'climate change', which considered global data (green); M, moderate vulnerability (yellow); grey cells denote attributes ranked high as a precaution because of a lack of data.

found to be widespread across mainland Southeast Asia, particularly in the Mekong River basin across Laos, Thailand, and Cambodia, with downstream consequences likely in Vietnam. The Pearl River basin in China was also heavily dammed.

Of the three factors defining water quality, agriculture was most intense in India, Bangladesh, China, and Australia (Table S15, Supporting information). Mining was most prevalent in China and Indonesia, although both Brunei and Cambodia were also considered to be at high vulnerability because of poor water quality, as the precautionary principle was applied owing to a lack of data on the extent of mining in these nations. Human population density was highest in Bangladesh, with India ranked as moderate, and with all other nations ranked lower in comparison.

Of the nations assessed, inland fishing pressure was lowest in Bangladesh, India, Laos, Pakistan, and Papua New Guinea, and moderate or high in all other nations (Table 12). However, the documented inland fisheries production is low in all nations, excluding Myanmar and Cambodia, which were ranked high, and Brunei was also ranked high owing to a lack of data. Thus, the overall fisheries threat rankings in most nations were based on moderate levels of aquatic protein consumption, which helps to capture unreported fishing effort.

3.4 | Overall conservation priority

Considering the results from both the ESA and the ESP, *G gangeticus*, *H. bennetti*, *P. pristis*, and *U. polylepis* were categorized as priority 1 for conservation (Table 13). All freshwater obligate rays, along with *C. leucas*, were categorized as priority 2 for conservation, and the remaining euryhaline generalists (*G. garricki*, *G. glyphis*, and *U. dalyensis*) were categorized as priority 3.

4 | DISCUSSION

A key objective of this study was to adapt existing vulnerability assessment frameworks to the complex and data-poor context of non-marine elasmobranch species in the Indo-West Pacific. Building on robust and widely used ESA and ESP frameworks (e.g. Stobutzki et al., 2002; Chin et al., 2010; Hobday et al., 2011; Walker et al., 2021), the key factors and attributes were identified for each component, based on the biological and ecological data available across all study species. This study provides a template that may be applied to other data-poor species or areas, allowing users to easily conceptualize the framework, understand the significance of each attribute, identify the relevant biological and ecological information, and apply the available data for their given scenario.

The results of the ESA–ESP analysis generally reflect the IUCN Red List status of the study species. Species ranked as priority 1 were mostly listed as Critically Endangered on the IUCN Red List (e.g. *G. gangeticus*, *P. pristis*, and the freshwater population of *H. bennetti*, whereas *U. polylepis* was also ranked as priority 1). Species ranked as priority 2 are all listed as Endangered, with the exceptions of *M. chindwinensis*, which is listed as Data Deficient, and *C. leucas*, which is listed as Vulnerable. Species ranked as priority 3 were those

TABLE 13 Overall relative conservation priority of all species, based on the vulnerability assessments for both ESA and ESP assessments.

Species	Ecological group	ESA relative conservation priority	ESP relative conservation priority	Overall relative conservation priority	IUCN Red List status
Glyphis gangeticus	EG	H	M	1	CR
Hemitrygon bennetti	FO	H	M	1	VU[a]
Pristis pristis	EG	H	M	1	CR
Urogymnus polylepis	EG	M	H	1	EN
Carcharhinus leucas	EG	M	M	2	VU
Fluvitrygon kittipongi	FO	H	L	2	EN
Fluvitrygon oxyrhynchus	FO	H	L	2	EN
Fluvitrygon signifer	FO	H	L	2	EN
Hemitrygon laosensis	FO	H	L	2	EN
Makararaja chindwinensis	FO	H	L	2	DD
Glyphis garricki	EG	M	L	3	VU
Glyphis glyphis	EG	M	L	3	VU
Urogymnus dalyensis	EG	M	L	3	LC

Note: The table also includes the ecological category of each species (freshwater obligate, FO; euryhaline generalist, EG) and its IUCN Red List status (Critically Endangered, CR; Endangered, EN; Vulnerable, VU; Least Concern, LC; Data Deficient, DD).
Abbreviations: ESA, exposure sensitivity adaptability; ESP, exposure susceptibility productivity; H, high vulnerability; L, low vulnerability, relative to other species considered in the present study; M, moderate vulnerability. Red cells denote species categorised as priority 1 for conservation, yellow cells denote species categorised as priority 2, and green cells denote species categorised as priority 3.
[a]The overall IUCN extinction risk for *H. bennetti* considers its marine conspecific populations. The closed freshwater population of this species assessed here has undergone population reductions of ≥80% over the past three generations, consistent with Critically Endangered criteria (Rigby et al., 2020).

listed as either Vulnerable or of Least Concern. Although *H. bennetti* is listed as Vulnerable on the IUCN Red List, the isolated freshwater population considered in this study has experienced severe population declines (80%–90%), and in line with Criterion A2 (population size reduction) would probably meet the IUCN Red List criteria for Critically Endangered, if assessed independently from conspecifics elsewhere in the species range (Rigby et al., 2020). Therefore, the results of the ESA and ESP assessments are generally congruent with the IUCN Red List status of each species, whereby the most vulnerable species identified in the present study are those currently facing the highest risks of extinction.

In interpreting these results, it is important to consider the differences between vulnerability assessments (i.e. ESA and ESP) and extinction risk assessments (i.e. IUCN Red List). The IUCN Red List uses a range of quantitative criteria to assess the risk of extinction of a taxon through changes in population size over a standardized time frame, or through considerations of restricted geographical range and population fragmentation (IUCN, 2022b). In this sense, the IUCN Red List tracks quantifiable changes in population size or species range in response to threats (Collen et al., 2016), whereas vulnerability assessments consider the exposure and vulnerability of the species to those threats and the potential to affect future population size or geographical range. Although only *M. chindwinensis* has been assessed as Data Deficient on the IUCN Red List, most of the study species are poorly studied, and the actual threats to their populations are data limited (Grant et al., 2019; Kyne & Lucifora, 2022). Therefore, the conservation management value of the present ESA–ESP assessment is that it has been able to consider a range of direct and indirect data sources to provide a 'best indication' of the vulnerability of each species to the relevant threats to which they are exposed, and has used alternative data sources to the IUCN Red List assessments. In doing this, these vulnerability assessments are complementary to the IUCN Red List assessments as they have: (i) identified the key threats that species face; (ii) identified the factors (biological and environmental) that contribute to their vulnerability; (iii) clarified key knowledge gaps; and (iv) prioritized future research and management requirements. In addition, this study also rendered a large volume of data to profile the environmental and fisheries pressures for the nations where these species occur.

4.1 | Environmental threats

The species most vulnerable to environmental threats were the freshwater obligate species. This can be explained by their low salinity tolerance and confinement to freshwater habitats, making them highly sensitive to river habitat degradation (Kyne & Lucifora, 2022). Poor distributional flexibility and limited mobility also restrict their capacity to relocate. The key difference among freshwater obligate species was the increased rarity of *H. bennetti*, *H. laosensis*, and *M. chindwinensis*, which are each restricted to a single river basin, compared with the more widely distributed *Fluvitrygon* species that occur in fragmented populations across the study area (Grant et al., 2019). This aligns with a general pattern of greater extinction risk among freshwater fishes with small endemic ranges (Purvis et al., 2000; De Silva, Abery & Nguyen, 2007).

In contrast with the freshwater obligate species, only two euryhaline generalist species (*G. gangeticus* and *P. pristis*) were also found to be ranked as highly vulnerable to environmental threats. Although *P. pristis* can tolerate a broad salinity range, it occupies fresh water for the first 4 or 5 years of life, before migrating downstream to marine environments (Thorburn et al., 2007). This catadromous-like life history requirement may restrict its ability to adapt to local environmental pressures, which has affected its sensitivity and adaptability in the present study. Meanwhile, the key factor leading to high vulnerability to environmental threats for *G. gangeticus* was its rarity, as it is highly depleted throughout its small and fragmented range (Rigby et al., 2021).

Habitat use patterns, including the ability to move between marine and freshwater environments, were a key characteristic in determining the vulnerability of a species to environmental threats for euryhaline generalists. When faced with poor conditions such as pollution or eutrophication, euryhaline generalists were considered to have a much greater potential to respond by relocating via coastal waters to a nearby river, although we note that this is not something that has yet been observed. For example, *Glyphis* species in Australia and Papua New Guinea display high site fidelity (Lyon et al., 2017; Dwyer et al., 2020; Grant et al., 2023) and movement to neighbouring rivers is considered to be uncommon (Kyne et al., 2021a). The greatest flexibility in this respect probably occurs in *C. leucas* that, unlike *Glyphis* species, has been observed to use a range of environments from freshwater to marine as juveniles (Heupel et al., 2010; Ballantyne & Fraser, 2012). Although *U. dalyensis* and *U. polylepis* and were both deemed to be moderately vulnerable to environmental threats, *U. dalyensis* was considered less adaptable owing to its increased population site fidelity within rivers, compared with *U. polylepis*, which seems to occur more commonly in inshore marine environments as well as in rivers (Kyne, 2016; Grant et al., 2021b). Our results support the suggestion of Compagno & Cook (1995) that obligate freshwater elasmobranchs with limited geographical ranges, together with euryhaline generalists that require access to freshwater environments as juveniles (e.g. *P. pristis*), have greater vulnerabilities to riverine environmental pressures compared with euryhaline generalist species that can occur across wider estuarine salinity gradients throughout their life histories.

4.2 | Fisheries threats

The main attributes driving the susceptibility of a species to fisheries threats were the productivity of the species and the behaviour of fishers in each nation. The freshwater obligates have relatively low vulnerability to fisheries compared with the other species assessed. Although most of the freshwater obligate species are highly exposed to fishery pressures, and are all highly susceptible to fisheries mortality, they were also found to be the most productive of all species considered. However, this finding is founded on the assumption that their small body size indicates higher productivity and greater tolerance to withstand fishing mortality (this assumption is further discussed in Section 4.4.2). In support of this assumption, Lucifora, Scarabotti & Barbini (2022) found that the maximum body size appears to be a good general indicator of productivity for potamotrygonid rays in South America. However, it should be noted that smaller bodied potamotrygonid species have still been subject to fisheries-induced population declines (Lucifora et al., 2017). This highlights the need for greater research into the life history and demography of freshwater rays to estimate productivity accurately and to provide informed fisheries management advice.

The interspecific differences in fisheries vulnerability between *Urogymnus* species and *Glyphis* species highlight the differences in fishery characteristics within the nations considered in the study region. As with environmental threats, *G. gangeticus* is more vulnerable to fisheries pressure than *G. garricki* or *G. glyphis*, despite their similar biology and level of exposure. This may be attributed to geographical differences in the respective ranges of the species, and related differences in national fishery characteristics and uses of non-marine elasmobranchs (Lucifora et al., 2019). *Glyphis gangeticus* has a fragmented distribution across Pakistan, India, Malaysia, and Borneo, where it is caught as by-catch in both commercial and small-scale fisheries, and is retained for its meat, fins, and skin (Rigby et al., 2021). *Glyphis glyphis* and *G. garricki*, although caught and retained in Papua New Guinea (Grant et al., 2021d), are also protected and are not as commonly caught or retained in their expansive northern Australian range (Kyne et al., 2021b). Similarly, *U. dalyensis* is also distributed in northern Australia and Papua New Guinea, and was the only other euryhaline generalist species considered to have low vulnerability to fishery threats. Although it is likely that this species is exposed to a moderate degree of fishing activity, particularly recreational, it is not known to be retained commonly in Australia (Kyne, 2016). This contrasts with *U. polylepis*, the only species found to be highly vulnerable to fisheries pressure. Distributed throughout much of southern and Southeast Asia, *U. polylepis* is exposed to a broad range of fishing gear, and is frequently retained either for food or the aquarium trade throughout its entire range (Grant et al., 2021b).

Pristis pristis was considered to be moderately vulnerable to fishing pressures. This may appear to contradict its Critically

Endangered IUCN Red List status (Kyne, Carlson & Smith, 2013), and its listing as the highest ranked species on the Evolutionarily Distinct and Globally Endangered species list (EDGE, https://www.edgeofexistence.org). Particularly unexpected was its moderate ranking for fisheries selectivity, as the species is known to be highly susceptible to capture in nets owing to its long toothed rostrum (Espinoza et al., 2022). Although *P. pristis* undoubtedly has exceptionally high susceptibility to net-based fishing activity, which probably outweighs its lack of susceptibility to other fishing gear commonly used in river environments (e.g. line, trap, and electro-fishing), this was not captured by the descriptive criteria used to assess the attribute, which considers only the variety of gears to which a species is exposed within its range. This result highlights a limitation of the framework (which is discussed further in Section 4.4). However, it should be noted that *P. pristis* was still listed in the highest overall conservation priority ranking, which is in line with its international conservation concern. This demonstrates that although the present study is limited in some respects, the overall conservation priority rankings delivered intuitive results that correspond with other conservation assessments (e.g. IUCN Red List and EDGE) using alternative data.

4.3 | Geographical trends

With the exception of Malaysia and Papua New Guinea, all of the nations considered in this study were found to have high levels of environmental threats. The Pearl River in China was found to be most under pressure, with extremely high levels of damming, poor water quality from mining and agriculture, and severe projected climate change impacts. Overall, climate change was found to be the most widespread threat affecting these species, and action is needed to address the severity of future climate change and the forecasted environmental degradation impacts on freshwater environments (Lennox et al., 2019). Potential impacts include changes to the frequency and intensity of drought and flood events and exacerbating the physiochemical variability of these environments (Lennox et al., 2019; Tickner et al., 2020). Globally, 10 of the 14 nations considered are in the top one-third of nations predicted to suffer economic and social losses from extreme weather events driven by climate change (Eckstein & Kreft, 2020). This indicates a need to direct local management efforts to focus on mitigating the impact of other sources of mortality and environmental degradation, such as damming, mining, and fisheries, so that population resilience is maximized to counter the occurrence of unpredictable events driven by climate change. The present study indicates that the greatest imperative exists for Pakistan, Myanmar, the Pearl River in China, and the Mekong River basin (Laos, Thailand, Cambodia, and Vietnam). The mitigation of damming impacts into the future is particularly important in the Mekong River basin, where a large number of hydropower dams are planned for construction (De Silva, Abery & Nguyen, 2007; Grill et al., 2019). Little is known about the extent to which fish passage facilities can be designed to be effective for freshwater elasmobranchs.

The nations with the highest fisheries threats are Myanmar, Cambodia, and Malaysia, and concerted efforts to protect non-marine elasmobranchs in these nations are needed to reduce continuing population declines. This is particularly significant for the conservation of *M. chindwinensis*, a poorly documented species considered to be endemic to the Chindwin River in Myanmar (Roberts, 2007). The species is Data Deficient on the IUCN Red List, with only two specimens scientifically recorded to date (Grant et al., 2021a). However, given its rarity, and the apparent local extinctions of other non-marine elasmobranch species in the Ayeyarwady River basin (e.g. *G. gangeticus* and *P. pristis*), *M. chindwinensis* is likely to be at risk of extinction owing to fisheries exploitation and requires concerted conservation attention (Grant, Mizrahi & Mather, 2022).

4.4 | Considerations for future application

There are several general considerations in applying the adapted ESA–ESP framework developed in this study. The present study has a broad scope (13 species distributed across 14 nations of the Indo-West Pacific) and provided an overview of the vulnerability of each non-marine elasmobranch species, and the nations with highest vulnerability required the use of broad data sources. The intention is to help guide future allocation of conservation effort and resources to high-priority species and nations. It does not, however, precisely capture fine-scale information, and national conservation priorities are likely to be further refined through localized and species-specific research activities.

To maintain consistency across such a broad study area, widely available measures of environmental degradation factors (e.g. intensity of damming; Grill et al., 2019) and fisheries pressure indicators such as inland fisheries production (Funge-Smith, 2018) were used. In the absence of more detailed information to inform rankings for each exposure attribute, quantitative categories were based on dividing the range of values across study nations into equal thirds. This follows the approach used by Chin et al. (2010) and Walker et al. (2021) and allows a comparison of relative vulnerability among study species; however, it also results in a loss of detail for particular attributes. For example, owing to the extremely high human population density of Bangladesh, it was the only nation ranked as high for this attribute. Other nations were clustered into lower rankings, and a result of this was that Australia was assigned the same ranking as comparatively densely populated nations such as Pakistan and Vietnam. Broad-scale risk or vulnerability assessment is a necessary first step towards guiding the allocation of conservation resources in data-poor situations (such as encountered at present for non-marine elasmobranchs). It would be improved by greater research into how widely available data can be applied to accurately reflect real-world situations (Harry & Braccini, 2021).

Another element not captured by this assessment is governance. Vulnerability assessments only consider the exposure of species to environmental and human threats, and do not incorporate management actions in response to those threats (Chin et al., 2010; Walker et al., 2021). It is well known that weak governance structures and systems (e.g. leading to issues such as corruption, weak regulations, poor compliance, and limited enforcement) are often related to biodiversity loss (Smith et al., 2003) and have been specifically implicated in the endangerment of habitat and species (Ayambire & Pittman, 2022). In some cases, the existing national-level policy may be acting to ameliorate threats considered in this study. For example, *F. oxyrhynchus*, *F. signifer*, and *U. polylepis* are protected from targeted capture and retention in Indonesia under the Ministry of Environment and Forestry decree no. P.20/2018 and the Ministry of Marine Affairs and Fisheries decree no. 1/2022; however, awareness and compliance with these protections are low (Iqbal et al., 2020). At present, there is a lack of information on the efficacy of species and environmental protections in the nations included in this study. Future efforts that explore and consider the role of governance could be valuable for better capturing the vulnerability of different species on a regional basis.

In addition, the framework does not account for species such as *P. pristis*, which possess unique morphological traits influencing their interactions with fishing gear. For example, when determining trophic specificity, the criteria do not account for the rostrum of *P. pristis*, which may be used to stun larger fish (Wueringer et al., 2012), potentially expanding its range of prey items compared with the other species considered. The rostrum also disproportionately increases the catchability of *P. pristis* in net fisheries (Dulvy et al., 2016), although most other species ranked higher in selectivity as various gears were considered, and no weighting of the specific susceptibility to certain gears was used in calculations. As such, future applications of the framework could account for species that are uniquely susceptible to particular fishing gear (e.g. sawfishes), either through modified descriptive criteria, or a logic rule. However, caution is needed to avoid the introduction of biases in data-poor situations. Similarly, detailed information on some aspects of the biology and ecology of the species could not be included in the assessment, to maintain consistency with lesser studied species. For example, physiological studies have provided precise data on the salinity tolerances of *F. signifier* in laboratory environments (Tam et al., 2003); however, these data were not available for other freshwater obligates and were therefore excluded.

To overcome limitations of broad data uses and applications, the next step would be to conduct a more spatially or taxonomically focused analysis. The focus may be on a selection of the most vulnerable species, nations, or individual river basins. The ability to investigate local environmental and fisheries pressures in more detail would provide more meaningful results for management at the local or national scale. For example, in one reach of the Mekong River alone there are more than 40 different fishing gears used (Phen & Nam, 2011). It should be noted that this assessment does not account for the sublethal impacts of environmental stressors on the species, and only accounts for the increased mortality resulting from direct impacts or reductions in fitness. For example, Lear et al. (2020) demonstrated how the magnitude of rainfall in the wet season can affect the body condition of juvenile *P. pristis* in the dry season, and such sublethal effects may influence population dynamics.

4.4.1 | ESA assessment

There are several limitations to the attributes representing exposure to environmental threats in the ESA assessment. First, when assessing damming intensity, all dams were considered equal, although in reality this is not the case. The type (e.g. hydropower or irrigation), capacity, and location of the dam within the river basin can all influence how it affects local species (Dudgeon, 2002; He et al., 2019). Furthermore, dams located in the main stem of a river basin have a larger impact on connectivity in the river, inhibiting migrations as well as altering flow regimes and water quality. This effect would be particularly strong in dams located closer to river mouths, limiting the availability of freshwater habitats not only through blockages of migration, but also through saltwater intrusions linked with reduced freshwater flows (Gardner & Finlayson, 2018). For example, the range of *F. signifer* in the Perak River, Peninsular Malaysia, is severely limited by the Chendoroh Reservoir and tidal intrusion from the sea (Grant et al., 2021c). In future applications, it may be possible to consider the positioning of dams and their potential for differing magnitudes of impact. Second, the environmental impact of a mine may depend on its spatial footprint, extraction/production volume, the integrity of a tailings dam, or its waste products (particularly chemicals used or leached in ore extraction and processing). The environmental protections imposed on the mine and how well these are adhered to play a major part in its environmental impact (Storey et al., 2009). With no universal measure of the environmental impact of mining at the scale of this study, this study used the number of mining features, and as with dams, there was no capacity to distinguish between the environmental impacts that different mines pose. More specific measures of mining impact may be possible if assessing a small area, with fewer mines to consider. Third, the best index available to assess the intensity of impacts from climate change in each nation was based on loss of lives and economic impacts, rather than environmental parameters (Eckstein & Kreft, 2020). Greater research is required to understand how climate change will affect freshwater environmental factors such as temperature and rainfall across the Indo-West Pacific (Lennox et al., 2019).

4.4.2 | ESP assessment

There are also some considerations regarding the productivity component of the ESP analysis. This component was measured using body size as a proxy, based on a known relationship between increasing body size and declining productivity in chondrichthyan species (Dulvy et al., 2014). This, combined with the logic rule that all components are weighted equally and combined multiplicatively, could be superficially interpreted to mean that the smallest bodied species (the freshwater obligate rays) have low vulnerability to fishing (i.e. they are sufficiently productive to withstand or recover from high fishery pressures, despite also being highly susceptible to fisheries mortality). This is not the case. Although it is likely that the smaller bodied ray species are more productive than the larger bodied elasmobranchs, the actual rates of reproduction and natural mortality are not known. As such, it is not clear how they compare with rates of fisheries mortality in these species, a variable which is also unknown. This is a major assumption of the current model. However, the need to make this assumption highlights the need for further research into the life history and fisheries mortalities of these species, so that more informative measures of productivity and fisheries resilience can be estimated. Until better information is available, future applications of this model could benefit from the ability to weight certain components more heavily than others (Stobutzki et al., 2002; Griffiths et al., 2006). The information available, the scope of the study, and the intended level of resolution needed to meet the objective of the study must be considered carefully in such applications.

4.5 | Conclusions and future research

This study has provided a useful indication of the species and nations of highest conservation priority across the Indo-West Pacific. Furthermore, the congruence between the calculated species vulnerabilities and their IUCN Red List status provides confidence that the resulting conservation priority species list is sound and reflects our present, albeit limited, understanding. This is significant as the ESA and ESP assessments are based on alternative data compared with the IUCN Red List assessments. Therefore, the present study has demonstrated the value of vulnerability assessments for data-poor species groups and regions, and their complementary value for more commonly used and considered extinction risk assessments.

This study has also made a valuable contribution to clarifying future research and management requirements for Indo-West Pacific non-marine elasmobranchs. Here we indicate that large-bodied euryhaline species occurring in southern and Southeast Asia are of greatest conservation concern, and coupled with their present extinction risks they require the most urgent conservation attention. There is also considerable concern for freshwater obligate rays in Southeast Asia, which are exposed to high levels of environmental and fishery threats. There is a pressing need to understand the life history of these species to inform their resilience to these threats, and their ability to recover once depleted. Relevant to all species considered in this study was an absence of data on the magnitude of how non-marine environmental threats may be affecting populations. There are many dam infrastructures already in place throughout the Indo-West Pacific, and with further structures planned in the near future there is uncertainty about the cumulative impacts of these activities on non-marine elasmobranchs. There is a need to understand the habitat use patterns of non-marine elasmobranchs in riverine environments so that the maintenance of essential habitat types can be included in habitat management (e.g. restoration) and impact mitigation planning. Furthermore, there is a need to understand population dynamic responses with respect to year-to-year environmental fluctuations (e.g. how the magnitude of the wet season affects populations). This information would allow greater forecasting of potential impacts of extreme weather events and fluctuations resulting from climate change, which is a factor that will have increasing relevance to the conservation management of non-marine elasmobranchs in the future. At present, the future outlook of non-marine elasmobranchs in this region is concerning. Despite its limitations, the framework presented in this study provides a valuable 'big picture' view of the status of non-marine elasmobranchs in the Indo-West Pacific, and will be useful for guiding future research and allocating conservation resources to priority species and nations experiencing high levels of threats.

AUTHOR CONTRIBUTIONS

Michael I. Grant and Andrew Chin conceived the study. Rachel Mather compiled the data and conducted the analysis, with support from Andrew Chin, Cassandra Rigby, and Michael I. Grant. Andrew Chin, Cassandra Rigby, Michael I. Grant, and Rachel Mather interpreted the data. All authors critically revised the methodology and contributed to writing and drafting the article.

ACKNOWLEDGEMENTS

The authors thank the Save Our Seas Foundation for the continued support of our research activities on non-marine elasmobranchs in the Indo-West Pacific. We thank Catherine Sayer and Philip Boon for their time and helpful comments in the revision of this article, and also thank Catherine Sayer for advice on using IUCN Red List data. Open access publishing facilitated by James Cook University, as part of the Wiley - James Cook University agreement via the Council of Australian University Librarians.

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The results are reproducible from the data, equations, algorithms, and cited references presented in article or Supporting information figures and tables.

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How to cite this article: Mather, R., Chin, A., Rigby, C., Cooke, S.J., Fahmi, Haque, A.B. et al. (2024). Murky waters: Assessing the vulnerabilities of Indo-West Pacific non-marine elasmobranchs to inform future conservation planning priorities. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 34(1), e4039. https://doi.org/10.1002/aqc.4039