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Cataloguing and mapping cumulative human impacts on marine biological and functional diversity to inform conservation management

A Dissertation submitted in partial satisfaction of the requirements for the degree Doctor of Philosophy in Environmental Science and Management

by

Casey C. O'Hara

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December 2022

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Casey C. O'Hara

Vita of Casey C. O'Hara

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Education

PhD Environmental Science and Management (2022)
Bren School of Environmental Science & Management, University of California, Santa Barbara
Committee: Dr. Benjamin Halpern (chair), Dr. Halley Froehlich, Dr. Christopher Costello
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Environmental science and management

Researcher, Ocean Health Index (January 2015 – present) National Center for Ecological Analysis and Synthesis - Santa Barbara, CA
AAAS Mass Media Science Fellowship (June 2014 - September 2014) *The Oregonian* - Portland, OR
Program Consultant (June 2013 - August 2013) The School for Examining Essential Questions of Sustainability (SEEQS) Charter School - Honolulu, HI
Masters Thesis Group Project (April 2013 - June 2014) UCSB Bren School - Santa Barbara, CA "Offshore wind energy in the context of multiple ocean uses on the Bermuda platform." Client: Department of Environmental Protection, Bermuda

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- Advanced Data Analysis (ESM244) (Winter 2022)

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- Statistics & Data Analysis for Environmental Science & Management (ESM206) (Fall 2019, 2021)
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Group Project Ph.D. Mentor

- Developing a site suitability framework for shellfish aquaculture on Canada's Pacific Coast (2021-2022)
- Spatial Analysis to Inform Policy Recommendations for Shark and Ray Protection in Mozambique (2020-2021)
- Where the Wind Goes: Motivating Low Ecological Risk Wind Development (2018-2019)

See also *STEM Education and Engineering*

Working groups

- **Functional Interactions and Biodiversity Targets** (April 2021, ongoing) National Center for Ecological Analysis and Synthesis - Santa Barbara, CA
- **Species Vulnerability Working Group (National Philanthropic Trust)** (February 2020) Matadradra Serua, Fiji
- **Coastal Outcomes Working Group (SNAPP)** (April 2019) National Center for Ecological Analysis and Synthesis - Santa Barbara, CA
- **Ocean Futures Working Group (SNAPP)** (July 2018) National Center for Ecological Analysis and Synthesis - Santa Barbara, CA

Relevant technical skills

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- Git/GitHub version control and project management
- MATLAB, Stata, C/C++, HTML, JavaScript, LaTeX
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Publications

- Reyes-García, V., Rodrigo Cámara-Leret, R. , Halpern, B.S., **O'Hara, C.C.**, Renard, D., Zafra-Calvo, N. (Accepted). Biocultural vulnerability exposes threats of culturally important species. PNAS.
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STEM education and engineering

Secondary education experience

- Program Consultant (June 2013 - August 2013) The School for Examining Essential Questions of Sustainability (SEEQS) Charter School - Honolulu, HI
- Science Teacher: Physics, Integrated Science, Engineering & Green Tech (August 2004 - June 2012) Carlmont High School - Belmont, CA
- Education Liaison (November 2009 - December 2009) Amundsen-Scott South Pole Station, Antarctica

Secondary education leadership and honors

- "Where the Wonder Went" documentary short film, Santa Barbara International Film Festival (2014)
- Senior Fellow, Knowles Science Teaching Foundation (2009 - present)
- Teaching Fellow, Knowles Science Teaching Foundation (2004 - 2009)

- Exploratorium Teacher Institute (2004 - 2013)
- Innovative Teacher of the Year, Carlmont High School (2011)
- Amgen Award for Science Teaching Excellence (2011)
- Certification: National Board for Professional Teaching Standards (Science - Adolescent/Young Adult) (2009)

Engineering experience

- Mechanical Engineer (May 2000 - December 2003) St. Jude Medical, Inc. - Sunnyvale, CA
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ABSTRACT

Cataloguing and mapping cumulative human impacts on marine biological and functional diversity to inform conservation management

by

Casey C. O'Hara

People around the world depend on healthy oceans for sustenance, employment, culture, and identity, among other valuable ecosystem services. Anthropogenic impacts from human activity on land and sea, coupled with increasing effects of climate change, drive declines in the health of marine biodiversity throughout the world's oceans, which puts at risk those ecosystem services we value. Effective marine conservation efforts depend on understanding where and to what degree anthropogenic stressors are impacting marine ecosystems. In this dissertation, my colleagues and I catalogued and compared the activities and stressors contributing to marine biodiversity loss, noting those stressors imposing the greatest impacts and those for which risk of impact is poorly understood. We then mapped the footprint of cumulative impacts across ranges of 1,271 threatened and near-threatened marine species on a global scale from 2003 to 2013. We found that on average, species are substantially affected by human stressors across more than half their range, and these impact footprints expanded in scale and increased in intensity over the study period. Building upon a trait-based framework for estimating species vulnerability to human stressors, we expanded our mapping methodology to 21,267 marine animal species, examining patterns of impact through lenses of species richness, functional vulnerability, and representative habitats. I conclude by examining the current literature on applying machine learning methods to estimate species conservation status based on information on species traits, stressors, and environmental conditions. Using a value of information framework, I explore the improvement in expected outcome of conservation management decision based on incorporating additional predictor data or increasing the number of species used to train the model. The resulting conceptual model can help identify optimal investment in data collection and formal assessment of currently data-deficient species to accelerate our understanding of extinction risk of marine biodiversity. In all, the concepts and methods presented here can inform effective, equitable, and ecologically representative conservation efforts toward the goals proposed in the draft of the United Nations Convention on Biological Diversity Post-2020 Global Biodiversity Framework.

Table of contents

Introduction

Humans are an integral part of marine ecosystems, for centuries deriving great benefit from the oceans in terms of food, natural resources, employment, recreation, and cultural value. Our activities on the oceans, coupled with impacts arising from land-based activities, pollutants, and fossil fuel use, increasingly threaten the health and resilience of the biodiverse ecosystems that generate these services [1–3]. But returning to a pristine ocean condition is clearly a non-starter - as we cross the threshold of 8 billion people on the planet, ocean fisheries and aquaculture provide nearly one fifth of high quality animal protein directly for people around the world [4]; ocean-related goods and services generate $2.5 trillion annually, $1.1 trillion from coastal and marine tourism alone [2018 figures, 5]; and oceans absorb nearly a quarter of global carbon emissions [6] and half of excess heat [7], greatly moderating the global impacts of anthropogenic climate change.

My work on the Ocean Health Index [8–10] convinces me that somewhere between an unrealistic vision of pristine oceans and an unacceptable future of collapsed marine ecosystems lies a balance to ensure a sustainable coexistence of people and ocean. To find such a balance we must understand the impacts we are currently imposing and are expected to impose on marine ecosystems in the coming decades, to better design conservation strategies to prevent the worst outcomes while supporting adaptive and resilient ecological and social-ecological communities.

The United Nations (UN) Convention on Biological Diversity (CBD) is working to develop a Post-2020 Global Biodiversity Framework (GBF) for planned adoption in December 2022. One set of targets in the current draft of the GBF focuses on a supertarget of reducing threats to biodiversity, including spatial planning to retain existing intact and wilderness areas, restoration of at least 20% of degraded ecosystems focusing on priority ecosystems, conservation of 30% of land and sea areas through effective, equitable, and ecologically representative networks of protected areas, and management actions to enable the recovery and conservation of species and genetic diversity [11]. The four chapters of my dissertation expand the scope of our understanding of human impacts on marine biodiversity by estimating risk of impact across multiple stressors at the resolution of species.

The first chapter of my dissertation, “Anticipating the Future of the World’s Ocean” [12], published in *Annual Review of Environment and Resources* in October 2022, catalogs a broad suite of anthropogenic stressors, considering the human activities, the stressors they generate, and the impact of those stressors on marine biodiversity. We considered the current impacts, near term trends, and uncertainty in both the estimates and mechanisms by which the stressor harms marine life. Based on this catalog, we highlighted well characterized stressors such as fisheries, shipping, and marine plastics for which further research should prioritize implementation of policy and development of institutions, and highly uncertain stressors such as chemical pollutants, seabed mining, and mesopelagic fisheries where funding should prioritize primary research to characterize vulnerability and potential species- and ecosystem-level impacts.

My second chapter, “At-risk Marine Biodiversity Faces Extensive, Expanding, and Intensifying Human Impacts” [3], published in *Science* in April 2021, leveraged species-specific threat information from IUCN Red List assessments of 1,271 threatened and near-threatened species to map species ranges against distributions of stressors to which the species are vulnerable. Using a time series of stressor distributions from 2003 to 2013, we found that on average, these at-risk species are subjected to impacts across more than half their native ranges, and that these impacts are expanding in scope and increasing in intensity. Understanding where and to what degree human activities and climate change are affecting threatened species is a necessary step in identifying where reactive area-based protections may allow for recovery of heavily impacted marine ecosystems.

My third chapter, “Cumulative human impacts on global marine fauna highlight risk to fragile functional diversity of marine ecosystems,” expands upon chapter 2 by incorporating a trait-based framework to estimate species vulnerability to anthropogenic stressors to allow for mapping of impacts across the ranges of more than 21,000 species. In addition to species-by-species impacts, we examined the spatial distribution of impacts on vulnerable functional groups, and compared the results to an established habitat-based method for ecosystem-level cumulative impact mapping. Where the methods diverge in their estimation of impacts may indicate otherwise healthy ecosystems made fragile by impacts on particularly vulnerable functional groups, potentially suggesting opportunities for targeted interventions rather than broad area-based measures.

Finally, in my fourth chapter, “Improving expected benefit of species conservation status predictions using a value of information framework,” I examine the potential for the use of machine-learning (ML) models to predict species conservation status, i.e., threatened or not threatened, based on a training set of species with known conservation status. The current literature shows the promise of ML methods for faster and more cost-effective understanding of threatened status for data deficient species, but predictive uncertainty may reduce the value of conservation decisions made using these predictions. We can improve predictive accuracy by incorporating additional predictor data in a ML model, and/or by increasing the set of formally assessed species used to train the model, but additional formal assessments and acquisition of new predictor data are both costly. I develop a value of information framework connecting ML predictions to potential conservation outcomes, to conceptually explore the value of reducing uncertainty in conservation status predictions relative to the quality of conservation decisions that result.

All the work presented here relates to that first supertarget of the GBF - reducing threats to biodiversity. Another GBF supertarget calls for ensuring that equitable and sustainable management is designed to meet the needs of people, including food security, nutrition, medicines, and livelihoods, especially for the most vulnerable [11]. Fundamentally, conservation is about preserving our relationship with nature, whether instrumental, cultural, or existence value. Modern conservation philosophy generally strives to account for equity and inclusion to counteract historic institutional injustices in ocean governance, captured in phrases such as "ocean equity" [13] or "blue justice" [14], and enshrined directly into the Post-2020 GBF, goals 3, 9, 13, 20, and 21 among others [11]. While debate continues around the balance of social/environmental win-wins or tradeoffs in marine conservation [15], long-term effectiveness of conservation policy depends on local support which in turn depends on managing social impacts and applying best practices of governance [16]. While the ideas, methods, and data I present in my dissertation can provide valuable guidance toward identifying conservation priorities, they are not sufficient - they must be coupled with understandings of the social, economic, and cultural needs of the people most affected by conservation decisions to provide the greatest benefits from conservation action.

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Anticipating the future of the world's ocean

Casey C. O'Hara, Benjamin S. Halpern

Abstract

Oceans play critical roles in the lives, economies, cultures, and nutrition of people globally, yet face increasing pressures from human activities that put those benefits at risk. To anticipate the future of the world's ocean, we review the many human activities that impose pressures on marine species and ecosystems, evaluating their impacts on marine life, the degree of scientific uncertainty in those assessments, and the expected trajectory over the next few decades. We suggest fundamental research should prioritize areas of high potential impact and greater uncertainty about ecosystem vulnerability, such as emerging fisheries, organic chemical pollution, seabed mining, and the interactions of cumulative pressures, and deprioritize research on areas that demonstrate little impact or are well understood, such as plastic pollution and ship strikes to marine fauna. There remains hope for a productive and sustainable future ocean, but the window of opportunity for action to achieve this outcome is closing.

1. INTRODUCTION

Widespread scientific research and many synthetic reports are raising increasing concern about the fate of the oceans. Once thought to be too big to be susceptible to human impacts, oceans are showing many signs of significant change resulting from climate change, overfishing, offshore energy, invasive species, coastal development, and more (1). The most recent IPCC report declared a code red for humanity given the scope and impact of climate change on our planet (2). The analogous report for biodiversity and ecosystem services highlighted the negative trends for ocean biodiversity and related services to people (3, 4). The recently released Second World Ocean Assessment catalogued the many ways that human activities are benefiting humanity but are also putting significant pressure on ocean ecosystems (1, 5). The overarching theme to these reports is that human impacts on the ocean have led to biodiversity loss and shifts in ecosystem functioning, in turn reducing the ocean's contributions to people (4).

Amidst these sobering reports, research is also showing the potential for a healthy and resilient future for the oceans if smart action is taken. Fisheries management reform and sustainable aquaculture development can lead to more food produced with less environmental impact (6, 7). Well-designed networks of marine protected areas can boost fisheries, support biodiversity and protect stored carbon (8). Modest reductions in ship speeds can reduce harm and mortality to whales, greenhouse gas emissions, and noise pollution (9).

Taken together, what do all of these assessments and recent scientific findings tell us about the future of the oceans? What are and will be the major issues that the oceans, and thus humanity, face, and what can and should we be doing to address these issues now in order to make a better future? And similarly, what are issues that are sufficiently well known that we can act now and shift research attention elsewhere?

In this review we focus on highlighting what we know a lot about with respect to human pressures on marine species and ecosystems, where lurking issues remain that merit more attention, and where things are likely headed in the next few decades, and what this work tells us about anticipating the near-term future of the world's ocean. In doing so we aim to move beyond cataloguing the state of the oceans and towards a synthetic understanding of where things are headed and what we can and should be doing to tip that trajectory towards the most sustainable possible future.

1.1. Framework for anticipating the ocean's future

To guide our discussion, we use a simple conceptual model of human impact on marine ecosystems, in which human activities result in pressures that adversely affect vulnerable marine species or ecosystems:

$$I_j(t) = \sum_{i=1}^{I}\left[A_i(t) \times p_{ij}(t)\right] \times \sum_{k=1}^{K} v_{kj} \qquad 1.$$

in which $A_i(t)$ represents current intensity of activity i; p_{ij} represents the marginal contribution of activity i to pressure j, generally in the form of an unintended (indirect) rather than intended (direct) effect; v_{kj} is the vulnerability of some ecological entity k (e.g., a species, taxon, or functional group) to pressure j based on its physiological and life history traits (10); and $I_j(t)$ is the overall impact of pressure j on a given set of ecological entities. In some cases, one activity (e.g., bottom trawl fishing) may drive multiple pressures (e.g., intentional biomass removal, unintentional bycatch, habitat destruction, noise pollution), while in other cases, one pressure (e.g., nutrient pollution) may be driven by multiple activities (e.g., agricultural runoff, municipal wastewater, atmospheric deposition of combustion byproducts). The trajectory of future impacts is driven by changes over time in the intensity of an activity ($A_i(t + \Delta t)$) and/or in the pressures associated with an activity ($p_{ij}(t + \Delta t)$), often due to regulation, technological innovation, or economic demand. While this simple model elides complexities such as non-linearities and interactions among pressures, it incorporates several key issues that are necessary to anticipate the future of the ocean: 1) activities and pressures currently impacting marine ecosystems will remain consequential for the future ocean unless immediate action is taken to reduce the intensity of the activity or mitigate its contribution to pressures; 2) increasing intensity of human activities and expansion into more vulnerable ecosystems will exacerbate current impacts and introduce emerging impacts; 3) uncertainty in our estimate of the state of the marine system (state uncertainty), driven by environmental stochasticity and the challenge of obtaining precise measures, can confound effective policy and decision making; and 4) uncertainty in our understanding of the processes by which activities generate stressors, or more commonly how pressures generate impacts (process uncertainty), especially related to ecological vulnerability to emerging and/or rapidly increasing pressures, will be critical for managing for future impacts and thus should be a priority for future research.

To evaluate the future state of the ocean, we assess the main activities and pressures that are affecting the oceans now and likely to do so in the future. We draw in particular on recent work by the Second World Ocean Assessment (1, 5) and our own work cataloguing pressures to oceans (11–14) to structure the list of activities and pressures. The focus on activities in some cases and pressures in others is motivated by how data are typically collected and reported and how pressures connect to the oceans (e.g., fishing directly kills organisms, while land-based pollution is integrated via watersheds before pouring into coastal oceans). Activity-based assessments are thus focused on fishing, aquaculture, and offshore ocean activities (e.g., shipping, mining), while pressure-based assessments are focused on those derived from land-based activities, climate change, and other types of pollution (e.g., noise, light).

For each pressure or activity, we discuss and assess three axes of information that are critical for anticipating how human activities will affect the future of the ocean: 1) impact of the activity or pressure on natural systems (I_j in equation 1), 2) expected trajectory of pressures in the coming twenty years under business as usual assumptions (changes in A or p in the future), and 3) current areas where uncertainty remains, particularly process uncertainty in terms of ecological vulnerability (v). Because many recent reports have comprehensively addressed the impact of human activities and pressures on the ocean, in particular the Second World Ocean Assessment (1, 5), we limit our treatment of the impact axis to brief summaries. Where appropriate, we evaluate coastal versus offshore areas separately given the large differences in their exposure to activities and pressures. To address expected change in pressure intensities in the future, we assess the likely trajectories of activities that lead to changes in pressures over the coming decades. To address scientific uncertainty, we identify gaps in basic understanding of processes that govern system dynamics (process uncertainty, which is best addressed through investment in fundamental research) rather than gaps in knowledge that arise from data limitations (state uncertainty, which can be addressed through investment in data collection infrastructure). For each axis – impact, trajectory, and uncertainty – we use categorical evaluations (low, medium, high) based on review of the literature and our own expert judgement.

2. WILD-CAPTURE FISHERIES

Marine capture fisheries are a critical resource to meet nutritional, social, and economic well-being of billions of people globally. The great majority of global marine fisheries production, estimated at 84 million tonnes (1 million tonnes = 1 teragram, Tg) in 2018 (15), goes to human consumption, with the remainder to non-food or indirect food uses such as feed inputs for aquaculture or livestock (16). Fisheries provide nearly one fifth of animal-based protein for global diets, and are especially critical for food security (15) and micronutrients for coastal developing nations (17). Additionally, fisheries employ 39 million people globally (15), with another 80 million people employed in secondary seafood sectors, about 90% of these in small-scale fisheries in developing countries (18).

The undeniable benefits derived from fisheries do not come without cost, and unique among human activities that affect the marine system, the negative impacts of fishing on marine biomass are direct, intentional, and unavoidable. In addition to direct removal of targeted biomass and non-targeted biomass (bycatch), fishing activity results in habitat destruction (14), loss of trophic supports for other fished and non-fished species (19, 20), introduction of marine debris and plastics from lost and discarded fishing gear (21), noise pollution (22), light pollution (23), and disruption of other critical ecosystem functions such as carbon sequestration in seabed sediments (8). Aside from the pervasive effects of climate change, fisheries impose the greatest impact on marine ecosystems (14) and at-risk marine biodiversity (24).

The scientific and economic foundation of sustainable fisheries management is well established (25). Strong fishery management measures implemented at both stock level and national level have been shown to slow negative trends in stock health and facilitate recovery of depleted stocks (26, 27). Scientifically assessed stocks have on average improved since 2005 (15, 26). However, even in these well-managed fisheries, management decision methods may be particularly sensitive to state uncertainty inherent in assessing status of stocks, introducing substantial uncertainty in expectations of stock recovery (28, 29).

Sustainable management of fisheries varies tremendously with a large divide between industrial fisheries in developed economies vs. small scale fisheries in developing economies (15, 30). Even as scientifically assessed fisheries are improving, stocks in unassessed or poorly managed fisheries are generally thought to be in poor health and/or declining (31). Important levers to reduce uncertainty in the ecological and economic sustainability of global fisheries lie in developing technical and institutional capacity to implement effective management of currently poorly-managed and unassessed fisheries.

Small-scale fisheries important to the developing world are often characterized by lack of data to inform stock assessment (32) and less strict management, driving ever-increasing fishing effort on overexploited stocks (33). These complex social-ecological systems display broad diversity across inputs, assets, markets, institutions, and specialization (34), making one-size-fits-all solutions impossible. However, several avenues of action show promise: implementation of rights-based fisheries management such as territorial user rights fisheries (TURFs) (30), improvements in data-limited stock assessment techniques (32), and development of technical and institutional capacity (33, 35). Such investments may seem costly but are likely to pay off relative to the long-term costs of a depleted fishery (30, 32).

Over the next several decades, large changes in total harvest from wild-capture fisheries are not likely, even under significant fisheries reform. While reforms may result in production gains due to increased biomass of rebuilt stocks and harvest from currently underfished stocks, a recent study estimated that ecological limits impose an upper limit on such gains at 16% when maximizing food production, and only 4% when accounting for economic rationality (6). However, fisheries reforms aimed at recovering stocks and maximizing yield will result in reduced fishing intensity, which in turn reduces unintended impacts of fishing including bycatch (36).

Several other trends are likely to become increasingly important. Climate change will shift stock distributions (see Section 7.1), changing beneficiaries of fishery value resulting in winners and losers as species ranges shift across political boundaries (37). Technological advances such as real-time satellite-based tracking of fishing vessels will enable transparent and effective governance of transboundary and high seas fisheries (38–40) and greatly enhance global capacity for enforcement against illegal, unreported, and unregulated fishing (41) and forced labor (42). Finally, there is growing interest in the vast potential of mesopelagic fisheries to enhance global seafood production, though primarily for fish meal and oil rather than direct consumption (43). Exploitation of mesopelagic stocks bears risks due to state uncertainty around biomass estimates, as well as process uncertainty around the contribution of these stocks to carbon sequestration and trophic support of other commercially and ecologically important species (43, 44).

3. AQUACULTURE

Farmed seafood, or aquaculture, plays a significant role in the global food system, contributing more than half of all directly-consumed seafood globally and nearly half of all aquatic production (6, 7). In 2017 total aquaculture production was 112 Tg, valued at $250 billion, with roughly two-thirds of this production as food fishes and one-third as aquatic plants. Roughly 45 Tg of this total production is freshwater fishes, and ~18 Tg each of molluscs and other marine species (7, 15).

The potential impacts to ocean ecosystems from aquaculture vary substantially depending on the type of species being grown and the resulting methods and infrastructure used to grow them. Finfish and crustaceans (fed species) often create nutrient pollution, increase risk of pathogen spread and genetic escapes, produce greenhouse gas emissions, and destroy key habitats such as mangroves, especially for shrimp ponds (although this pressure has abated recently; (7)). They also require feed, and this feed is fast becoming the dominant source of environmental pressure from fed aquaculture through impacts from land-based agriculture and harvest of forage fish (45, 46).

Shellfish and algae have many fewer potential pressures associated with their production, in particular because they are not fed, and indeed can create positive outcomes from carbon sequestration, nutrient uptake in eutrophic waters, and habitat creation (47). The main concerns for negative effects are introduction of non-native species and modest habitat loss from farm infrastructure, as well as overharvest of wild seed for stocking shellfish farms. When unfed aquaculture is produced in extremely high densities, for example in some places in China, the uptake of nutrients by seaweed and primary productivity by shellfish can be substantial (48), which could reduce trophic resources necessary to support other endemic wildlife.

Despite the critical role that aquaculture plays in our global and local food systems, it receives a fraction of the attention that fisheries do in the scientific literature or from research funding (49). As such, although research and development work on specific cultivation practices for key species is well known, a wide range of questions about how aquaculture will interact with other ocean uses, especially fisheries, and its potential impact on or benefit to marine systems remain understudied.

In particular, key unknowns about potential innovations in aquaculture limit our ability to anticipate future impacts from production. Very few species have had their life cycle ‘closed,’ where all life stages are reared in captivity. Doing so removes the need to harvest wild seed to restock farmed populations. Innovations in pen design are allowing farms to move further offshore, which significantly reduces many of the environmental impacts from raising high concentrations of animals (50). And perhaps most importantly, rapid advances in alternative feeds suggest a potential future where the need for forage species and agricultural products is significantly reduced, helping mitigate the pressures from the capture and production of those feed components (51).

There is no doubt that historic growth in aquaculture over the past 30 years will continue into the future. With demand for seafood increasing and human population growing, and with wild fisheries effectively at their maximum production, aquaculture is the only way to meet this demand. Indeed, demand for and production of aquaculture is expected to nearly double current levels by 2050, with a majority of this increase in fed species (6).

4. OCEAN-BASED ACTIVITIES

The last few decades have seen increasing use of the oceans for a wide range of uses beyond fishing (Section 2) and aquaculture (Section 3), including transport, energy, resource extraction, bioprospecting, tourism, and more. Technological advances, societal needs, and the push towards blue economies are increasing the intensity of such activities and driving their impacts deeper and farther into the oceans.

4.1. Shipping

Commercial shipping is one of the dominant uses of the ocean, with nearly 2.0 billion dead-weight tons of capacity for goods shipped around the world in 2019 by more than 96,000 ships (1). Additionally, passenger and cruise ships constitute another roughly 5000 ships and primarily occur in coastal areas, with extensive traffic where they do occur. As one of the few uses of the oceans that traverses nearly every patch of space, the impacts from shipping have the potential to reach every species and ecosystem, with most of this impact in the northern hemisphere and along coastal shipping routes (14, 52).

Commercial ships are a dominant contributor to noise pollution (see also section 6.1), introduced and invasive species from ballast water, and air pollution and emissions. In coastal areas in particular, shipping also contributes to animal strikes, mainly of large cetaceans; for endangered populations like the Northern Right Whale, Fin Whale and the Blue Whale, these strikes can increase mortality by two to eight times as much (53). Shipping also puts modest amounts of pollution into the ocean from engines (oil and petroleum), antifouling materials, and waste dumped from the ships.

With automated ship tracking systems (AIS), satellite monitoring and open data platforms like global fishing watch, high temporal and spatial information on the location and speed of commercial ships is becoming increasingly available (54). With this information it becomes possible to predict where and how much each pollution type is occurring, where invasive species are most likely to emerge, where overlap with species movements are likely to lead to ship strikes, and how much reduced ship speed can reduce impacts (9, 55, 56), although many of these models are still under development.

The distribution and intensity of commercial shipping is expected to increase 2.5- to 12-fold by 2050 as the global economy increasingly depends on trade of goods (56). This growth will lead to new and larger ports and new shipping routes. In particular, the likely ice-free condition in the Arctic within the next decade will dramatically shift shipping into this previously low-traffic global region, altering patterns of shipping in other regions in response.

4.2. Offshore energy and resource extraction

For more than a century we have turned to the sea for oil and gas extraction, pushing further and deeper offshore as technology improved. Many of the largest and most productive oil fields are offshore, with 27% of global oil production and 30% of natural gas production occurring offshore in 2016 (1). This extraction has literally helped fuel the growth of national and global economies.

Pressure to shift energy production to sustainable sources has led to a dramatic increase in offshore renewable energy production and speculation. Though offshore wind energy currently contributes only 0.5% of global installed electricity production capacity, the International

Renewable Energy Agency has proposed a roadmap to increase capacity seven-fold by 2030 and an additional 8.5-fold between 2030 and 2050 (57). Much smaller efforts have focused on wave (surface and internal) energy, and tidal energy.

The ocean seafloor offers many other valuable resources for human uses. Offshore sand and gravel are extensively mined for beach replenishment and restoration efforts, as well as concrete production. More than 30,000 Tg of sand and gravel are extracted each year (58), with more than half now coming from the seabed. The rate of extraction far exceeds replenishment, such that it now functions as a non-renewable resource. More recently, with the depletion of precious and essential minerals from terrestrial mines, offshore mining has begun, primarily through leasing potential areas and exploratory extraction. The demand for rare earth minerals and other metals needed for electronic components is creating huge demand for these resources.

All these offshore activities involve building infrastructure or removing the benthic layer to extract resources, and in doing so they destroy the habitat where they occur. For energy infrastructure, there are also pipelines or cables that connect that infrastructure to the shore, further extending their benthic footprint and risking spills and fishing gear entanglement. Oil spills in particular present low frequency, high impact consequences; they have become much less frequent over the last few decades (59) but very large spills like Deepwater Horizon in the Gulf of Mexico remind us of the potential for catastrophic impacts. While under construction, and less so while under operation, offshore infrastructure also produces significant amounts of noise pollution (see Section 6). After construction, and because there are typically regulations against other uses accessing the space where the infrastructure sits, the artificial habitat and de facto protection can lead to some benefits to biodiversity (60).

The relatively extensive process for permitting offshore infrastructure and the environmental impact assessments that must be done as part of that process means we know a fair bit about the environmental impacts of these activities, although many details likely remain proprietary. In contrast, we know very little about deep sea mining impacts because of the limited scope of this mining to date and the difficulties in monitoring and observing at extreme depths. Some reports have found that although deep sea mining has impacts, these impacts may be less than equivalent mining on land (61).

Nearly all offshore uses are expected to increase in the near future, with offshore oil and gas extraction continuing to show sustained growth and substantial expansion of offshore wind expected due to strong, sustained winds offshore and fewer conflicting uses compared to on-land wind farms (1). Growth in nearly all types of mining is expected due to increasing demand and fewer on-land resources remaining. Growth in some types of mining, especially deep-sea mining, are less certain due to existing regulatory hurdles.

5. LAND-BASED

Coastal marine ecosystems are heavily impacted by pollutants and other stressors originating from land-based activities, including agriculture, mining, industrial manufacturing, fossil fuel combustion that contributes to atmospheric pollution, and urbanization. Chemicals and waste products from these activities generally aggregate in soils and surface water and are carried to the ocean via runoff and rivers, while airborne waste products are carried to the ocean via atmospheric transport and deposition. Because these pollutants are quickly diluted with depth and distance from the shore, the greatest impacts of these land-based stressors typically occur in coastal zones.

5.1. Nutrient pollution

Increases in the input of biologically reactive nitrogen (N) and phosphorus (P) to coastal marine waters since the mid-20th-century have resulted in coastal eutrophication, harmful algal blooms, and loss of biogenic habitats such as coral reefs and coastal wetlands (62), while human-driven shifts in the natural balance of N to P can disrupt the structure, diversity, and functioning of ecosystems (63). Major sources of anthropogenic N in the oceans come from agricultural runoff, fossil fuel combustion (via atmospheric deposition), livestock waste, and municipal wastewater (62). Fertilizers, livestock waste, and wastewater are also major sources of anthropogenic P pollution, along with industrial discharges and construction (64).

Anthropogenic nitrogen inputs doubled in the last half of the 20th century, approaching parity with natural sources of biologically reactive nitrogen, and are expected to increase to 120% of natural sources by 2050 (65). In the 21st century, fertilizer use increased by 42% globally between 2002 and 2012 (1); even accounting for increasingly efficient fertilizer use, N losses to the environment may increase by an additional 15% by 2050 under business as usual (66).

Policies and actions to curtail both N and P loading from point sources have proven quite successful in wealthier countries, though curtailing inputs from nonpoint sources (N and P from agricultural sources and N from fossil fuel combustion) has proven to be far more challenging (64, 67). In general, practices to mitigate N inputs also tend to reduce P, though the converse is not generally true (68). While impacts of nutrient over-enrichment on marine systems are generally well understood, climate-driven variation in patterns of precipitation, flooding, and drought will result in variation and state uncertainty around patterns of runoff and freshwater transport of nutrients to the ocean (69).

5.2. Organic chemical pollution

Synthetic organic chemicals including persistent organic pollutants (POPs) such as pesticides (e.g., DDT), industrial chemicals (e.g., polychlorinated biphenyls - PCBs), and industrial byproducts (e.g., dioxins); endocrine disrupting chemicals (EDCs), many of which are POPs;

and pharmaceutical and personal care products (PPCPs) intended for health care, cosmetics, and medical use are of increasing concern to marine ecosystems due to their persistence in the environment, bioaccumulation, long-range transport, toxicity, and disruption of biological and ecological processes (70–72). Organic pollutants enter the marine environment via agricultural runoff, industrial discharge, municipal wastewater, and atmospheric deposition, with high concentrations found in coastal areas near urban centers and areas of high industrialization and low concentrations persisting in remote marine ecosystems and organisms (1).

The Stockholm Convention targets a small but increasing number of POPs for elimination or reduction of production (73), and has proven successful in reducing loads of DDT and PCBs in the environment (1, 74). However, the rate of increase and diversification of synthetic chemicals is outstripping other major drivers of environmental change (75). Furthermore, management is hampered by substantial process uncertainty around the complex interactions among emissions, exposure, and toxicity, particularly when considering cumulative effects of exposure to multiple chemical pollutants (71, 75). Despite the rapid increase of potentially harmful pollutants, ecological research on effects of synthetic chemical contamination on biodiversity and ecosystems lags well behind research devoted to other drivers of global change (75).

5.3. Toxic metals

Elevated concentrations of heavy metals in the marine environment, even biologically essential metals (e.g., iron, manganese), can alter metabolism, reproduction, and behavior of marine species, and can be toxic at high enough concentrations (76). In particular, non-essential metals including cadmium, lead, and mercury are a major concern to marine ecosystems due to their toxicity and effects on neurology and development of marine organisms as well as humans (1, 76). Primary sources of heavy metals in the ocean include agricultural runoff, industrial discharge, wastewater discharge, dredging, mining, and atmospheric deposition from fossil fuel combustion and metal refining (76–78).

As measured in the marine system, concentrations of cadmium and lead have generally leveled off, though are still detectable above background levels; however, monitoring is concentrated around North America, Europe, and Arctic coasts (1), so regional variation is not adequately captured. Global production of cadmium and lead have remained consistent in recent years (1).

Human activity has elevated atmospheric mercury concentrations 450% above pre-industrial levels (78). Global anthropogenic emissions increased by 20% from 2010 to 2015; efforts to reduce emissions in Europe and North America were more than offset by increased emissions associated with increased economic activity elsewhere, particularly East Asia (78). As of 2015, only 30% of total annual atmospheric mercury emissions were attributed to current activity, with another 60% attributed to volatilization of legacy mercury deposited to soils and water from past human activity (78). Even as the Minimata Convention drives reductions in anthropogenic mercury emissions from current activities, legacy mercury will remain a significant source of mercury inputs into aquatic ecosystems (78).

While the individual toxicity of these metals has been well studied, complex mixtures of metals and other chemical pollutants introduces process uncertainty, confounding predictions of cumulative toxic risk and sub-toxic impacts, and bears further investigation (77).

5.4. Plastics - micro and macro

The rate of plastic production has increased dramatically over the past 50 years, with a cumulative total of more than 8,300 Tg produced globally by 2015, with roughly half of that production thrown away rather than recycled or incinerated (79). Of that waste, an estimated 5-12 Tg enters the oceans each year (80). Lost and discarded fishing gear is another significant source of marine plastic debris, making up nearly half the plastic waste found in the Great Pacific Garbage Patch (21). Of particular concern are microplastics, as they are already ubiquitous and macroplastic waste degrades into microplastics, and plastics are persistent in ecosystems for an extremely long time (81). In response to this growing pressure, both research on plastic pollution (82) and funding for plastic pollution mitigation in the ocean (49, 83) has increased dramatically in the past decade.

This high profile of plastic pollution gives the impression that it is having a huge impact on the oceans, yet evidence remains limited that marine organisms are yet negatively affected by them (84). Entanglement and ingestion of macroplastic by sea turtles, seabirds and other marine fauna can harm and often kill those individuals, while ingestion of microplastics can cause injuries and disrupt feeding and nutrient uptake (85). Microplastics can adsorb organic chemical pollutants and toxic metals (see Sections 5.2 and 5.3), though these toxins can be transported by natural sediment and organic matter as well, and microplastics will generally be a small fraction of natural suspended particulate matter (86). Despite the near omnipresence of plastics in the marine environment (85), it remains unclear whether these impacts are scaling up to population-level consequences. The marginal impact of an additional unit of plastic pollution (i.e., vulnerability, v_{kj} in Equation 1) appears to be very small, and further research is not likely to upend our understanding of the magnitude of vulnerability. On the other hand, the vast global production of plastics (A_i) and the contribution of that production to marine plastic pollution (p_{ij}) mean that the risk of impact cannot be ignored. This is especially relevant as plastic production continues to increase exponentially, and thus the amount of plastic waste entering the ocean is similarly expected to increase manyfold in the coming decades (80).

5.5. Changes to sediment dynamics

Anthropogenic changes in coastal sediment dynamics and sediment inputs threaten river deltas (87), sandy beaches (88, 89), and high-biodiversity coastal ecosystems (90, 91). Habitat loss and degradation can be driven by sediment input decreases (e.g., coastal erosion, beach retreat) or increases (e.g., smothering of coral reefs) (90), resulting in loss of nursery habitats for many species and reductions in productivity of coastal ecosystems (92), coastal protection ecosystem services (93), and resilience to climate change (87).

Changes in sediment supply driven by dams, urbanization, mining, and land-use change have reduced sediment flux for most of the world's major river deltas since 1970 (87), with additional drastic reductions for most major rivers projected by century's end (94). These changes in sediment flux, combined with coastal activities including development, sand mining, and sand nourishment, have driven erosion and accretion of sandy shorelines (88) and river deltas (87) globally. Coastal erosion in combination with unchecked sea level rise could drive half of the world's sandy beaches to disappear by 2100 (89). Sea level rise and climate-driven changes in precipitation patterns and coastal dynamics will likely elevate state uncertainty around sediment supply and transport (95, 96).

5.6. Direct human impact

Coastal zones are far more densely populated than the global average (97). Due to this substantial human presence, global coastlines and very nearshore coastal ecosystems often experience heavy impact and modification from coastal development, trampling from beach and coastal access and shoreline hardening to protect coastal infrastructure. For example, 14% of the shoreline of the United States has been hardened against erosion and flooding (98), many of the world's major coastal cities have hardened more than half their shoreline (99), and China has modified more than 60% of its coastline (100).

Some methods of shoreline engineering and infrastructure (e.g., seawalls) impose greater impacts on marine biodiversity than others (e.g., riprap revetments and breakwaters), though the effects are highly variable and may depend on such factors as taxonomy, structure design and placement, and sediment dynamics (99). Human presence from coastal tourism and recreation can lead to degradation of coastal ecosystems from trampling or species' behavioral shifts, but the nature and extent of these impacts is not well known. Process uncertainty in the impacts of species behavioral responses to human presence can result in failure to recognize and manage critical interactions, and conversely, wasting resources on managing interactions of little consequence (101).

Increasingly dense coastal populations and urbanization, along with the impacts of sea level rise and increasingly frequent and intense storms, are likely to motivate increased construction of engineered shorelines and infrastructure (102). Growing global commercial shipping and the need to build and expand ports that service those ships, especially along the emerging Arctic shipping routes, will increase shoreline hardening in many areas (56).

6. NOISE AND LIGHT POLLUTION

Sound can propagate very long distances in water, and for this reason animals from cnidarians to mammals have evolved to use sound as a primary sensory system for navigation, foraging, avoiding predators, mating, and finding settlement habitat, among other uses, especially over longer distances or where light visibility is low (22). The ocean is naturally noisy, cueing animals to the locations of for example coasts (via waves), storms, ice edges, and the many organisms making noise, intentionally or otherwise.

The last century in particular has seen the rapid increase in anthropogenic noise, or noise pollution, stemming from commercial shipping and transport (see also Section 4.1), fishing (see also Section 2), offshore energy construction and operation (see also Section 4.2), ocean exploration (seismic surveys), military activities (especially sonar), and airplane and coastal traffic (sound propagating into the water), among others (22). This cacophony of noise pollution now overwhelms natural noise in many parts of the ocean (1), drowning out the ability for animals to use sound as a cue.

Recent syntheses indicate that we understand with high certainty how noise impacts species (22). We know less about how and where noise propagates in the ocean because for many parts of the global ocean we do not have high spatial and temporal resolution data on water properties (temperature, salinity) that affect noise transmission, although the navy probably has this information.

Light pollution interacts with species in ways different from noise pollution. Many species - from larger animals like seabirds and sea turtles to microscopic organisms such as copepods - use light to navigate, hunt, avoid predators, and vertically migrate. The role of light as a cue is particularly important at night and at depth, where low levels of light allow organisms to hide while using light they produce or from the moon and stars above to navigate and hunt (103).

The footprint of light pollution is already substantial, affecting an estimated 22% of the world's coastal areas (23). The dominant source of this light pollution is urban and other human infrastructure along the coast, and light from these developments can reach tens of kms out to sea (14). Offshore light pollution comes primarily from oil and gas rigs and commercial fishing vessels, in particular squid boats that use light to attract squid (12). Light from these sources can be equivalent to major metropolitan areas and are easily visible from space.

Because we can measure the source and intensity of anthropogenic light from satellites, we know with very high precision where and how much light pollution reaches the ocean, and likely how much it penetrates into the water. In contrast, we know much less about the consequences of this light pollution. Although an increasing number of publications exist (103) across a wide range of taxa on the impacts of anthropogenic light (104), most attention has focused on terrestrial species. Much less is known about how marine species respond, where the properties of light transmission and the ecology and evolution of species in response to those differences diverge from terrestrial systems.

Both noise and light pollution are expected to increase. Already a majority of the world's population lives near the coast (102), such that both types of pollution are expected to increase substantially in the coming decades. Furthermore, with substantial increases expected in commercial shipping (see Section 4.1) and offshore energy (Section 4.2), there will be commensurate increases in noise pollution. Technology may help reduce these overall increases in noise, through innovations such as noise-reducing rotors for commercial ships, but these innovations are unlikely to be sufficient and widespread enough to compensate for the increase in overall volume.

7. CLIMATE

Since the advent of the industrial revolution in the late 1700s, fossil fuel combustion, deforestation, and other human activities have driven an unprecedented rise in atmospheric carbon dioxide from 280 ppm to over 410 ppm, still rising at 2.3 ppm per year. Excess carbon dioxide, along with methane and other greenhouse gases, are driving increasingly higher atmospheric temperatures globally. Even under scenarios of ambitious carbon mitigation, trends in atmospheric and oceanic temperature and chemistry will continue for the near future (2). Continued warming is exacerbated by positive feedback loops, including melting of reflective glaciers and Arctic sea ice. Even at modest levels of overall temperature rise, we may be approaching climate tipping points due to release of methane from thawing Arctic permafrost and undersea clathrates, global forest diebacks, and collapse of Greenland and Antarctic ice sheets (105). Process uncertainty around the existence of critical climate thresholds and the magnitude of consequences of exceeding such thresholds amplify the urgency of addressing climate impacts immediately and aggressively.

7.1. Changing ocean temperature and chemistry

Anthropogenic carbon emissions are driving three major threats to global marine ecosystems: increasing ocean temperatures; deoxygenation due to temperature-driven changes in solubility, stratification, and upwelling; and ocean acidification due to absorption of carbon dioxide into marine waters (106, 107). Changes in ocean temperature and chemistry will create novel marine climates with no analog in recent history, shifting the locations of habitable space for many species, and eliminating some existing climates that support marine biodiversity (108). Long-term trends will be accompanied by increasing frequency and intensity of short-term extreme heat, acidification, and hypoxic events (107).

Since 1900, average sea surface temperatures increased by 0.74°C, and are currently increasing 0.28°C per decade (109). These rising temperatures are driving shifts in species distributions generally poleward, on order of 50-100 km per decade, as organisms move or disperse into suitable areas (110), resulting in biodiversity losses near the equator and increases in higher latitudes (111). Future distributions will most likely be driven by changes in both temperature and oxygen supply as species strive to meet critical thermal tolerance and metabolic demands (110). Species ranges will shift differentially based on physiology, adaptive capacity, mobility, and dispersal capacity (110) and biogeographical constraints (112, 113), disrupting food webs as historic species interactions disappear and novel species interactions are introduced (110). Ecosystems and food webs are expected to be more resilient than individual species, even as some species are lost and others introduced (110).

Even as long-term temperature trends are driving species range shifts, marine heat waves on the timescale of days to months have increased in frequency and intensity over the past century (114), a trend that is expected to accelerate under continued global warming (115). Marine heat waves have resulted in physiological stress, mortality, and disruption of ecosystems, particularly coral reefs, kelp beds, and seagrass meadows (116, 117), impacting both biodiversity and provisioning of ecosystem services (116, 118). The drivers and ecological impacts of marine heat waves have been well studied, but better forecasting capacity would be valuable to inform conservation management and adaptation in the face of continued warming and heat waves (117).

Like marine heat waves, short-term marine hypoxic events are expected to increase in frequency and intensity under the current climate trajectory. Extreme hypoxic events negatively impact development, growth, metabolism, and survival of marine species across many taxa and regions. The severity of these impacts may eclipse those of acidification and warming; despite this, deoxygenation and hypoxia have received relatively scant attention in the scientific literature (107).

Ocean surface pH has declined by 0.1 since 1800 and is expected to decline by an additional 0.1-0.4 pH units by 2100 (109). Ocean acidification is a major concern to calcifying marine species, particularly shelled molluscs, as it impedes their ability to secrete calcium carbonate (119, 120). Changes in the marine carbonate system can impact non-calcifying species through behavior change, disruption of sensory capabilities, and reduction of fertilization success (120, 121) in animals and enhancement of photosynthesis in many seaweeds and phytoplankton species (120). Recent work highlights interactions among multiple mechanisms through which marine life will respond to changes in the seawater carbonate system (120).

To date, research on climate-driven marine species range shifts has focused on case studies and models based on projections of environmental parameters, but there remains substantial process uncertainty in demographic mechanisms - e.g., changes in reproductive success, larval dispersal, adult mobility, and trophic interactions - that underlie these range shifts. Trait-based approaches to understanding community dynamics under climate change may better inform predictions of the function and resilience of novel ecosystems (110). The effects of warming, acidification, and deoxygenation on marine species and ecosystems are likely to compound due to physical and physiological interdependence of these three stressors, but cumulative impacts have received little attention in the scientific literature (107).

7.2. Sea level rise

Sea level rise (SLR) driven by glacial melt and thermal expansion of warming ocean waters threatens low-lying coastal ecosystems by exacerbating coastal erosion, salinization of surface and ground water, increased flooding and storm surge, and degradation of coastal habitats including mangroves, salt marshes, and coral reefs (122, 123). These ecological impacts can in turn result in major impacts on coastal communities, cities, infrastructure, and low-lying island states (1). Sea levels have on average risen 90 mm since 1993, averaging 4.7 mm per year since 2010 and accelerating (1). Healthy coastal ecosystems are often resilient to modest SLR, but cumulative impacts of other pressures creates uncertainty in the capacity of these ecosystems to keep pace with accelerating SLR (124, 125). Mangroves and salt marshes have the capacity to build upward to keep pace with historic SLR, but subsidence and changes in sediment supply from human activities can overcome this process, resulting in wetland degradation (123, 124). Studies have shown that coral reefs can benefit from SLR through increased accommodation space for vertical and lateral expansion (126) and improved resilience to increasing temperatures (127). However, the rate of SLR in the next century is likely to outpace the vertical growth potential of many or most coral reefs, particularly in light of increasing bleaching and acidification (125).

7.3. Ultraviolet radiation

Widespread use of chlorofluorocarbon (CFC) chemicals throughout the 20th century reduced the ability of the stratospheric ozone layer to shield Earth's surface from harmful ultraviolet (UV) radiation. Increased UV exposure is harmful to marine organisms, particularly plankton and bacteria, affecting photosynthesis, mobility, growth rates, and metabolic function (128), reducing primary productivity at the ocean surface and altering the composition and biodiversity of marine communities (129). Ozone depletion and increased UV exposure vary greatly with latitude; effects are most pronounced in the southern hemisphere, particularly above the South Pole (129).

Since the adoption of the Montreal Protocol in 1987, use and production of CFCs and other ozone-depleting substances (many of which are also powerful greenhouse gases) have been dramatically curtailed. Stratospheric ozone concentrations are generally healing at 1-3% per year, and regional concentrations are expected to return to 1980 levels by the 2030s (mid-latitude Northern Hemisphere), 2050s (mid-latitude Southern Hemisphere), and 2060s (Antarctica) (130).

8. ANTICIPATING THE FUTURE OCEAN

The future of the world's ocean will be written by human choices as much as by nature's ability to respond and rebound from those choices. How much will we use (and use up) ocean resources, and can nature absorb those pressures? For many anthropogenic stressors, there is strong scientific understanding linking activities to associated pressures to impacts on species and ecosystems (low process uncertainty; high impact) and a reasonable estimate of future impacts (known trajectory). Impacts from industrial scale commercial fishing, aquaculture, nutrient pollution, altered sediment dynamics, commercial shipping, offshore energy, and plastic pollution are relatively well understood and thus potentially lower priorities for further research (Table 1), although their management remains a priority. In these many cases, the ability to anticipate the future of the oceans is not limited by scientific uncertainty about how the pressures affect biodiversity, but rather by the political and economic challenges of implementing effective policy.

In contrast, several pressures and activities stand out where high scientific uncertainty intersects with high ecological impact and potential for future change (Table 1). For these issues, investment in further research to reduce process uncertainty should take a high priority, as overly precautionary management is likely to be costly and inefficient, while undermanagement may result in catastrophic consequences. The future impacts of small-scale fishing are uncertain, given many data limitations, but are probably substantial and greater than today given increasing numbers of human communities dependent on coastal fisheries. Emerging fisheries like mesopelagics have potentially huge impact on species and systems about which we currently know little. Land-based pollution from inorganic and organic pollutants already heavily impact coastal systems in many parts of the world, and the rapid development of new compounds with unknown consequences for species creates a high-risk scenario. Ocean acidificiation is a known threat to calcifying organisms in particular, but the capacity of species to adapt to changing conditions remains less well known, and the potential consequences of major ecosystem impacts would be profound. Seabed mining (particularly of sand and gravel) currently has a large footprint, and there is substantial risk from growing commercial interest to expand into deep sea areas where we know almost nothing about potential ecological consequences.

Many human impacts on the ocean can be directly managed, when impact can be attributed to specific human activity, and curtailing the activity results in direct curtailing of the impact. Where impact is known to be large and likely increasing, management can work to reduce the extent or intensity of the activity, implement policies or technologies that reduce the pressures associated with a given unit of activity, or both. Climate stressors, on the other hand, stand apart from most other activities and pressures listed above, in that the drivers (greenhouse gas emissions) are global and diffuse, and the persistence of elevated CO_2 in the atmosphere ensures that stressors will continue to impact the oceans for decades even under the most ambitious management plan. While climate stressors may be effectively beyond management, reducing impacts attributable to manageable activities will be important to avoid compounding the effects of warming, acidifying, rising seas, and to improve resilience of marine ecosystems to climate change.

Perhaps one of the greatest process uncertainties is how multiple stressors interact to create cumulative effects. There is some evidence about the frequency of additive, synergistic and antagonist pressures, but we know very little about how multiple stressors interact with more than two stressors present (131), and most parts of the ocean experience far more than two stressors at a time (12). The potential for cumulative effects to lead to nonlinear responses in ecosystems, most notably tipping points that push ecosystems past an irreversible point, seems likely (105), but we know little about whether tipping points are common or rare (132), or whether changes are actually irreversible. All of these uncertainties make anticipating the future of the ocean particularly difficult.

Beyond the uncertainties connected to specific stressors, there are key areas of uncertainty at the intersection of stressors and social science disciplines. Interactions between human and ecological systems are fundamental to anticipating the future of the ocean, and the complexity of these interactions leads to additional layers of uncertainty around outcomes of any given management action for species, ecosystems, people, and communities. This uncertainty is compounded by mismatches in the spatial and temporal scale of individual experience, which is determined by how people perceive change in their surroundings; the scale of management action, which is determined by jurisdictional boundaries; and the scale of ecological impact, which is determined by natural processes and human interactions with those processes. Attention to procedural, distributional, and recognitional equity in the (re-)allocation of resource rights of people and communities can avoid social harms, including conflict, disempowerment, human rights abuses, and widening of economic inequality, while at the same time improving conservation outcomes by increasing local support for and participation in conservation (133). Even so, unalloyed synergies in conservation are not common; the balance between synergies and tradeoffs in social and ecological well-being depends on historical context, resource dependence, and asymmetries of power in governance (134). Considerations of equity and human well-being in conservation action become even more critical in the face of accelerating climate change (135). Better understanding issues of inequity and their interactions with resource management will allow for better forecasts and, in turn, effective management decisions and resource policy.

New and emerging uses of marine resources that we know we know little about, such as potential widespread fishing of mesopelagic fish stocks or deep-sea mining, play an important role in our imprecision in predicting ocean health in the next few decades. Equally important are the many things we do not even know are on the horizon, in particular new technologies or resource needs not yet imagined. For example, interest in deep sea mining is being driven in part by the need for the rare metals used in solar panels, electric cars and wind turbines, among other uses. Future technologies, whether ocean related or not, may require materials and resources that are more abundant in the ocean, and thus push human activities and associated pressures offshore. Accounting and planning for these unknowable parts of the future can only be done effectively with adaptive management.

The best strategies to improve the health of the future ocean depend on the intersection of potential impact, uncertainty, and trajectory (Table 1). For the most part, we know how different activities (A_i in equation 1) produce different amounts of stressors (p_{ij}), such that relatively little uncertainty remains at the global scale, although local-scale contributions to each will likely vary substantially and thus need to be measured. In contrast, in many cases we do not know how the full diversity of species responds to a given stressor (v_{kj}). More importantly, for many pressures we know the consequence for individual organisms or sometimes whole populations, but rarely whether these impacts translate into larger population or ecosystem scale changes (101).

Determining whether it is strategic to invest in reducing uncertainty, and how, depends on which type of uncertainty exists. In general, we suggest that the priority for future scientific research should focus on issues where substantial process uncertainty remains. However, we also recognize that reducing uncertainty about the state of the marine system is critical to informing effective and efficient management and conservation, and so investment in improved data collection and monitoring technology should be a priority for policymakers (136). In particular, local data can help tailor strategies for a specific place, and local priorities might differ from the big-picture priorities.

These are questions of how to make research and data investment as strategic as possible. In contrast, altering the impact or trajectory of activities and stressors relies on policy action and technological innovation rather than scientific research. Where potential impact is high and/or trajectory is high, action needs to focus much less on additional research and primarily on reducing the growth and intensity of activities. Ultimately, even with perfect knowledge about how pressures from activities impact species and the likely trends in those activities and pressures, our efforts to change the trajectory of the future of the ocean depend on how well we can design, implement and enforce different management strategies.

In addition to support from governmental agencies (the National Science Foundation and the National Oceanic and Atmospheric Administration in particular), a substantial amount of funding (US$1.2 billion in 2020) for ocean-related research and conservation in the United States comes from philanthropic organizations (49), whose priorities may be driven as much by public perception and donor preference as by scientific urgency. In addition to funding of basic science (28% of funding in 2020), philanthropy has been heavily focused on a few specific topics over the past decade, namely marine protected areas and habitat protection (14% of funding), fisheries (10%), and industrial pollution/stressors (14%, dominated by an annual grant from an association of energy companies toward oil spill response capacity). Since 2010 philanthropic funding has increased five-fold for aquaculture initiatives, ten-fold for climate initiatives, and twenty-fold for small-scale fisheries (49). Overall, philanthropic funding for ocean issues in general has doubled since 2010. Still, current funding is woefully insufficient to achieve conservation goals and avoid costly future impacts. Emerging “blue ocean” mechanisms can remove barriers to public and private investment in sustainable ocean-based economic activity to help fill this funding gap (137). Such finance projects are likely to prioritize data collection and monitoring toward feasibility analysis and risk reduction (138) rather than primary research to reduce process uncertainty.

In some cases there seems to be a mismatch between scientific understanding and public perception of the magnitude of impact/concern. For example, plastic pollution receives widespread public and scientific attention (139, 140), and foundation funding has increased seven-fold since 2010 to nearly half the funding allocated to fisheries and parity with funding for ocean climate concerns (49) – this despite little evidence of substantial impact on marine ecosystems (84), particularly compared to impacts from fishing or climate change (11, 141). Ultimately, we suggest that current funding and research priorities may need to be realigned to help achieve a healthy ocean. A high priority should be placed on primary research in areas where both process uncertainty and potential for impacts are high, such as mesopelagic fisheries, organic chemical pollutants, and cumulative impacts across multiple stressors. As process uncertainty is reduced, funding for high-impact pressures should shift toward implementation, such as monitoring and enforcement for fisheries and marine protected areas.

The ocean has maintained its potential for resilience in the face of the many pressures humans place on it - to date very few marine species have gone extinct (142), and the fact that humans do not live in the ocean seems to have helped maintain sufficient refuge. But our footprint in the ocean is expanding and the individual and cumulative pressures from our activities are intensifying (14). The ocean cannot maintain its function and vitality much longer in the face of these pressures. The window of time for action is rapidly closing to sustain healthy oceans.

SUMMARY POINTS

- Anticipating the future of the ocean requires understanding whether and how anthropogenic pressures impact ecosystems, the degree of uncertainty in those assessments, and the expected trajectory of human uses of the ocean.
- Most research on pressures to oceans has focused on how individuals or populations respond to the presence and intensity of pressures, without further exploring whether these changes translate into wider ecosystem consequences; this uncertainty is critical to resolve for both scientific understanding and more strategic management and conservation.
- Several pressures, including those from shipping, certain types of aquaculture, and overfishing in wild-capture fisheries, are well understood and are known to have large and likely increasing impacts; these pressures can be effectively managed.
- Several other pressures, including ocean plastic pollution and offshore renewable energy, are known to have relatively little impact despite their high profile in public attention.
- Climate pressures, particularly rising ocean temperatures, marine heat waves, and ocean acidification, are effectively unavoidable in the next few decades even under aggressive carbon reduction scenarios; therefore, other pressures must be managed to improve ecosystem resilience to these inevitable impacts.
- Research and funding priorities may need to be realigned to account for magnitude of process uncertainty and potential for impacts: resources for primary research should focus on pressures where both process uncertainty and potential for impacts are high, while resources for effective management should be focused on well-understood and high-impact pressures.

FUTURE ISSUES

- The complexity of interactions among multiple pressures, even among pressures whose individual impacts on marine ecosystems are well understood, remains a critical source of uncertainty in the cumulative impact of human activity on marine ecosystems, and should be a high priority for future research.
- Emerging human activities, including mesopelagic fisheries, seabed mining, and an ever-increasing array of organic chemical pollutants, carry substantial uncertainty around risk of impacts; research to understand potential impacts of these activities, coupled with a precautionary approach to management, will be critical to minimizing risk to vulnerable marine species and ecosystems.
- Systematic trait-based methods of estimating vulnerability of marine species to anthropogenic pressures would greatly enhance our ability to anticipate and manage the impacts of human activity, including novel and emerging stressors.
- Managing human activities to support healthy ocean ecosystems will require robust understanding of the complex ways in which ecological condition, resource use policy, and economic incentives interact within and across scales, from local to national to regional to global.
- Policy and action to better manage human impacts on our oceans will inevitably result in changes in allocation of resource use rights within and among coastal communities; careful attention to the equity implications of conservation policy and marine resource management must be a high priority for an equitable, just, and sustainable future ocean.

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KEY TERMS AND DEFINITIONS

- **Pressure:** A factor that can cause environmental change; anthropogenic pressures are generated by human activity on land or sea.
- **Impact:** Mortality or reduction of fitness of an individual, population, or community due to vulnerability and exposure to an anthropogenic pressure.
- **Vulnerability:** The magnitude of potential impact from a pressure, conditional upon exposure, on an individual, population, or community
- **State uncertainty:** Uncertainty about the state of the ecological system due to environmental stochasticity and the challenge of obtaining precise measures
- **Process uncertainty:** Uncertainty about the mechanism or degree of vulnerability of an individual, population, or community to a pressure

Category	Activity/pressure	Process uncertainty	Change (~20y)	Ecological impact	
				Coastal	Offshore
Fishing	Industrial fishing	low	low	high	high
	- Transboundary species	low	med	high	high
	- Emerging fisheries	high	med	low	high
	Small-scale fishing	med	med	high	med
Aquaculture	Finfish/fed shellfish	low	high	med	med
	Bivalves/non-fed	low	high	low	low
	Seaweed	low	high	low	low
Ocean-based	Shipping (strikes)	low	med	low	low
	Shipping (invasives)	med	med	med	low
	Seabed mining	high	med	med	med
	Offshore renewable energy	low	med	low	low
	Offshore nonrenewable energy	low	med	low*	low
Land-based	Nutrient pollution	low	high	high	low
	Organic chemical pollution	high	high	high	low
	Toxic metals	high	med	med	low
	Plastic pollution	low-med	high	low	low
	Sediments	low	high	high	low
	Direct human impact	low	high	high	N/A
Noise and light pollution	Noise pollution	med	med	low	low
	Light pollution	med	med	low	low
Climate	Temperature	low	high	high	high
	Ocean acidification	med	high	high	high
	Sea level rise	low	high	med	N/A
	Ultraviolet	low	low	low-med	low-med

* For offshore nonrenewable energy, if there is an oil spill then coastal impact is high

Table 1. Estimates of ecological impact, the expected trajectory in the coming 20 years, and scientific uncertainty in how each activity or pressure affects species and ecosystems.

At-risk marine biodiversity faces extensive, expanding, and intensifying human impacts

Casey C. O'Hara, Melanie Frazier, Benjamin S. Halpern

Abstract

Human activities and climate change threaten marine biodiversity worldwide, though sensitivity to these stressors varies considerably by species and taxonomic group. Mapping the spatial distribution of 14 anthropogenic stressors from 2003 to 2013 onto the ranges of 1,271 at-risk marine species sensitive to them, we find that on average species face potential impacts across 57% of their ranges, that footprint is expanding over time, and those impacts are intensifying across 37% of their ranges. While fishing activity dominates the footprint of impacts in national waters, climate stressors are driving the expansion and intensification of impacts. Mitigating impacts on at-risk biodiversity is critical to supporting resilient marine ecosystems, and identifying co-occurrence of impacts across multiple taxonomic groups highlights opportunities to amplify benefits of conservation management.

The impact on the world's oceans of human activities including fishing (*1*), land-based development and runoff (*2*), and ship strikes (*3*), coupled with the accelerating effects of climate change (*4*), are pervasive and increasing (*5*). Impacts from these anthropogenic stressors threaten marine species across taxa, driving thousands toward extinction (*6*, *7*) and jeopardizing the sustainability of coastal social-ecological systems (*7*, *8*).

Species respond differently to stressors, and multiple stressors can have cumulative impacts on threatened marine species (*9*). Efforts to assess cumulative human impacts on marine species have been single snapshots in time limited to a few specific taxa and stressors (e.g., (*10–13*)), leaving the vast majority of species unassessed. A recent comprehensive species-level assessment of cumulative impacts on at-risk terrestrial vertebrates (*14*) does not include marine species and does not capture changes in impact over time. Assessments of the distribution and rate of change of cumulative human impacts on global marine habitats (*5*, *15*) provide valuable insights into ecosystem-level concerns, but habitat-focused assessments do not capture the heterogeneity of species' vulnerability (*4*, *11*), which is crucial for designing conservation strategies.

Here we present a global assessment of cumulative human impacts on at-risk marine species, and changes in those impacts over recent time. For each of 1,271 threatened and near-threatened marine species comprehensively assessed and mapped for the IUCN Red List of Threatened Species (*16*) (hereafter "at-risk species"), we identified sensitivity to 14 anthropogenic stressors. We then intersected species range maps with relevant maps of annual stressor intensity from 2003 to 2013 to determine the extent of potential impacts (*sensu* (*17*), hereafter simply "impacts") across species' ranges, as well as how rapidly these impacts have been expanding in extent and increasing in intensity.

Mapping potential impacts to at-risk species requires understanding which stressors threaten the species (sensitivity) and where those stressors overlap the species' range (exposure) (*17*). We identified sensitivity to various stressors for each at-risk species, based on threat information from IUCN Red List assessments (*16*). Of 1,271 marine species identified as at-risk, 1,036 (82%) are sensitive to one or more of our suite of 14 anthropogenic stressors (Tables S1, S2), with 865 species (68%) sensitive to multiple stressors (Fig. 1). The remaining 235 species (18%) were not classified as sensitive to these stressors, being classified as either sensitive to others (e.g., invasive species, terrestrial hunting) or having insufficient information to determine sensitivity. The greatest proportion of at-risk species are sensitive to artisanal fishing (59%), direct human disturbance (e.g., trampling or coastal development, 46%) and sea surface temperature extremes (42%). Overall, 70% of at-risk species are sensitive to one or more fishing stressors (Fig. 1).

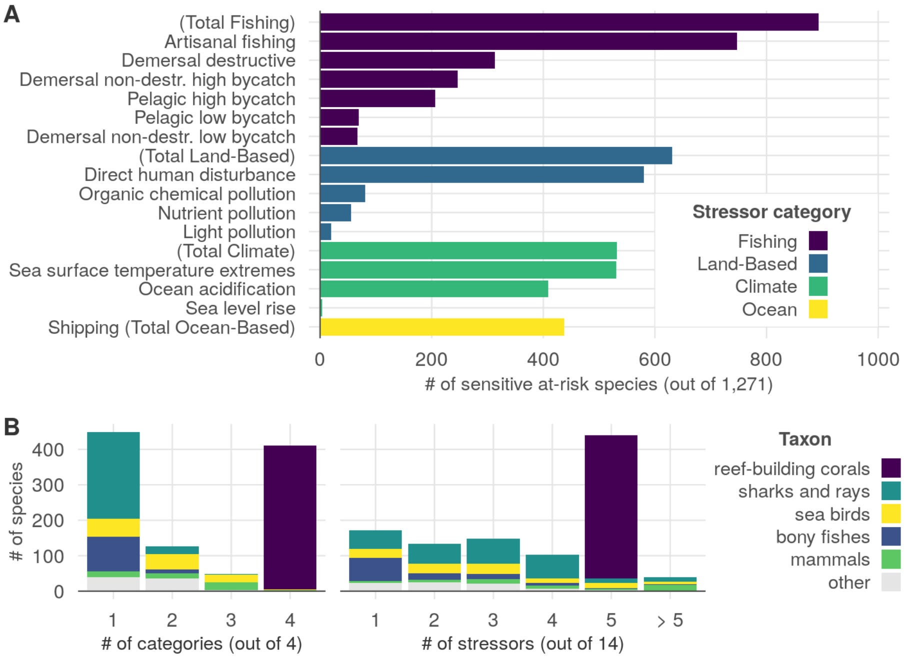

Fig. 1. Number of stressors and stressor categories (fishing, ocean, land-based, and climate) impacting at-risk species. A) Count of species classified as sensitive to each anthropogenic stressor or category; category totals count species sensitive to one or more stressors in the category. B) Counts of species by number of stressor categories (left) or stressors (right) to which each is sensitive; the five largest taxa are highlighted.

We then assessed where the range for each at-risk species intersected with the spatial extent of stressors to which it is sensitive (i.e., footprint of potential impacts on species range, hereafter "impacted range") and found highly heterogeneous patterns, with a much higher number of impacted species occurring in the Central Indo-Pacific and Coral Triangle region (Fig. 2A). This result accords with general understandings of global marine species richness (*18*) and patterns of threatened status of marine species (*19*). Adjusting for local richness of at-risk species (Fig. S1), we find additional areas with a high proportion of impacted species in the North Atlantic, North Sea, and Baltic Sea; international waters in the eastern Atlantic; and the western Pacific and tropical Indo-Pacific (Fig. 2B).

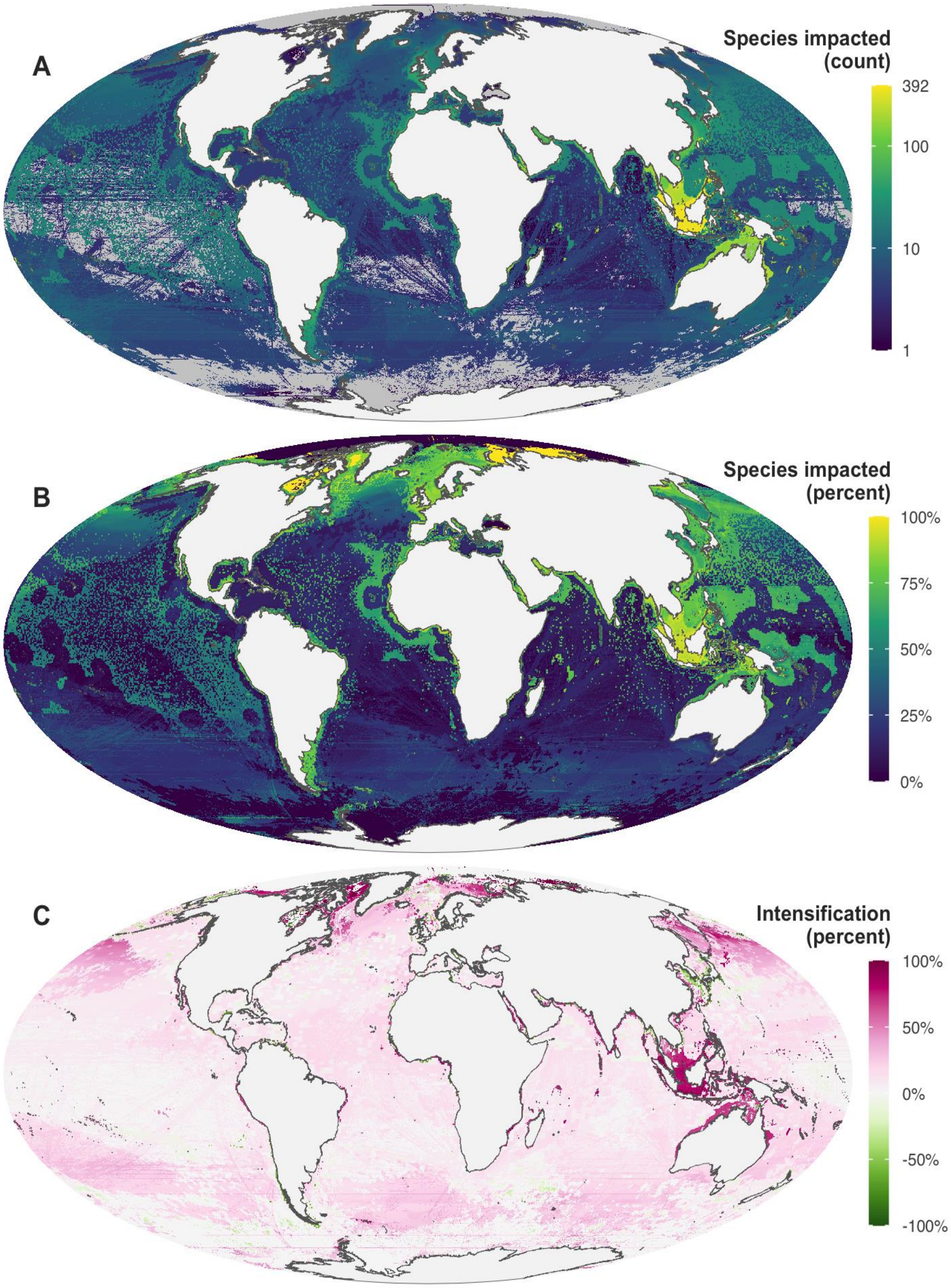

Fig. 2. Proportion of species impacted and with intensifying impacts. A) Number of threatened species impacted by one or more stressors in 2013, the most recent

year of assessment; grey indicates no impacted species. B) Proportion of threatened spp, relative to at-risk species richness, impacted by one or more stressors. C) Net proportion of impacted at-risk species where stressors are intensifying at a rate ≥0.1% per year over the period 2003 to 2013. See Fig. S2 for insets highlighting areas of high intensification and abatement.

Areas with a high proportion of impacted at-risk species (≥50% of species present in a cell were impacted) cover 22% of the global ocean, while areas with a low proportion of impacts (≤10% of species impacted) cover 26% (Fig. 2B). These regions represent areas of particularly high concern and potentially lower concern, respectively, for managing at-risk species. In 14% of the ocean, including some high biodiversity areas in Australia's northern waters, no at-risk species were impacted (Fig. 2B), highlighting potential refugia. Fishing stressors dominate impact footprints in most national exclusive economic zones (EEZs); however there are areas where this pattern is reversed and low fishing effort within certain EEZs gives way to unrestricted effort in areas beyond national jurisdiction (Fig. S3A). The footprint of climate stressors on at-risk species range is particularly notable in temperate and polar regions, as well as the Coral Triangle (Fig. S3B).

Human impacts on at-risk species are changing over time. From 2003-2013, impacts were intensifying (i.e., one or more stressors significantly increasing in intensity faster than 0.1% per year) for at least one at-risk species in 70% of the global ocean, and in 4% of the ocean a high proportion (>50%) of species were experiencing intensifying impacts (Figs. 2C, S2; Fig. S4 by stressor group). Only 4% of the ocean had areas where impacts were abating for at least one at-risk species, and a high proportion of abatement occurred in only 0.5% of the ocean (Figs. 2C, S2).

The footprint of impacts on species ranges is extensive and varies considerably by taxonomic group (Fig. S5). In the most recent year of assessment (2013) impacts occurred across

57±42% (mean±sd) (median 73%) of the total range of at-risk marine species, with a mean of 19±35% of range impacted by two or more stressors (Fig. 3A). Impacts exceed half the total range for 59% (n=744) of at-risk species, and 90% of total range for 42% (n=540) of species; for 7% (n=92) of species, the entire range is impacted. Corals and mangroves bear the largest cumulative impact footprints (99±2% and 89±18% of range, respectively).

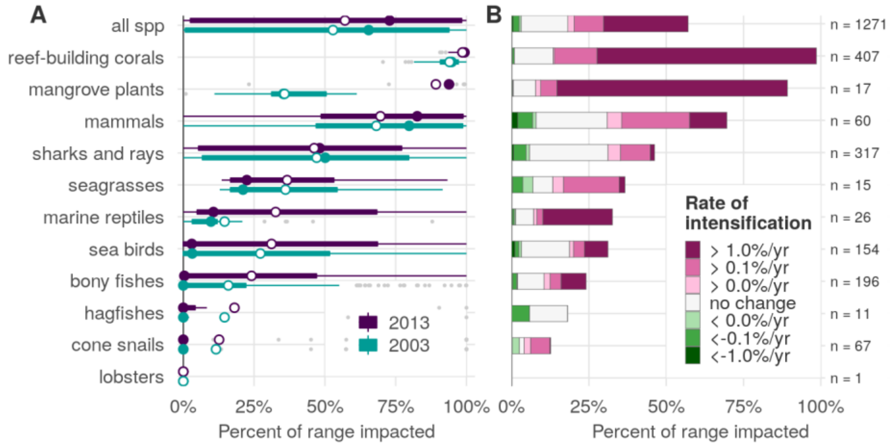

Fig. 3. Proportion of range impacted, including intensifying and abating impacts, by taxonomic group. A: Boxplots of impacted range and expansion per taxon, for 2003 and 2013. Hollow point is mean, solid point is median, thick line spans interquartile range (IQR), thin lines extend to the last observation within 1.5 × IQR. Grey points represent outliers. B: Taxon-level mean impacted range (2013) and average portion of that range intensifying or abating.

Because greater exposure to pressures likely increases extinction risk, there is an expectation that the percent range impacted should correlate positively with IUCN risk category. Such a relationship is evident for small-ranged species (those with range areas in the bottom quartile, <113,000 km^2) (Fig. S6A). However, this correlation breaks down for mid-ranged species (second quartile), and for large-ranged species, impacted range ostensibly seems to correlate negatively with extinction risk. A likely driver of these results is that, as range size increases, extinction risk becomes predicted less by overall impact footprint and more by impacts on critical habitats or life stages (*20*, *21*), particularly as stressors and species are concentrated in coastal areas. Focusing on species/stressor interactions in neritic waters, the results for small-ranged species are essentially unchanged, but the counterintuitive patterns for larger-ranged species are subdued (Fig. S6B). Importantly, large-ranged species at lower extinction risk are dominated by coast-hugging corals, widely impacted by the stressors included in this assessment, while large-ranged Endangered and Critically Endangered species include a higher proportion of pelagic-ranging turtles and sea birds harmed by terrestrial threats, e.g., hunting and invasive species, that are not assessed here (Fig. S6C).

Across all included species, average impacted footprint increased over time, from 53±41% in 2003 to 57±42% in 2013 (Fig. 3A), but varied dramatically among taxonomic groups. Mangroves (impacted footprint +53%), marine reptiles (+18%), and bony fishes (+8%) showed dramatic expansion of mean impacted footprint from 2003 to 2013; mean impact footprint for mammals, seagrasses, cone snails, and hagfishes did not significantly change. Notably, the impact footprint of sharks and rays shows a mild contraction over time, driven by shifting patterns of fishing pressure.

On average, impacts experienced by at-risk species intensified faster than 0.1% per year in 37±39% of their ranges, and faster than 1% per year in 27±35% of their ranges. Overall, only 2±6% of species' ranges experienced abating impacts, and only 1±2% were abating rapidly (Fig. 3B). Mangrove plants and corals in particular experienced intensifying impacts across their ranges (80±16% and 85±11%, respectively), largely driven by climate stressors. While the impact footprint on sharks and rays contracted by a small amount overall (Fig. 3A), impacts intensified over 11±15% of their ranges (Fig. 3B), particularly from small-scale fishing. On average, intensifying range exceeds abating range by a factor of 15.

While species ranges are dictated by ecological boundaries, effective management of activities that impact those species is dictated by political boundaries. At-risk species in the eight most-impacted EEZs on average suffer impacts across 88% of their ranges within those EEZs. In the largest EEZs, mean impacted footprint varies considerably, e.g., Indonesia (84%) vs. French Polynesia (12%). Uninhabited or sparsely inhabited islands make up the regions with the smallest mean footprint; within the eight least-impacted EEZs, species are on average impacted across 8% of their ranges. (Fig. 4, Table S3).

Fig. 4. Mean footprint of impacts on at-risk species ranges by EEZ. Each panel shows the area-weighted mean proportion of species range impacted within each EEZ, by stressor category. Yellow and green bars indicate the eight EEZs with the highest and lowest mean cumulative impacted footprint, respectively. Purple bars indicate the eight largest EEZs by area, which do not coincide with the eight highest or lowest scoring EEZs. Narrow grey bars indicate other EEZs within each geographic region.

Fishing activity, due to its broad reach (Fig. S3) and preponderance of sensitive species (Fig. 1), is the dominant contributor to cumulative impact to species' ranges in most EEZs, with some notable exceptions (e.g., Jordan and Australia; Fig. 4). Climate impacts are the second-largest contributor, followed by ocean-based impacts. Land-based impacts are most extreme in very small EEZs (e.g., Jordan, Singapore, Oecussi Ambeno, and Bosnia & Herzegovina; Fig. 4), but in general are the smallest contributors to species range impacts because they are limited to coastal areas, and absent for uninhabited islands.

IUCN Red List assessments (*16*) have long provided critical information on the status and key threats to at-risk species. Leveraging that work and recent advancements in mapping the location and pace of change of human induced stressors to the oceans (*5*), we show where species are being impacted and how the impacts are changing in intensity over time. This spatially and temporally resolved information helps inform conservation strategies aimed at species and locations with greatest conservation need. It can also inform effective ecosystem-based management strategies such as protections for flagship or keystone species, or taxa-specific mandates such as the Marine Mammal Protection Act of the United States, that leverage particular species to benefit the ecosystem more broadly. Co-occurrence analysis of taxa-level impacts highlights where such species-based strategies potentially confer co-benefits broadly across the ecosystem. For example, conservation efforts to reduce pressures on corals can simultaneously generate considerable benefits for marine mammals, bony fishes, sharks, seabirds, and marine reptiles (Fig. S7, Table S4). Additionally, by assessing at-risk marine species across all comprehensively-assessed taxa, our approach provides a window into broader ecosystem health with greater resolution into impacts across ecosystem structure complementary to impacts mapped onto representative habitats. Stressors that selectively impact some species over others potentially disrupt the 'biostructure' of an ecosystem (*22*), resulting in reductions in biomass of exploited species (*23*), reduced ecosystem functioning (*22*, *24*), and general loss of resilience (*25*) that can lead to ecosystem collapse to an undesirable stable state (*25–27*).

Reactive conservation measures are urgent where impacts on at-risk species are pervasive and intensifying (*28*) to allow for ecosystem recovery (*29*). Of particular concern is the tropical Indo-Pacific where accelerating climate impacts are exacerbated by intensifying fishing, shipping, and land-based stressors affecting most species (Fig. S4). Areas of low and/or abating impacts may indicate opportunities for proactive conservation to maintain existing patterns and trends (*28*); for example, the legal designation of the Phoenix Islands Protected Area in 2008 locked in already low impacts to species and enabled further reductions in impacts over time.

As most marine species ranges cross international boundaries (*30* (preprint)), effective conservation in one country may be undone by ineffective management in the next - the fate of an at-risk species depends on managing impacts throughout its range. For example, despite low fishing pressure in Jordan's waters (mean impacted range due to fishing 18%, Fig. 4), higher fishing pressures in bordering Egypt (32%), Israel (68%), and Saudi Arabia (82%) (Table S3) may reduce capacity of at-risk populations to rebuild following a regional disturbance. Quantifying effects of marine, land-based, and climate change stressors helps link drivers of impacts to management actions best suited to address them (*31*, *32*). Because climate impacts do not respect political boundaries, it is especially important to manage those impacts that can respond to localized policy, e.g. MPAs or fisheries management, to improve the resilience of at-risk species and populations to climate change (*33*).

Within the 1,271 species included in our study, marine vertebrates are well represented; this includes most large marine predators (e.g., sharks, cetaceans), which are widely considered as useful proxies for ecosystem health (*34*) (Table S5). Habitat building species are also well represented, including reef-building corals, seagrasses, and mangroves (Table S5). Sharks and rays (n=312) and corals (n=407) together represent 56% of at-risk species included. Although range maps and occurrence data exist for many more marine species than are included here, our dataset is limited by current state of knowledge of threatened species and species-specific sensitivity to anthropogenic stressors. While frameworks have been developed to estimate species sensitivity to climate stressors (e.g., (*4*, *17*)), a general framework for estimating species sensitivity to a comprehensive set of stressors, based on physiological and life history traits, would enable a thorough global assessment across many more species and taxonomic groups.

Our analysis reveals that human activity and climate change are impacting at-risk marine species within most of the global ocean and across a majority of their ranges, and these impacts are expanding and increasing in intensity for most species. However, areas of the ocean remain that harbor at-risk species free of impacts, including areas rich in biodiversity. If we hope to reverse the course of species extinction and recover populations of at-risk species, we need to know where species are exposed to the threats to which they are sensitive and how those threats are changing. Our results here provide that information and can embed within a wide range of management and conservation strategies, including marine protected areas, fisheries reform, land-sea conservation, and climate change mitigation efforts.

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Supporting Materials

At-risk marine biodiversity faces extensive, expanding, and intensifying human impacts

Materials and Methods

Impact on a species due to a stressor is a product of both sensitivity and exposure (*17*). Sensitivity was determined from threat information according to the IUCN Red List of Threatened Species ("Red List"), while exposure was determined based on overlap between spatial distribution of stressor and species range.

We crosswalked the threats listed by IUCN to stressor data available from an assessment of global cumulative human impacts (CHI) on marine habitats (*5*) (Tables S1, S2). For land-based and ocean-based stressors, the IUCN threat description mapped unambiguously onto a CHI stressor (Table S1). To match IUCN-noted fishing threats (differentiated by large/small scale and intentional/unintentional) to CHI fishing stressors (based on specific gear types), threat narratives were searched for particular gear-related key words and regular expressions patterns to ensure appropriate assignment of sensitivity to a specific stressor; similarly for climate-related threats and stressors. Of the 1,271 threatened or near-threatened marine Red List species, 1,036 were determined to be sensitive to one or more included stressors (Table S1).

Exposure to a threat was determined by overlapping a map of species range with maps of distributions of anthropogenic marine stressors. Stressor maps (*5*) describe the rescaled intensity of 14 anthropogenic stressors (Tables S1, S2) annually from 2003 to 2013. Data are presented on a global grid at ~1 km resolution in the WGS84 Mollweide coordinate reference system, an equal area projection that retains considerable accuracy in area at polar latitudes.

Stressor maps from Halpern et al. (*5*) include four general categories:

- Fishing: commercial demersal destructive, commercial demersal nondestructive high bycatch, commercial demersal nondestructive low bycatch, pelagic high bycatch, pelagic low bycatch, artisanal
- Climate change: sea surface temperature, ocean acidification, sea level rise
- Ocean: shipping
- Land-based: nutrient pollution, organic chemical pollution, human population, light pollution

Here we briefly restate the methods to generate stressor maps presented in Halpern et al. (*5*); detailed methods and references for data sources can be found in the supporting information for that assessment.

Stressors were rescaled to have values between 0-1. Rescaling allows for direct comparison among drivers with dramatically different units of measurement. With the exception of ocean acidification, Halpern et al. (*5*) rescaled each stressor layer by normalizing by the 99.99th percentile (to eliminate extreme outliers) across all global raster cells and years for that stressor, with the result capped to a maximum of 1. This approach assumes a linear relationship between the magnitude of the stressor and the impact on the ecosystem. This assumption ignores thresholds that likely exist but are known for very few stressors. For the ocean acidification stressor, Halpern et al. (*5*) rescaled the data based on biological thresholds for aragonite saturation.

For many stressors, the distribution of values was highly skewed such that extreme values dictated the rescaling value. In these cases, Halpern et al. (*5*) log-transformed stressor values prior to rescaling. Table S2 describes the transformations, where applicable, and rescaling values for all stressor layers; further detail can be found in the methods in (*5*).

To determine the pace of change of stressor intensity over time, Halpern et al. (*5*) estimated per-cell annual change in stressor intensity by applying a linear regression model to each raster cell, i.e., $stressor \sim \beta_0 + \beta_1 \cdot year$, across years 2003 to 2013.

For the purposes of our analysis, we flattened each of these stressor maps from Halpern et al. (*5*) to a simple presence/absence by first aggregating (using mean value) to a ~10 km grid, then calculating a minimum threshold based on a 95% volume contour across the entire sequence of years (2003-2013) for the stressor. Species range maps (*16*, *35*)) were reprojected and rasterized to the same ~10 km grid to indicate species presence/absence. Note that species range maps outline regions where species are likely to be present, though they do not distinguish between core habitat and fringe habitat; additionally, these range maps are static in time and do not account for climate-driven range shifts. These were subsequently clipped to a bathymetric to constrain neritic and shallow-water species to areas no deeper than 200 m. Resolution of species range maps can have important implications for minimizing commission errors (*36*); this ~10 km resolution was chosen as a tradeoff between inclusion of finer-resolution stressor data and reduction of range map commission errors.

Species level impacted ranges were calculated by intersecting the gridded species range map and flattened stressor map for each stressor to which the species is sensitive. Following Allan et al. (*14*), the impacted range of a species is the logical sum of all stressor/species intersection maps: a cell is impacted if the species suffers potential impacts from one or more stressors in that location, avoiding assumptions about an additive/synergistic/antagonistic nature of cumulative impacts. Impacted range maps were calculated for each species at three levels of aggregation: individual stressor, stressor category (fishing, ocean, land-based, and climate), and cumulative across the full suite of stressors.

Summing the impacted range maps across all at-risk species (as well as taxonomic groups), we mapped the spatial distribution of the number of impacted species in each cell; we then calculated the proportional impact based on the number of impacted species found in the cell relative to the total number of at-risk species in the cell, with values ranging from 0 to 1. The proportional impact more closely approaches the method of habitat-based cumulative human impacts presented by Halpern et al. (*5*), in which the impact score of a cell is the average impact across all habitats present in the cell.

For each species, the cumulative impacted footprint for a suite of stressors is simply the proportion of range that is impacted by one or more stressors. Rate of expansion of impacted footprint was estimated from a simple linear model, $footprint \sim \beta_0 + \beta_1 \cdot year$, across the 2003-2013 range of data. Note that species range maps used in this analysis are static, therefore expansion of impacted footprint does not take into account account potential shifts in species ranges.

To identify areas of impact intensification, we again used the time series of stressor maps, this time using the rescaled stressor intensity to calculate per-cell trend in stressor intensity. For each stressor, we performed a per-cell linear regression of $intensity \sim \beta_0 + \beta_1 \cdot year$ across the time series. We reclassified cells based on statistical significance ($p < 0.05$) and ecological significance (rate of change of ±0.1% per year or greater, and ±1.0% per year for rapid change). Next, for a given species, we identified all relevant stressor trend layers (via sensitivity), and per cell, classified any cell where at least one stressor was significantly increasing and none were significantly decreasing as an area of intensifying impact; the converse (one or more significantly decreasing and none increasing) was classified as an area of abating impact. For cells with one or more stressors increasing and one or more decreasing, we classified the effect on cumulative impact as indeterminate, resulting in a conservative estimate of areas of intensifying or abating impact. Note that for a given species in a given cell, these categories are mutually exclusive, but a species could simultaneously be experiencing intensifying impacts in one part of its range and abating impacts in another.

Finally, to quantify the overall effect of intensifying and abating impacts in a location, we calculated the difference between the counts of species with intensifying impacts and those with abating impacts in a particular location, and divided by the total species richness, i.e. intensification score $= \frac{n_{cell,intensifying} - n_{cell,abating}}{n_{cell}}$ with values ranging from +1 (all species subject to intensifying impacts) to -1 (all species subject to abating impacts).

Mapping impacts on all species in each taxon across the four stressor categories and the full suite of stressors, we defined areas of substantial taxon-level impacts as any cells in which at least 25% of the local taxonomic assemblage were impacted. Using these taxa-level impact maps, we calculated co-occurrence of taxon-level impacts using a cell-wise pairwise comparison. Distribution of co-occurring impacts was mapped as the number of different taxonomic groups substantially impacted in each cell.

Impact scores for national Exclusive Economic Zones (EEZs) were calculated first by determining the EEZ-specific impact footprint for each species, based on the species' range falling within the EEZ and the impacts on that portion of range, and then calculating the area-weighted average footprint across all at-risk species present within the EEZ. Unimpacted species were scored as zero and included in the average. These were calculated for the cumulative footprint across all stressors, as well as for the four stressor categories.

All analysis was coded and calculated in R version 3.6.3 (*37*), using the `tidyverse` (*38*), `raster` (*39*), `sf` (*40*), and `widyr` (*41*) packages. Figures were generated in R using the `ggplot2` (*42*), `ggforce` (*43*), and `cowplot` (*44*) packages, and tables were generated using the `flextable` package (*45*). All code and processed data can be found at https://github.com/oharac/bd_chi.

SI Tables

Table S1: IUCN threat categories mapped to cumulative impact stressors.

Methods and descriptions of cumulative impact stressors from Ref. (5) are detailed in Table S2. Stressors that match to multiple threat categories are marked with an asterisk.

Threat category	Threat subcategory	Stressor	spp
1. Residential & commercial development	1.1. Housing & urban areas	Direct human disturbance*	501
	1.2. Commercial & industrial areas		468
	1.3. Tourism & recreation areas		451
2. Agriculture & aquaculture	2.4. Marine & freshwater aquaculture	Nutrient pollution*	36
4. Transportation & service corridors	4.3. Shipping lanes	Shipping	438
5. Biological resource use	5.4. Fishing & harvesting aquatic resources• 5.4.1 Intentional use: subsistence/small scale• 5.4.2 Intentional use: large scale• 5.4.3 Unintentional effects: subsistence/small scale• 5.4.4 Unintentional effects: large scale	Artisanal fishing	747
		Demersal destructive fishing	313
		Demersal non-destructive high bycatch fishing	246
		Demersal non-destructive low bycatch fishing	67
		Pelagic high bycatch fishing	206
		Pelagic low bycatch fishing	69
6. Human intrusions & disturbance	6.1. Recreational activities	Direct human disturbance*	460
	6.3. Work & other activities		20
9. Pollution	9.1. Domestic & urban waste water	Organic chemical pollution	7
	9.2. Industrial & military effluents		74
	9.3. Agricultural & forestry effluents		7
	9.1. Domestic & urban waste water	Nutrient pollution*	19
	9.3. Agricultural & forestry effluents		9
	9.6. Excess energy	Light pollution	20
11. Climate change & severe weather	11.1. Habitat shifting & alteration	Ocean acidification	2
	11.3. Temperature extremes		406
	11.5. Other impacts		2
	11.1. Habitat shifting & alteration	Sea level rise	3
	11.5. Other impacts		1
	11.1. Habitat shifting & alteration	Sea surface temperature extremes	92
	11.3. Temperature extremes		472
	11.5. Other impacts		8

Table S2: Overview of methods to generate stressor distribution maps (from Ref. (5)).

Stressor	Preparing data	Gapfilling	Transform	Rescaling (0 to 1)	Potential species-level impacts
Sea surface temperature	Number of extreme SST weeks during a five-year period subtracted from the number of extreme SST weeks during a baseline 5 year period (1985-1989). An extreme week is defined as (weekly SST - weekly climatological SST) exceeding 1 SD of anomalies calculated across 1982-2017 for that week.	Coastal cells without data estimated using mean of surrounding cells, gapfilling performed on total annual extreme events	NA	Normalized by raster value corresponding 99.99th quantile across all years	Physiological stress or mortality
Ocean acidification	Monthly aragonite saturation values (Ω) averaged to obtain annual estimates.	Coastal cells without data estimated using inverse distance weighting of rescaled data	NA	Cell stressor score = 1 when Ω ≤ 1; otherwise, stressor score = (Ω_current - Ω_ref) / (1 - Ω_ref) where Ω_ref = average from 1880-1889	Disruption of calcium structure formation, physiological stress or mortality
Sea level rise	Monthly anomalies averaged to obtain annual mean sea level anomaly. 5 year mean of annual data used to smooth large yearly variation.	Estimated missing coastal data using inverse distance weighting of 5 year mean anomaly data	NA	Normalized by raster value corresponding 99.99th quantile across all years	Flooding, habitat disruption
Fishing: artisanal	Total tonnes of catch from nonindustrial fisheries calculated for each year (Watson 2018, 0.5° resolution). Catch divided by corresponding year's Net Primary Productivity (monthly data averaged for yearly NPP estimate) to standardize by region's productivity.	Fisheries catch and NPP gapfilled using average of nearest neighbors	NPP log10, catch not transformed	Normalized by raster value corresponding 99.99th quantile across all years	Biomass removal, bycatch
Fishing: demersal destructive	Total tonnes of catch for industrial demersal fishing using gear types causing habitat destruction calculated for each year. Catch divided by corresponding year's Net Primary Productivity (monthly data averaged for yearly NPP estimate) to standardize by region's productivity.	Fisheries and NPP gapfilled using average of nearest neighbors	NPP log10, catch not transformed	Normalized by raster value corresponding 99.99th quantile across all years	Biomass removal, habitat destruction
Fishing: demersal nondestructive high bycatch	Total tonnes of catch for industrial demersal fishing using high bycatch practices calculated for each year. Catch data divided by corresponding year's Net Primary Productivity (monthly data averaged for yearly NPP estimate) to standardize by region's productivity.	Fisheries and NPP gapfilled using average of nearest neighbors	NPP log10, catch not transformed	Normalized by raster value corresponding 99.99th quantile across all years	Biomass removal, bycatch
Fishing: demersal nondestructive low bycatch	Total tonnes of catch for industrial demersal fishing using low bycatch practices calculated for each year. Catch data divided by corresponding year's Net Primary Productivity (monthly data averaged for yearly NPP estimate) to standardize by the region's productivity.	Fisheries and NPP gapfilled using average of neighbors	NPP log10, catch not transformed	Normalized by raster value corresponding 99.99th quantile across all years	Biomass removal

Table S2: Overview of methods to generate stressor distribution maps (from Ref. (5)).

Stressor	Preparing data	Gapfilling	Transform	Rescaling (0 to 1)	Potential species-level impacts
Fishing: pelagic high bycatch	Total tonnes of catch for industrial pelagic fishing using high bycatch practices calculated for each year. Catch data divided by corresponding year's Net Primary Productivity (monthly data averaged for yearly NPP estimate) to standardize by region's productivity.	Fisheries and NPP gapfilled using average of nearest neighbors	NPP log10, catch not transformed	Normalized by raster value corresponding 99.99th quantile across all years	Biomass removal, bycatch
Fishing: pelagic low bycatch	Total tonnes of catch for industrial pelagic fishing using low bycatch practices calculated for each year. Catch data divided by corresponding year's Net Primary Productivity (monthly data averaged for yearly NPP estimate) to standardize by region's productivity.	Fisheries and NPP gapfilled using average of neighbors	NPP log10, catch not transformed	Normalized by raster value corresponding 99.99th quantile across all years	Biomass removal
Nutrient pollution (runoff)	Intensity of pollution from modeled plumes of land-based fertilizer pollution (Halpern et al. 2008), based on country level fertilizer use (UN 2016), land cover data (Friedle et al. 2010), and elevation data (USGS 2004)	NA	ln(x + 1)	Normalized by raster value corresponding 99.99th quantile across all years	Eutrophication, harmful algal blooms, physiological stress or mortality
Organic chemical pollution (runoff)	Intensity of pollution from modeled plumes of land-based pesticide pollution (Halpern et al. 2008), based on country level pesticide use (UN 2016), land cover data (Friedle et al. 2010), and elevation data (USGS 2004)	NA	ln(x + 1)	Normalized by raster value corresponding 99.99th quantile across all years	Toxins, hormone disruption, physiological stress or mortality
Direct human disturbance	Density (people per km2) converted to population (people per raster cell). Intervening years (i.e., years outside of 2000, 2005, 2010, 2015, 2020) interpolated using a linear model. For each raster cell, coastal human population summed for 10 km radius. Data cropped to include only cells 1km from the coast.	NA	ln(x + 1)	Normalized by raster value corresponding 99.99th quantile across all years	Intertidal habitat destruction, coastal development, habitat fragmentation
Light pollution	Non-calibrated radiance values from satellite data calibrated across year/satellite following methods of Elvidge et al. 2009.	The dataset does not include the north and south pole regions, and these were estimated as zero	NA	Normalized by raster value corresponding 99.99th quantile across all years (excluding zero values)	Disruption of navigation

Table S2: Overview of methods to generate stressor distribution maps (from Ref. (5)).

Stressor	Preparing data	Gapfilling	Transform	Rescaling (0 to 1)	Potential species-level impacts
Shipping	Tournadre (2018) data used to create yearly rasters describing annual proportional change in shipping relative to 2011. Multiplied yearly proportional change raster with high resolution shipping raster (Halpern et al. 2015 and Wallbridge 2013) to estimate shipping traffic over time.	Outer border of shipping data was gapfilled using mean of nearest neighbors; NA values for yearly shipping density were estimated as the total global change in shipping relative to 2011	ln(x + 1)	99.99th quantile determined for each year (1992-2016) and the average of these values used to rescale data	Ship strikes, noise pollution, chemical pollution

Table S3: Mean proportion of in-region species range impacted

EEZ/Region	cumulative	fishing	climate	land-based	ocean	N spp
Global	0.367	0.192	0.184	0.013	0.131	1271
Bosnia and Herzegovina	1.000	1.000	0.200	1.000	0.200	5
Singapore	0.945	0.934	0.754	0.538	0.762	408
Malaysia	0.929	0.742	0.740	0.052	0.677	465
Oecussi Ambeno	0.909	0.905	0.630	0.393	0.649	388
Cameroon	0.906	0.900	0.021	0.016	0.055	72
Jordan	0.903	0.183	0.699	0.753	0.704	186
Brunei	0.901	0.792	0.679	0.075	0.679	409
Bahrain	0.882	0.880	0.455	0.066	0.395	98
Iraq	0.881	0.877	0.437	0.054	0.471	91
Kuwait	0.879	0.876	0.441	0.086	0.465	94
Vietnam	0.873	0.683	0.600	0.025	0.590	340
Guernsey	0.871	0.871	0.034	0.010	0.074	42
Saudi Arabia	0.866	0.802	0.556	0.048	0.462	230
Belgium	0.864	0.787	0.151	0.042	0.102	32
Jersey	0.857	0.857	0.144	0.019	0.072	42
United Arab Emirates	0.854	0.840	0.453	0.050	0.471	116
Sudan	0.852	0.799	0.540	0.034	0.415	195
Netherlands	0.848	0.765	0.151	0.023	0.113	33
Slovenia	0.845	0.845	0.076	0.126	0.049	52
Thailand	0.842	0.552	0.549	0.045	0.483	427
Indonesia	0.842	0.707	0.632	0.077	0.455	523
Poland	0.839	0.771	0.185	0.078	0.003	10
Philippines	0.838	0.254	0.589	0.168	0.376	471
Estonia	0.837	0.797	0.266	0.042	0.003	10
Germany	0.836	0.749	0.099	0.045	0.112	33
United Kingdom	0.824	0.722	0.149	0.014	0.099	67
Iran	0.824	0.741	0.396	0.020	0.410	131
Denmark	0.820	0.734	0.067	0.029	0.122	37
Lithuania	0.814	0.792	0.250	0.059	0.003	8
Latvia	0.807	0.790	0.222	0.037	0.004	9
Cambodia	0.806	0.433	0.486	0.029	0.453	266

Table S3: Mean proportion of in-region species range impacted

EEZ/Region	cumulative	fishing	climate	land-based	ocean	N spp
Croatia	0.801	0.776	0.058	0.028	0.041	58
Djibouti	0.798	0.555	0.495	0.070	0.291	218
Myanmar	0.794	0.675	0.548	0.055	0.092	280
Tunisia	0.788	0.760	0.053	0.010	0.034	69
Norway	0.775	0.482	0.312	0.005	0.178	47
Sweden	0.754	0.687	0.133	0.036	0.038	34
Qatar	0.752	0.499	0.454	0.034	0.461	99
Eritrea	0.751	0.136	0.664	0.035	0.497	216
China	0.751	0.714	0.125	0.022	0.166	198
Faeroe Islands	0.742	0.454	0.268	0.001	0.178	34
Morocco	0.740	0.631	0.100	0.007	0.056	95
Iceland	0.732	0.360	0.313	0.001	0.194	35
Finland	0.729	0.649	0.234	0.052	0.004	10
Mayotte	0.720	0.525	0.167	0.035	0.207	199
Turkey	0.719	0.673	0.058	0.046	0.055	61
East Timor	0.716	0.450	0.577	0.270	0.327	398
Gibraltar	0.714	0.624	0.098	0.044	0.036	65
Papua New Guinea	0.712	0.286	0.371	0.049	0.283	435
Oman	0.711	0.623	0.153	0.011	0.178	161
Ghana	0.701	0.618	0.051	0.004	0.080	77
Bangladesh	0.686	0.642	0.065	0.027	0.024	97
Ireland	0.664	0.494	0.160	0.006	0.093	62
Greenland	0.653	0.111	0.452	0.001	0.172	25
Argentina	0.646	0.556	0.119	0.002	0.037	95
Russian Federation	0.643	0.306	0.363	0.002	0.116	79
France	0.637	0.522	0.126	0.021	0.065	90
Republic of Korea	0.632	0.538	0.085	0.022	0.100	100
Albania	0.629	0.563	0.050	0.035	0.041	62
Jan Mayen	0.614	0.062	0.384	0.000	0.186	15
Pakistan	0.600	0.529	0.134	0.013	0.172	131
Algeria	0.590	0.484	0.091	0.016	0.044	67
Saint Pierre and Miquelon	0.590	0.409	0.220	0.007	0.118	41
Taiwan	0.586	0.315	0.261	0.040	0.296	384
Japan	0.586	0.399	0.184	0.028	0.180	402
Egypt	0.583	0.330	0.301	0.018	0.282	239
Nigeria	0.581	0.509	0.046	0.006	0.073	78

Table S3: Mean proportion of in-region species range impacted

EEZ/Region	cumulative	fishing	climate	land-based	ocean	N spp
Guinea	0.580	0.481	0.081	0.005	0.063	81
Lebanon	0.576	0.509	0.063	0.017	0.059	54
Montenegro	0.568	0.503	0.053	0.019	0.042	59
Italy	0.555	0.457	0.074	0.016	0.047	75
Canary Islands	0.554	0.424	0.096	0.002	0.057	82
Canada	0.552	0.232	0.275	0.005	0.118	87
India	0.547	0.467	0.142	0.019	0.156	284
Republique du Congo	0.546	0.476	0.031	0.004	0.071	74
Yemen	0.545	0.350	0.311	0.031	0.322	250
Syria	0.545	0.484	0.065	0.025	0.057	50
Belize	0.542	0.406	0.132	0.043	0.134	76
Democratic Republic of the Congo	0.535	0.460	0.031	0.006	0.075	71
Mauritania	0.533	0.429	0.088	0.001	0.068	83
Ukraine	0.524	0.324	0.221	0.116	0.000	8
Democratic People's Republic of Korea	0.522	0.421	0.072	0.023	0.074	59
Spain	0.520	0.378	0.114	0.011	0.061	94
Greece	0.498	0.396	0.059	0.014	0.067	68
Togo	0.492	0.394	0.051	0.006	0.082	75
Northern Saint-Martin	0.492	0.298	0.144	0.022	0.184	63
Mozambique	0.489	0.359	0.282	0.030	0.217	267
United Republic of Tanzania	0.487	0.438	0.275	0.085	0.080	212
Monaco	0.481	0.340	0.085	0.066	0.038	61
Australia	0.476	0.014	0.346	0.005	0.384	446
Andaman and Nicobar	0.475	0.411	0.261	0.034	0.099	210
Angola	0.473	0.391	0.039	0.004	0.074	89
Gambia	0.460	0.356	0.082	0.009	0.066	85
Senegal	0.459	0.340	0.088	0.006	0.068	102
Sierra Leone	0.457	0.337	0.094	0.005	0.072	79
Guinea Bissau	0.457	0.345	0.082	0.008	0.062	82
Saint Lucia	0.447	0.308	0.066	0.022	0.122	65
Uruguay	0.446	0.352	0.073	0.005	0.044	97
Venezuela	0.439	0.329	0.087	0.015	0.123	96
Malta	0.434	0.336	0.053	0.003	0.053	61
Israel	0.432	0.339	0.071	0.022	0.067	231
Benin	0.431	0.330	0.050	0.008	0.080	75

Table S3: Mean proportion of in-region species range impacted

EEZ/Region	cumulative	fishing	climate	land-based	ocean	N spp
Kenya	0.429	0.370	0.259	0.052	0.042	209
Sri Lanka	0.424	0.331	0.195	0.037	0.169	256
Madagascar	0.424	0.199	0.306	0.032	0.197	262
Ivory Coast	0.420	0.314	0.052	0.004	0.078	77
Cyprus	0.411	0.282	0.071	0.008	0.071	52
Solomon Islands	0.401	0.071	0.304	0.047	0.115	352
Madeira	0.387	0.201	0.113	0.001	0.078	81
Western Sahara	0.387	0.253	0.087	0.001	0.057	84
Portugal	0.387	0.241	0.103	0.005	0.071	81
Guyana	0.386	0.296	0.055	0.003	0.067	65
Montserrat	0.372	0.261	0.066	0.010	0.120	63
Nicaragua	0.371	0.214	0.131	0.007	0.126	105
Libya	0.365	0.269	0.055	0.003	0.053	66
Fiji	0.362	0.077	0.287	0.028	0.158	274
United States of America	0.357	0.201	0.087	0.004	0.096	206
Saba	0.352	0.178	0.114	0.001	0.160	64
Dominica	0.349	0.215	0.055	0.013	0.112	70
Brazil	0.349	0.252	0.050	0.003	0.067	141
Mexico	0.345	0.235	0.070	0.004	0.090	164
Haiti	0.343	0.245	0.071	0.023	0.101	74
Vanuatu	0.342	0.016	0.292	0.034	0.117	258
Liberia	0.340	0.198	0.082	0.002	0.077	81
Comoro Islands	0.335	0.235	0.157	0.040	0.190	200
Maldives	0.334	0.093	0.203	0.054	0.150	173
Ecuador	0.333	0.276	0.016	0.003	0.058	108
New Caledonia	0.325	0.001	0.266	0.008	0.167	285
Georgia	0.325	0.044	0.235	0.103	0.002	4
Gabon	0.319	0.231	0.028	0.002	0.075	77
El Salvador	0.310	0.153	0.107	0.006	0.105	61
Suriname	0.310	0.216	0.052	0.002	0.065	66
Panama	0.305	0.141	0.106	0.013	0.090	119
Honduras	0.304	0.172	0.102	0.010	0.146	103
Peru	0.304	0.257	0.005	0.004	0.055	89
Guadeloupe and Martinique	0.293	0.151	0.060	0.010	0.113	73
Sint Eustatius	0.292	0.101	0.120	0.016	0.164	63
Seychelles	0.291	0.067	0.186	0.002	0.130	216

Table S3: Mean proportion of in-region species range impacted

EEZ/Region	cumulative	fishing	climate	land-based	ocean	N spp
Falkland Islands	0.288	0.106	0.165	0.000	0.037	42
Somalia	0.285	0.091	0.192	0.014	0.061	229
Equatorial Guinea	0.285	0.180	0.033	0.001	0.082	78
Samoa	0.284	0.147	0.190	0.028	0.072	178
Northern Mariana Islands and Guam	0.283	0.075	0.135	0.004	0.114	171
Saint Kitts and Nevis	0.283	0.136	0.079	0.021	0.130	64
Sao Tome and Principe	0.281	0.163	0.049	0.001	0.080	57
Grenada	0.280	0.137	0.069	0.016	0.120	82
Kerguelen Islands	0.277	0.003	0.252	0.000	0.022	27
Trinidad and Tobago	0.276	0.108	0.115	0.018	0.152	85
Heard and McDonald Islands	0.275	0.000	0.262	0.000	0.013	22
Aruba	0.275	0.166	0.060	0.008	0.116	88
British Indian Ocean Territory	0.274	0.000	0.228	0.000	0.068	203
Curaçao	0.274	0.155	0.053	0.009	0.109	86
Cape Verde	0.273	0.091	0.106	0.001	0.080	79
Azores	0.270	0.091	0.086	0.001	0.100	57
Wake Island	0.267	0.062	0.135	0.000	0.072	51
Antigua and Barbuda	0.267	0.132	0.060	0.003	0.109	73
Marshall Islands	0.265	0.055	0.180	0.018	0.062	227
South Georgia and the South Sandwich Islands	0.264	0.037	0.215	0.000	0.025	23
Palau	0.260	0.049	0.148	0.013	0.108	275
Juan de Nova Island	0.256	0.029	0.143	0.000	0.174	196
Romania	0.254	0.092	0.183	0.038	0.003	8
Jamaica	0.251	0.129	0.056	0.008	0.117	74
Dominican Republic	0.248	0.127	0.056	0.013	0.113	75
Glorioso Islands	0.247	0.048	0.145	0.000	0.081	216
Crozet Islands	0.245	0.000	0.229	0.000	0.016	27
Micronesia	0.242	0.069	0.125	0.007	0.076	289
Puerto Rico and Virgin Islands of the United States	0.242	0.107	0.052	0.009	0.111	77
New Zealand	0.242	0.075	0.134	0.001	0.039	108
Tristan da Cunha	0.236	0.007	0.202	0.000	0.030	38
American Samoa	0.230	0.053	0.139	0.001	0.058	180
Prince Edward Islands	0.228	0.000	0.204	0.000	0.024	28
Tonga	0.226	0.009	0.168	0.010	0.082	148

Table S3: Mean proportion of in-region species range impacted

EEZ/Region	cumulative	fishing	climate	land-based	ocean	N spp
Bouvet Island	0.222	0.000	0.194	0.000	0.027	17
Guatemala	0.218	0.095	0.061	0.007	0.094	103
Sint Maarten	0.212	0.000	0.127	0.021	0.170	62
Cuba	0.211	0.056	0.092	0.031	0.092	86
Chile	0.210	0.114	0.056	0.002	0.049	114
Bulgaria	0.205	0.080	0.107	0.055	0.005	8
South Africa	0.202	0.059	0.065	0.005	0.101	199
Saint Vincent and the Grenadines	0.201	0.053	0.060	0.018	0.117	70
Niue	0.199	0.005	0.144	0.001	0.051	120
Anguilla	0.195	0.065	0.049	0.003	0.104	72
Barbados	0.193	0.046	0.058	0.003	0.097	68
Clipperton Island	0.192	0.044	0.087	0.000	0.064	58
French Guiana	0.186	0.048	0.066	0.001	0.080	65
Norfolk Island	0.183	0.000	0.117	0.000	0.071	91
Tuvalu	0.181	0.039	0.128	0.006	0.023	234
Amsterdam Island and Saint Paul Island	0.181	0.000	0.159	0.000	0.021	35
Turks and Caicos Islands	0.181	0.049	0.051	0.002	0.112	72
Mauritius	0.180	0.021	0.102	0.004	0.113	223
British Virgin Islands	0.179	0.052	0.046	0.005	0.104	73
Réunion	0.177	0.019	0.059	0.012	0.128	201
Cook Islands	0.175	0.023	0.112	0.001	0.043	124
Colombia	0.174	0.030	0.070	0.008	0.091	131
Kiribati	0.174	0.073	0.089	0.019	0.017	232
Bahamas	0.172	0.021	0.081	0.004	0.133	93
Bermuda	0.168	0.020	0.049	0.001	0.100	56
Costa Rica	0.168	0.061	0.039	0.004	0.075	127
Wallis and Futuna	0.167	0.007	0.136	0.008	0.031	197
Nauru	0.165	0.061	0.084	0.001	0.021	218
Namibia	0.160	0.053	0.042	0.000	0.072	78
Tokelau	0.155	0.011	0.115	0.003	0.034	129
Bassas da India	0.152	0.000	0.028	0.000	0.124	46
Bonaire	0.150	0.012	0.060	0.009	0.111	85
Cocos Islands	0.148	0.012	0.066	0.001	0.071	78
Christmas Island	0.145	0.038	0.040	0.001	0.070	83
Ascension	0.137	0.037	0.069	0.000	0.032	38

Table S3: Mean proportion of in-region species range impacted

EEZ/Region	cumulative	fishing	climate	land-based	ocean	N spp
Macquarie Island	0.129	0.000	0.121	0.000	0.008	32
Cayman Islands	0.128	0.000	0.039	0.004	0.098	69
Johnston Atoll	0.124	0.078	0.005	0.000	0.043	69
Palmyra Atoll	0.123	0.064	0.005	0.000	0.062	74
French Polynesia	0.116	0.010	0.066	0.004	0.054	142
Pitcairn	0.114	0.030	0.020	0.000	0.066	72
Ile Europa	0.113	0.000	0.040	0.000	0.079	167
Ile Tromelin	0.090	0.000	0.036	0.000	0.057	174
Saint Helena	0.083	0.011	0.040	0.000	0.032	34
Howland Island and Baker Island	0.081	0.059	0.002	0.000	0.023	129
Jarvis Island	0.073	0.043	0.000	0.000	0.030	55
Line Group	0.059	0.022	0.004	0.000	0.034	129
Phoenix Group	0.057	0.027	0.012	0.000	0.020	144
Pacific Western Central	0.585	0.458	0.091	0.000	0.051	68
Pacific Northwest	0.449	0.194	0.168	0.000	0.094	63
Pacific Northeast	0.392	0.055	0.220	0.000	0.117	40
Atlantic Eastern Central	0.351	0.208	0.082	0.000	0.071	55
Atlantic Northeast	0.300	0.006	0.158	0.000	0.136	52
Pacific Eastern Central	0.278	0.190	0.037	0.000	0.056	74
Pacific Southeast	0.257	0.168	0.062	0.000	0.032	79
Atlantic Northwest	0.251	0.049	0.093	0.000	0.112	49
Atlantic Western Central	0.238	0.091	0.063	0.000	0.089	44
Pacific Southwest	0.207	0.003	0.174	0.000	0.030	91
Indian Ocean Eastern	0.186	0.031	0.120	0.000	0.036	77
Atlantic Southwest	0.156	0.020	0.099	0.000	0.037	84
Atlantic Southeast	0.149	0.013	0.092	0.000	0.044	76
Indian Ocean Western	0.146	0.026	0.078	0.000	0.043	74
Antarctica	0.139	0.004	0.118	0.000	0.017	44

Table S4: Total taxa-level impacted range within taxon and cooccurring between taxa.

Taxon	Taxon 2	all (km²)	climate (km²)	fishing (km²)	land-based (km²)	ocean (km²)
mammals	-	221,600,000	10,370,000	55,230,000	1,123,000	202,900,000
marine reptiles	-	203,900,000	200,100,000	18,890,000	2,559,000	
sea birds	-	160,800,000	148,600,000	21,850,000	1,647,000	82,990
sharks and rays	-	83,130,000		83,130,000	8,041	
bony fishes	-	76,570,000	63,820	76,760,000	10,020	
reef-building corals	-	10,930,000	10,370,000	4,929,000	1,004,000	8,281,000
mangrove plants	-	2,512,000	2,456,000		780,000	
seagrasses	-	2,074,000		193,600	681,900	1,436,000
hagfishes	-	7,810		7,810		
cone snails	-	2,814		1,910	903	
marine reptiles	mammals	143,900,000	2,384,000	18,240,000	1,061,000	
sea birds	marine reptiles	113,000,000	101,600,000	11,880,000	1,377,000	
sea birds	mammals	106,200,000	8,635,000	19,070,000	859,200	74,660
sharks and rays	bony fishes	76,380,000		76,590,000	13	
sharks and rays	mammals	76,040,000		53,170,000	3,008	
mammals	bony fishes	69,990,000	1,734	49,780,000	289	
sharks and rays	marine reptiles	53,820,000		18,440,000	7,948	
marine reptiles	bony fishes	51,190,000	63,820	17,140,000	9,409	
sharks and rays	sea birds	47,770,000		19,100,000	713	
sea birds	bony fishes	42,140,000	63,410	15,440,000	8,320	
reef-building corals	mammals	10,420,000	204,500	4,924,000	672,800	8,281,000
reef-building corals	marine reptiles	10,030,000	8,620,000	4,929,000	1,004,000	
sharks and rays	reef-building corals	8,378,000		4,929,000		
reef-building corals	bony fishes	7,430,000	63,820	4,923,000	289	
sea birds	reef-building corals	7,094,000	5,182,000	2,429,000	805,900	14,190
reef-building corals	mangrove plants	2,497,000	2,429,000		462,200	
marine reptiles	mangrove plants	2,480,000	2,089,000		655,900	
mangrove plants	mammals	2,449,000	1,417		471,400	
sharks and rays	mangrove plants	2,367,000			1	
mangrove plants	bony fishes	2,219,000	39,090			
seagrasses	marine reptiles	2,061,000		193,600	591,700	
sea birds	mangrove plants	2,058,000	1,631,000		416,800	
seagrasses	mammals	2,054,000		193,600	317,000	1,436,000
seagrasses	reef-building corals	1,781,000		184,800	270,300	1,315,000

Table S4: Total taxa-level impacted range within taxon and cooccurring between taxa.

Taxon	Taxon 2	all (km²)	climate (km²)	fishing (km²)	land-based (km²)	ocean (km²)
sharks and rays	seagrasses	1,757,000		193,600		
seagrasses	bony fishes	1,536,000		190,600		
seagrasses	sea birds	1,392,000		41,690	361,600	
seagrasses	mangrove plants	526,800			178,400	
marine reptiles	hagfishes	7,810		7,810		
sea birds	hagfishes	7,810		5,304		
sharks and rays	hagfishes	7,810		7,810		
mammals	hagfishes	7,735		6,400		
hagfishes	bony fishes	7,228		7,228		
reef-building corals	hagfishes	3,650		1,162		
marine reptiles	cone snails	2,814		1,910	903	
cone snails	bony fishes	2,676		1,910		
mammals	cone snails	2,676		1,910	213	
sea birds	cone snails	2,676		1,910	765	
sharks and rays	cone snails	2,676		1,910		
reef-building corals	cone snails	1,910		1,910		
seagrasses	hagfishes	462		90		

Table S5: At-risk species included

group	kingdom	phylum	class	order	species	subpops
reef forming corals (n = 407)	Animalia	Cnidaria	Anthozoa	Scleractinia	400	-
	Animalia	Cnidaria	Hydrozoa	Milleporina	6	-
	Animalia	Cnidaria	Anthozoa	Helioporacea	1	-
sharks, rays, and chimaeras (n = 312)	Animalia	Chordata	Chondrichthyes	Carcharhiniformes	76	-
	Animalia	Chordata	Chondrichthyes	Myliobatiformes	66	-
	Animalia	Chordata	Chondrichthyes	Rajiformes	50	-
	Animalia	Chordata	Chondrichthyes	Rhinopristiformes	39	6
	Animalia	Chordata	Chondrichthyes	Squaliformes	20	1
	Animalia	Chordata	Chondrichthyes	Torpediniformes	16	-
	Animalia	Chordata	Chondrichthyes	Orectolobiformes	15	2
	Animalia	Chordata	Chondrichthyes	Squatiniformes	14	-
	Animalia	Chordata	Chondrichthyes	Lamniformes	10	-
	Animalia	Chordata	Chondrichthyes	Chimaeriformes	3	-
	Animalia	Chordata	Chondrichthyes	Hexanchiformes	2	-
	Animalia	Chordata	Chondrichthyes	Pristiophoriformes	1	-
bony fishes (n = 196)	Animalia	Chordata	Actinopterygii	Perciformes	157	-
	Animalia	Chordata	Actinopterygii	Syngnathiformes	15	-
	Animalia	Chordata	Actinopterygii	Clupeiformes	12	-
	Animalia	Chordata	Actinopterygii	Tetraodontiformes	12	-
seabirds (n = 154)	Animalia	Chordata	Aves	Procellariiformes	86	-
	Animalia	Chordata	Aves	Charadriiformes	27	-
	Animalia	Chordata	Aves	Suliformes	18	-
	Animalia	Chordata	Aves	Sphenisciformes	13	-
	Animalia	Chordata	Aves	Anseriformes	7	-
	Animalia	Chordata	Aves	Gaviiformes	1	-
	Animalia	Chordata	Aves	Pelecaniformes	1	-
	Animalia	Chordata	Aves	Podicipediformes	1	-
cone snails (n = 67)	Animalia	Mollusca	Gastropoda	Neogastropoda	67	-
marine mammals (n = 57)	Animalia	Chordata	Mammalia	Cetartiodactyla	33	13
	Animalia	Chordata	Mammalia	Carnivora	20	1
	Animalia	Chordata	Mammalia	Sirenia	4	1
mangrove plants (n = 17)	Plantae	Tracheophyta	Magnoliopsida	Malvales	4	-
	Plantae	Tracheophyta	Magnoliopsida	Rhizophorales	3	-
	Plantae	Tracheophyta	Magnoliopsida	Lamiales	2	-
	Plantae	Tracheophyta	Magnoliopsida	Myrtales	2	-

Table S5: At-risk species included

group	kingdom	phylum	class	order	species	subpops
	Plantae	Tracheophyta	Liliopsida	Arecales	1	-
	Plantae	Tracheophyta	Magnoliopsida	Fabales	1	-
	Plantae	Tracheophyta	Magnoliopsida	Plumbaginales	1	-
	Plantae	Tracheophyta	Magnoliopsida	Primulales	1	-
	Plantae	Tracheophyta	Magnoliopsida	Scrophulariales	1	-
	Plantae	Tracheophyta	Magnoliopsida	Theales	1	-
seagrasses (n = 15)	Plantae	Tracheophyta	Liliopsida	Alismatales	15	-
marine reptiles (n = 15)	Animalia	Chordata	Reptilia	Squamata	8	-
	Animalia	Chordata	Reptilia	Testudines	6	12
	Animalia	Chordata	Reptilia	Crocodylia	1	-
hagfishes (n = 11)	Animalia	Chordata	Myxini	Myxiniformes	11	-
lobsters (n = 1)	Animalia	Arthropoda	Malacostraca	Decapoda	1	-

SI Figures

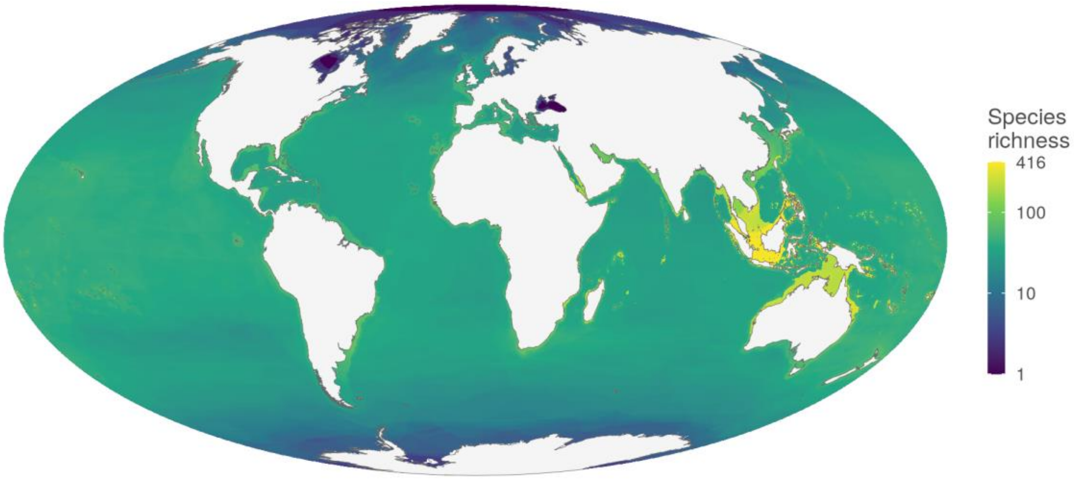

Fig. S1. Species richness, based on the number of at-risk species included in this assessment found in each cell.

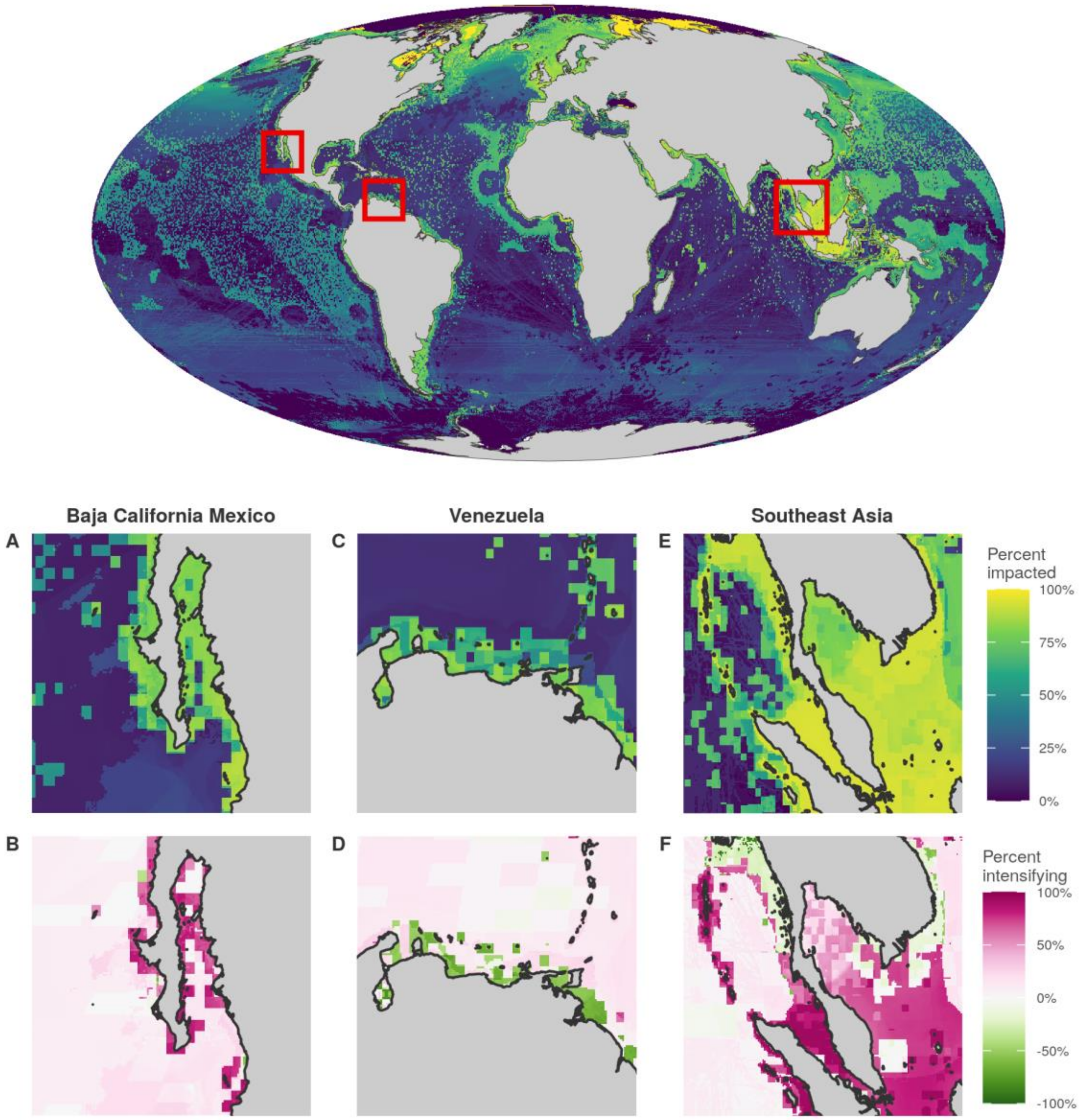

Fig. S2. Proportional impact and intensification for Baja California, Mexico; coastal Venezuela; and Southeast Asia. A high proportion of at-risk marine species in the coastal waters of Baja California are impacted by one or more stressors (A), and these stressors are increasing in intensity (B). Conversely, while Venezuela's coastal species are also highly impacted (C), stressor intensity decreased significantly over the study period (D). In Southeast Asia, most species ranges were again impacted by human activity (E), with stressor intensifying in Thai, Indonesian, and Malaysian waters (southern portion) while abating in coastal regions of Myanmar and Vietnam (F).

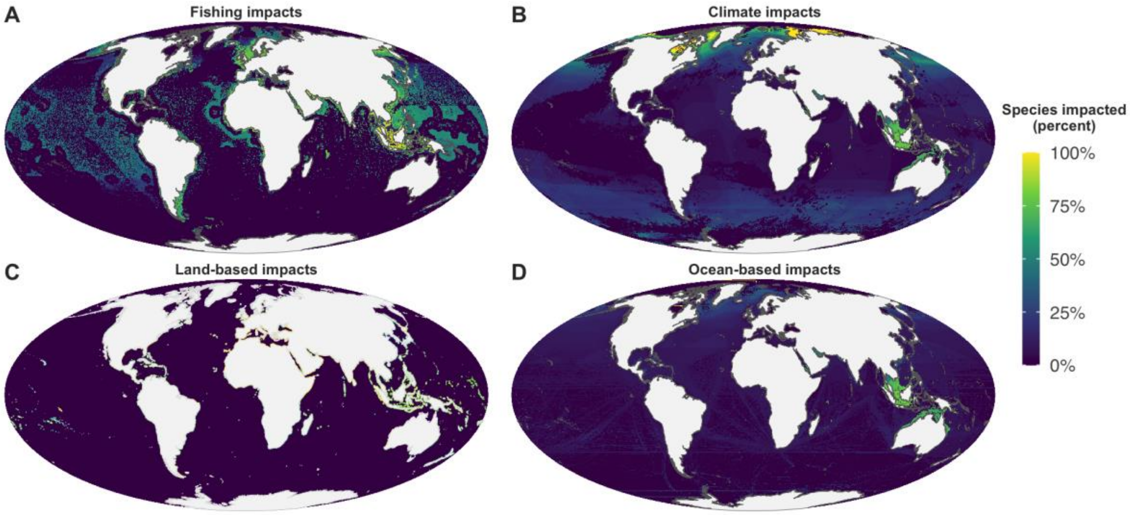

Fig. S3. Proportion of at-risk species impacted by stressor group. A) Impacts from fishing stressors: artisanal fishing, demersal destructive and non-destructive practices, pelagic high and low bycatch practices. B) Impacts from climate stressors: sea surface temperature, ocean acidification, sea level rise. C) Impacts from land-based impacts including direct human disturbance, nutrient runoff, and organic chemical pollution runoff. Note that pixel size is enhanced for better visibility. D) Ocean-based impacts from shipping.

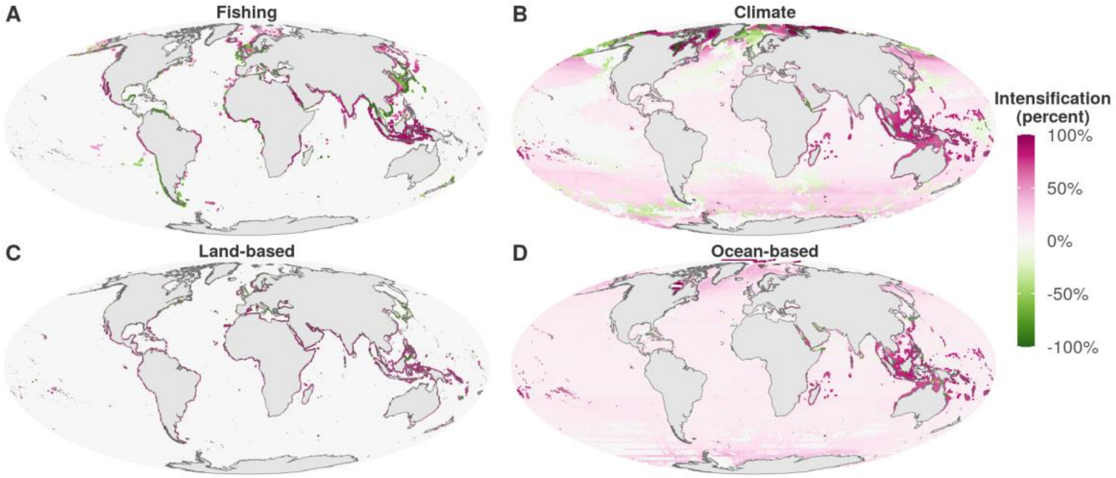

Fig. S4. Net proportion of at-risk species experiencing intensifying impacts (stressor intensity increasing by >0.1% per year) by stressor group. A) Intensification of fishing impacts: artisanal fishing, demersal destructive and non-destructive practices, pelagic high and low bycatch practices. B) Intensification of climate impacts: sea surface temperature, ocean acidification, sea level rise. C) Intensification of land-based impacts including direct human disturbance, nutrient runoff, and organic chemical pollution runoff. Note that pixel size is enhanced for better visibility. D) Intensification of ocean-based impacts from shipping.

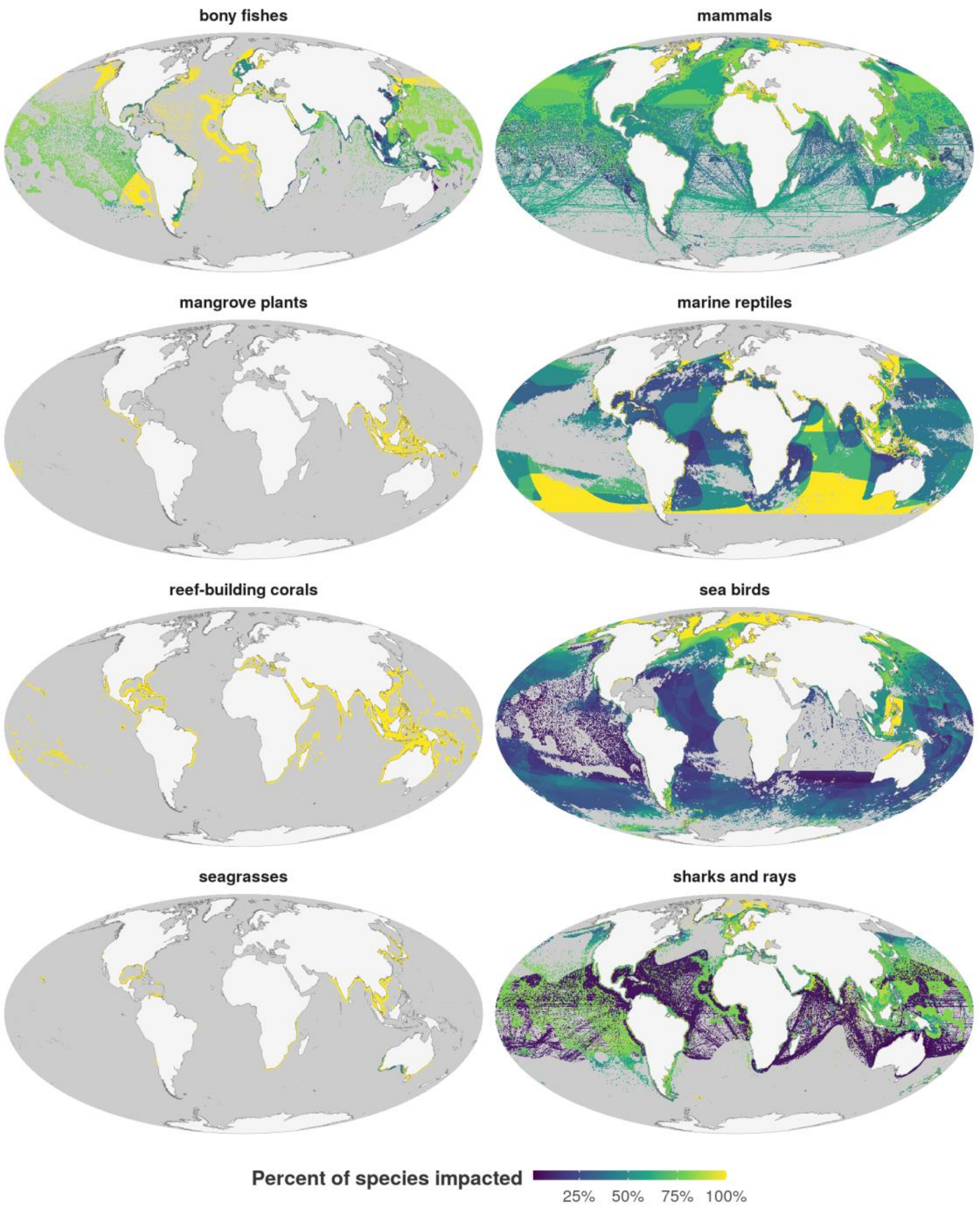

Fig. S5. Proportion of species impacted by one or more stressors, by taxonomic group. Grey represents zero impacted species present. Note that pixel size has been enhanced for reef-building corals, mangrove plants, and seagrasses for visibility. The abrupt transitions evident for marine reptiles is due to the small number of sea turtle species driving pelagic scores – a shift in presence of a single species can result in abrupt changes in proportion of species impacted. For example, the southern portion of the Indian Ocean (yellow) includes two impacted at-risk species (*Caretta caretta*, *Eretmochelys imbricata*), while the zone immediately to the north (green) includes the range of an unimpacted species (*Chelonia mydas*), dropping the proportion of impacted species to 67%. While included in calculations, maps for impacts on hagfishes and cone snails are omitted as ranges are too small to view at this scale.

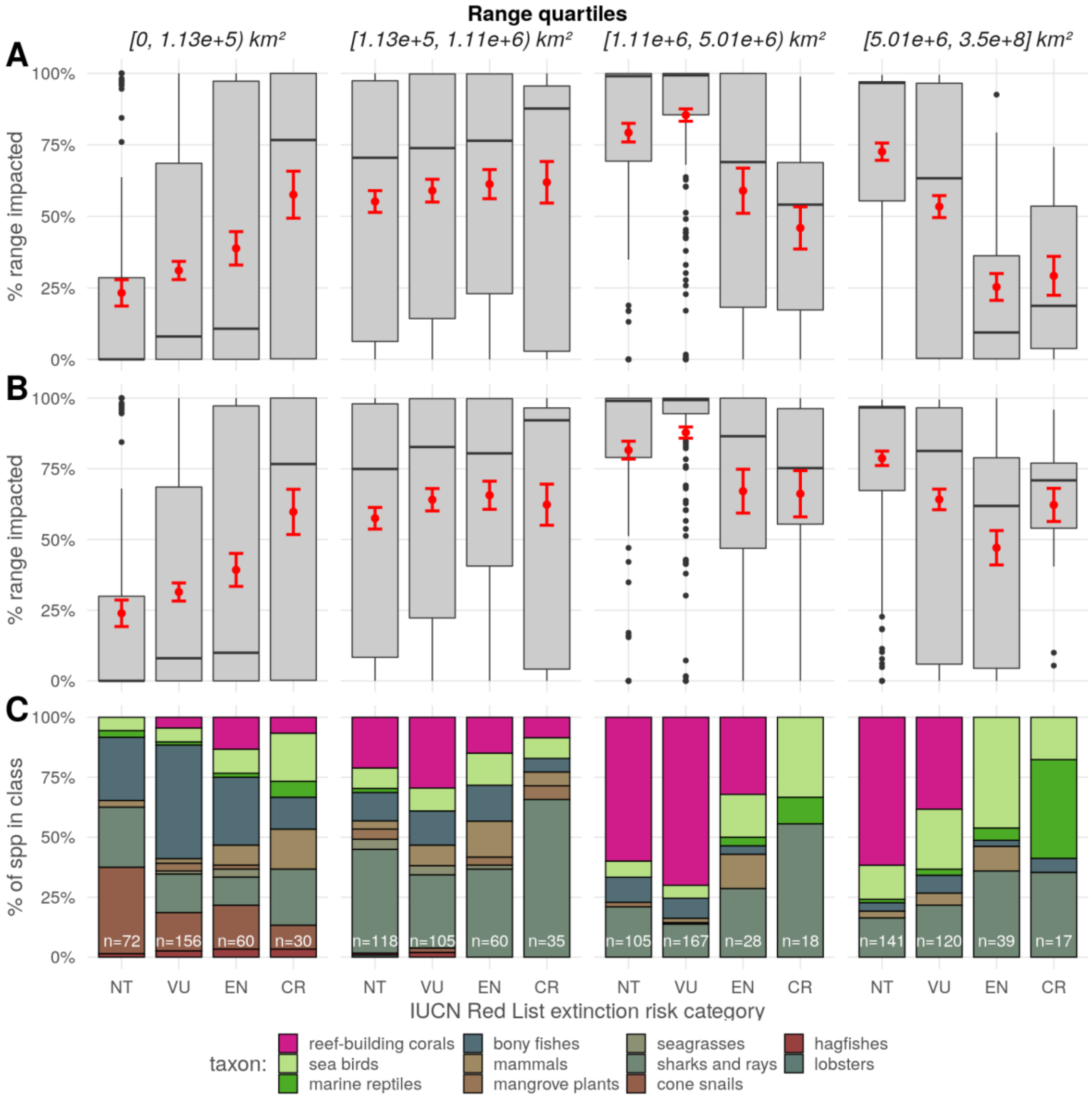

Fig. S6. Distribution and mean impacted range by range quartile and Red List extinction risk. A) Boxplot shows distribution of overall impacted ranges by range quartile and extinction risk; red point and error bars show mean ± standard error. B) Boxplot shows distribution of impacted coastal ranges (< 200 m depth); red point and error bars show mean ± standard error. C) Proportional representation of taxa within each class (range quartile and extinction risk).

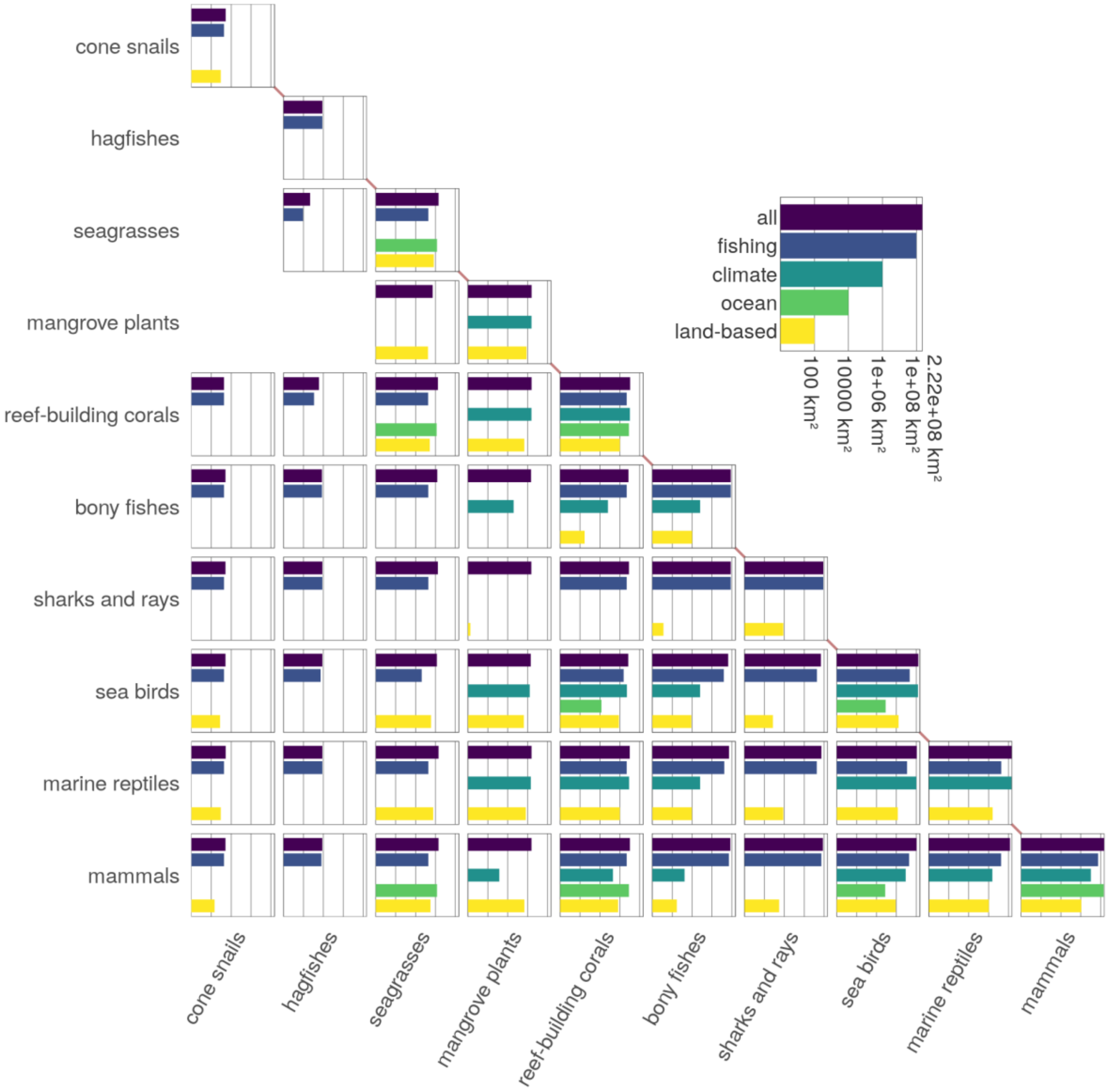

Fig. S7. Co-occurring areas of substantial taxa-level impact for 2013. Plots on the diagonal indicate, for a given taxon, the contribution of each stressor category to areas of high proportional taxa-level impact (cells in which ≥25% of species in the taxonomic group are impacted). Plots below the diagonal indicate footprints of co-occurring impacts for the intersecting pair of taxa. Bar length indicates area of impacted footprint for that category for that taxon pair. Note the log scale for area (on horizontal axis). Fishing stressors contribute substantially to the impacted footprint of nearly every taxon, but comprise almost the entire cumulative footprint for at-risk sharks, rays, and fishes. Stressors that affect multiple taxa across broad areas indicate where mitigation of key stressors can benefit multiple at-risk taxa. Areas of co-occurring fishing impacts are observed to some degree among nearly all taxonomic groups, particularly fishing pressures on sharks and rays overlapping with those on fish (77M km^2) and mammals (50M km^2). Climate-related impacts on seabirds largely co-occur with those on marine reptiles (102M km^2). Coastal and neritic taxa have much smaller impact footprints (Fig. S5) but these often co-occur mostly or entirely within the impacted footprint of wide-ranging pelagic taxa (Table S4).

Cumulative human impacts on global marine fauna highlight risk to fragile functional diversity of marine ecosystems

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Abstract

Healthy marine ecosystems provide critical benefits to people worldwide, but increasing threats from climate change and human activities disrupt ecosystem functionality and put these benefits at risk. Local and regional assessments have shown these impacts can be substantial, but we lack a global assessment of risk to marine biodiversity. Here we assessed risk of impact by intersecting spatial distributions of 21,267 marine animal species with distributions of 13 anthropogenic stressors according to each species' vulnerability, examining results through multiple lenses that connect to different conservation objectives: species, taxon, and functional vulnerability. Comparing our results to a broader ecosystem-wide analysis of impact on representative habitats, we found that species and functional entities were at higher risk from climate change, fishing, and nutrient pollution. We identify areas where high intensity stressors intersect with particularly vulnerable species, functional entities, and habitats, indicating ecosystems at greatest risk of biodiversity declines. Where multiple lenses of impact assessment indicate elevated risk, broad area-based protections may be warranted, but where impacts are focused on vulnerable functional entities there may be opportunities for more narrowly targeted conservation strategies such as local habitat restoration, assisted migration, or fishing gear restrictions. These results provide key insights at local to global scales on where and how to best meet conservation of species diversity and ecosystem function.

Introduction

Marine ecosystems provide critical benefits to people, including seafood, jobs and livelihoods, recreational value, and cultural value (1, 2). However, impacts from climate change, coupled with anthropogenic stressors from human activities on land and sea, drive degradation of coastal ecosystems, marine regime shifts, and increased extinction risk of threatened species (3–8), increasingly threatening the biological and functional diversity that underpin those benefits upon which we depend (2, 9–12). The United Nations (UN) Convention on Biological Diversity (CBD) is establishing ambitious area-based protection targets in the coming decade, toward the goal of curtailing extinction risk of species across all taxonomic and functional groups. Marine conservation efforts have typically focused on reducing threats to species and places identified for their implicit importance to ecosystem function; however, missing from this approach is an explicit assessment of threats to vulnerable functional groups, separate from species identity or habitat type, that are essential to supporting healthy and resilient ecosystems. To these ends, understanding where and to what degree anthropogenic stressors impose impacts on marine biological and functional diversity will be critical to designing, allocating, and monitoring effective and equitable conservation actions at scale.

Cumulative human impact models assess the risk of adverse impacts on elements of ecological concern (e.g., habitats, species, functional groups) based on vulnerability and exposure to anthropogenic stressors (13). Habitat-based estimates of ecosystem vulnerability to (e.g., (14)) and impact from (e.g., (9, 13, 15)) various stressors rely upon an understanding of fundamental structural and functional similarity between, say, a Caribbean coral reef and an Indonesian coral reef, or a Californian kelp forest vs. a Namibian kelp forest ecosystem, though there may be little overlap in the species that inhabit each system. Such a habitat-based approach provides valuable insights on impacts to the general trophic structure and functioning of an ecosystem, but it does not address the full spectrum of species diversity and may miss important differences in vulnerability stemming from heterogeneity of species composition between otherwise similar marine communities.

A species-based approach to estimating impacts may be better able to capture heterogeneity of species' vulnerability to stressors (5, 16–18), providing insights on impacts to individual species and the functional roles they fulfill. The diversity of ecological roles, or functional diversity, dictates the ability of communities to exploit resources, assimilate and transfer energy within and across ecosystems, and stabilize ecosystem processes (19). Thus, a species-based approach enables identification of functionally unique species and groups whose loss may pose greater risk to ecosystem functioning and resilience than similar impacts on functionally redundant species (20–22). Studies assessing anthropogenic impacts on marine species (e.g., (17, 23–26)) or functional diversity (e.g., (27–31)) generally have been limited in scope to a few select taxa and/or stressors, largely due to lack of a systematic means of estimating species vulnerability across multiple taxa and stressors (18, 31). O'Hara et al (5) parsed threat information from IUCN Red List assessments to estimate sensitivity and impacts from multiple anthropogenic stressors across multiple marine taxa globally over an eleven-year period, but that study was necessarily restricted to those species categorized as threatened and near-threatened, excluding the vast majority of marine species. However, a recently developed trait-based framework to estimate species vulnerability broadly across taxa and stressors (18) greatly expands the set of marine species available for such cumulative impact assessment.

Here we provide a taxonomically-diverse spatial analysis of cumulative human impacts of 13 anthropogenic stressors on 21,267 marine animal species and subpopulations. We then spatially aggregate species impact distributions through both a species (equal-weighted) and functional entity (*sensu* Mouillot et al. (20)) lens, providing a highly resolved understanding of how anthropogenic pressures are likely impacting marine biodiversity. Finally, we compare these results to those of habitat-based cumulative impact estimates to determine where and how species- vs. ecosystem-level vulnerability drives potential impact. The species, functional entity, and habitat approaches to estimating cumulative impact provide different but synergistic lenses through which to estimate our impact on marine ecosystems: areas of agreement between these methods reinforce urgency for conservation, while areas of disagreement may provide conservation insights by highlighting impacts on vulnerable and functionally important species in otherwise resilient marine ecosystems.

Results

We spatially modeled the cumulative human impact of 13 anthropogenic stressors (Table S1) on 21,267 marine animal species and subpopulations (Tables S2, S3) by mapping the spatial intersection of species distribution (presence/absence) (32–34) and stressor intensity (rescaled to be between 0 and 1) on a 10 km grid in Mollweide equal-area projection, weighting the results using trait-based vulnerability estimates of each species to each stressor (18). For each species, we calculated a range-level impact score as a weighted average of the impact across all grid pixels in the species' range as well as the coastal portions (depth < 200 m) of the species range. Because a species' abundance will vary throughout its range, we calculated the weighted mean based on net primary productivity (NPP) as a rough proxy for local abundance (e.g., biomass) and/or importance of an area to a species (e.g., feeding area) (35).

Productivity-weighted mean impacts across the extents of the assessed species varied dramatically across taxa as well as within taxa (Fig. 1). For species and taxa whose range extended beyond the continental shelf, coastal impacts from non-climate stressors were generally higher than average, though climate stressors were of similar magnitude. Corals were seen to be at greatest risk of impact on average, followed by other invertebrate groups, driven in large part by higher vulnerability to increasing sea surface temperature and ocean acidification. Of vertebrate taxa, elasmobranchs were on average at greatest risk, driven by rising temperatures and high fishing pressure. Average impact scores for vertebrate taxa fell below those of invertebrates, though there is considerable variation within each taxon, resulting in outliers: the top 1% of species by impact score (n = 213) contain a disproportionately high number of elasmobranchs (n = 68), corals (n = 19), and molluscs (n = 55) relative to their representation in the overall dataset (Table S2, S3).

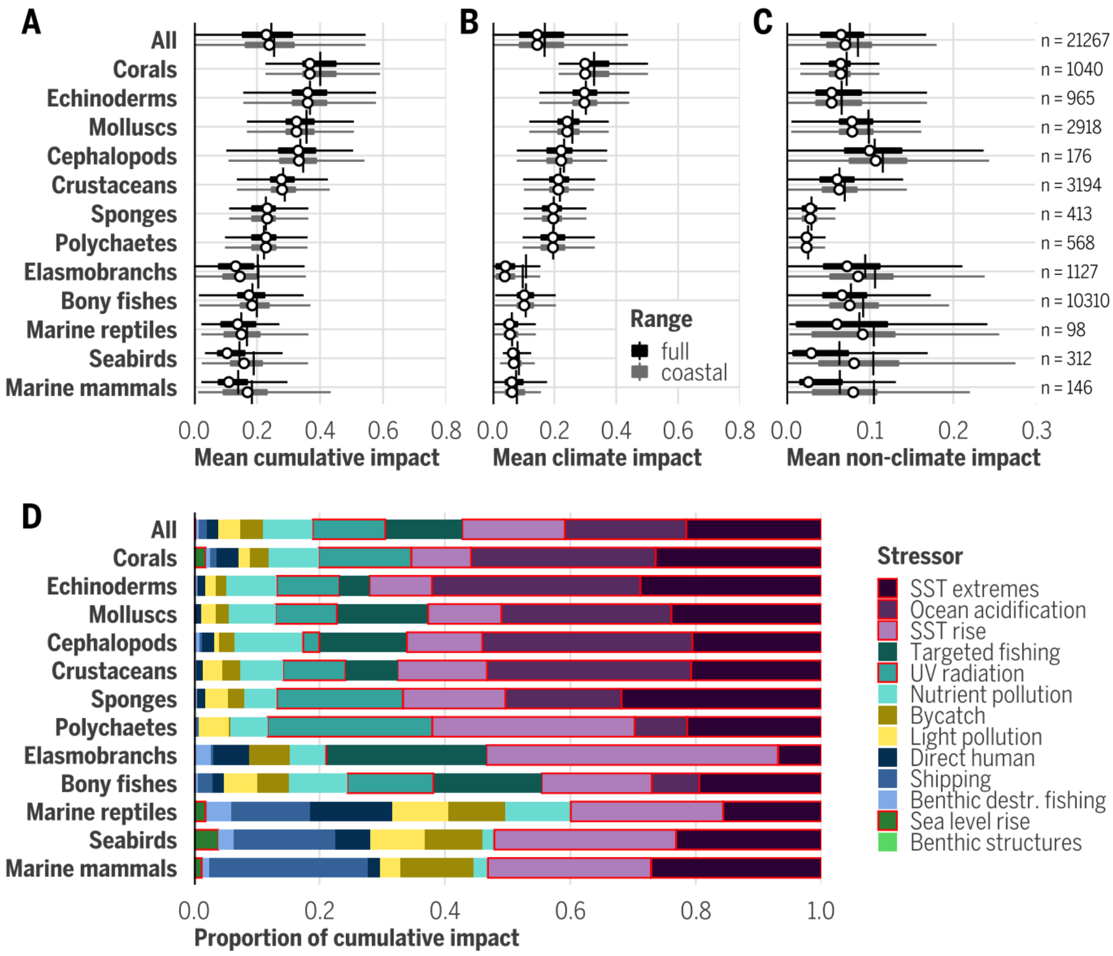

Figure 1. Cumulative productivity-weighted mean impacts on species ranges by taxon. (A) Distribution of mean predicted impact across species ranges (full range and coastal portions of range) from anthropogenic stressors by taxonomic group. (B)

Distribution of mean cumulative impact from five climate stressors. (C) Distribution of mean cumulative impact from eight non-climate stressors. IUCN-defined subpopulations are assessed individually where available. Vertical black line indicates mean across all species in taxon; white point indicates median. Boxes represent interquartile range (IQR, quartile Q1 to Q3); whiskers indicate observations 1.5x IQR below (above) Q1 (Q3) of box; outliers omitted from plot for clarity. (D) Contribution of individual stressors to mean cumulative impact across species ranges by taxon. Climate stressors outlined in red.

Sea surface temperature rise (long-term trends) and extremes (short-term events, e.g., marine heat waves) were substantial contributors to impacts across all taxa (Fig. 1D). Ocean acidification was a dominant stressor on all invertebrate species, but imposes little to no direct effect on vertebrates. Ultraviolet radiation impacted most invertebrates primarily due to vulnerability of planktonic larval life stages. Targeted fishing imposed the greatest average risk of impact of all non-climate stressors, even considering that many taxa are not targeted and thus not directly impacted. Fisheries bycatch impacted species broadly across all taxa.

To identify marine areas at greatest risk due to overlapping impacts from climate and human activity, we aggregated species-level distributions of cumulative impact in two ways. To estimate cumulative impact on global marine biodiversity considering all species as equally important, we calculated mean and variance of cumulative impact of all species in each 10 km x 10 km pixel. To estimate cumulative impact on functional diversity, we first assigned species to functional entities based on categorical values of four traits that roughly determine a species' ecological niche (maximum body size, adult mobility, position in water column, and adult trophic level) (36). For each pixel, we calculated the functional vulnerability (*sensu* (20)) of each functional entity based on the number of species representing that functional entity in that pixel: $FV =$

$\frac{1}{2^{N-1}}$, i.e., functional vulnerability drops rapidly as more species are included. Finally, the cumulative impact across functional entities was calculated as the functional vulnerability-weighted mean of cumulative impacts across all functional entities in each pixel.

The patterns of overlapping hot spots (cool spots) of climate and non-climate impacts (i.e., spatial cells in the top (bottom) quartile of global aggregated impact within each category) are largely similar whether viewed through the species lens or functional entity lens (Sørensen similarity index 71.0%) (Fig. 2). Averaging impact values of all species present in each spatial raster cell reveals 10.4% of ocean area where climate impact hot spots overlap with hot spots of non-climate impacts (e.g., Southeast Asia, East China Sea, Gulf of Mexico, Caribbean Sea, international tropical Pacific waters, Barents Sea, Bering Sea, Fig. 2A), and 9.4% of area where cool spots of climate and non-climate impacts overlap (e.g., Southern portions of Pacific, Atlantic, and Indian oceans; Weddell Sea; national waters for several southern Pacific and Atlantic small island states, Fig. 2A). Averaging impacts across all functional entities present in each cell, weighted according to functional vulnerability, better accounts for the risk of functional loss due to anthropogenic stressors. By this method, we found that climate and non-climate impact hot spots overlap in 10.3% of the ocean, while cool spots overlap in 6.3%, with spatial patterns similar to those for the species method (Fig. 2B).

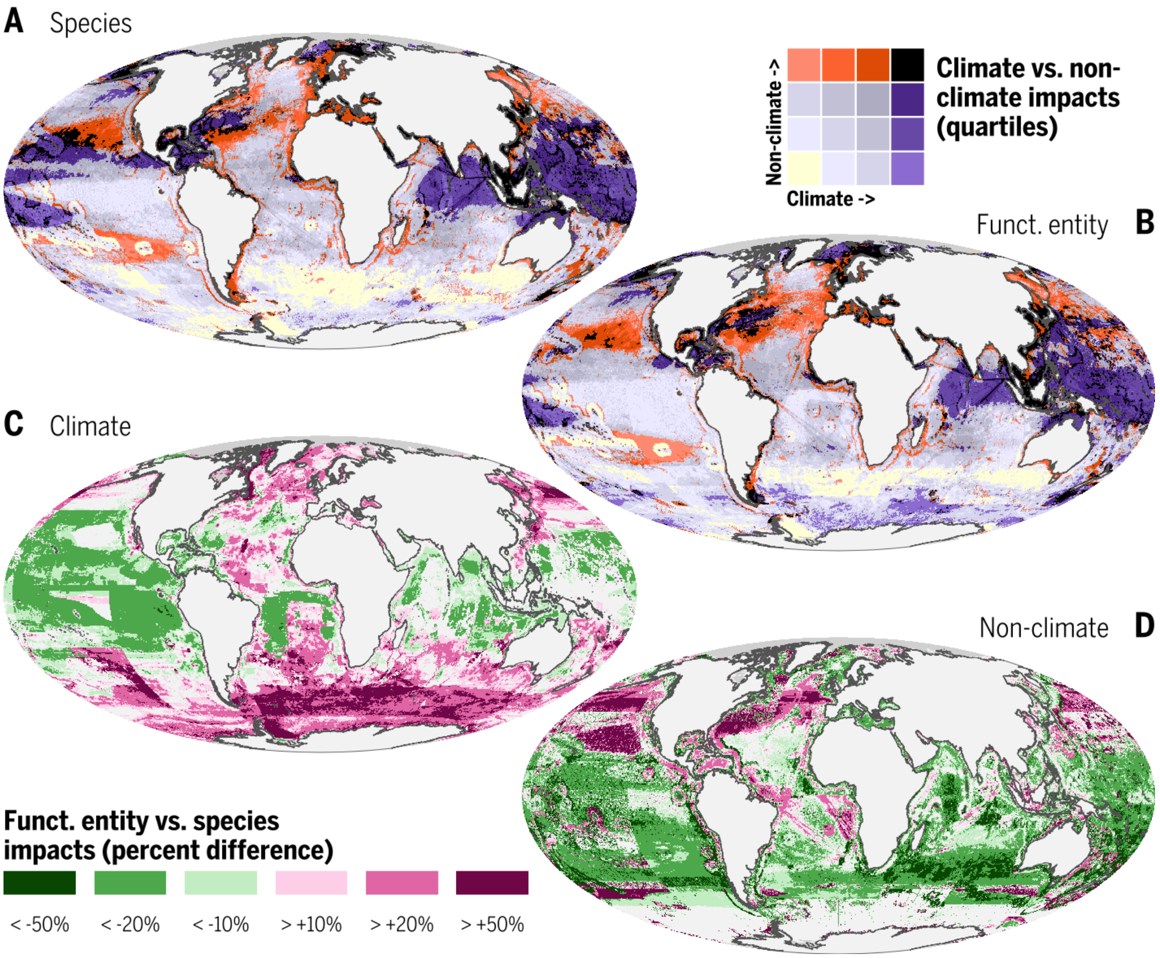

Figure 2. Comparison of mean impacts on species and functional entities from climate and non-climate stressors. Overlap of top quartile of impact from climate (purple tones) and non-climate (orange tones) stressors, based on (A) species method and (B) functional entity weighted mean method. (C) Proportional difference in intensity of climate impact between species and functional entity methods. Magenta indicates regions where impacts on vulnerable functional entities dominate impact across all species weighted equally, while green indicates the opposite. (D) Proportional difference in non-climate impact.

While patterns of hot spot and cool spots are largely similar between the two methods, the relative intensity of mean impacts varies considerably. Mean functional entity-level impacts exceed species-level impacts from climate stressors in 53% of the global ocean (Fig. 2C), indicating elevated functional vulnerability in areas of low current impact (e.g., Southern Ocean) and high current impact (e.g., Northern Europe, Philippine Sea). For non-climate stressors, functional impacts exceed species impacts in only 27% of the global ocean (Fig. 2D), though more often highlighting functional vulnerability in areas of higher current impact (e.g., temperate Northern Atlantic and Pacific, Caribbean Sea, Gulf of Mexico).

In addition to the species and functional entity lenses, we updated stressor layers and habitat maps from a recent global habitat-based cumulative impact study (9) to enable a comparison of areas where the three approaches concur and where differences may suggest alternate strategies for effective marine conservation. To facilitate comparisons of results among the species, functional entity, and habitat approaches, we converted impact scores (climate, non-climate, and overall) into percentile ranks based on the global distribution of scores by each method.

Overlapping hot spots and cool spots align well when comparing species-level impacts against functional entity-level impacts, but they differ substantially compared to estimates of impacts based on ecosystem-representative habitats (Fig.3A, Sørensen similarity index 44.6%; Fig. S1 for habitat analog to Fig. 2), driven by variations in vulnerability across species, function, and ecosystem. Comparing overlap between habitat and functional entity methods of climate hot spots/cold spots (Fig. 3A) reveals areas where the two methods disagree, indicating higher functional risk from climate change in equatorial Indian and Indo-Pacific waters (lighter orange tones) than in temperate Northern and Southern Pacific regions (lighter purple tones). For non-climate stressors (Fig. 3B), patterns of highest and lowest impact largely agree, though fishing pressure appears to impose relatively greater functional impacts (orange tones) in coastal Temperate Australasia and just beyond national waters of many southern African nations and Pacific small island states.

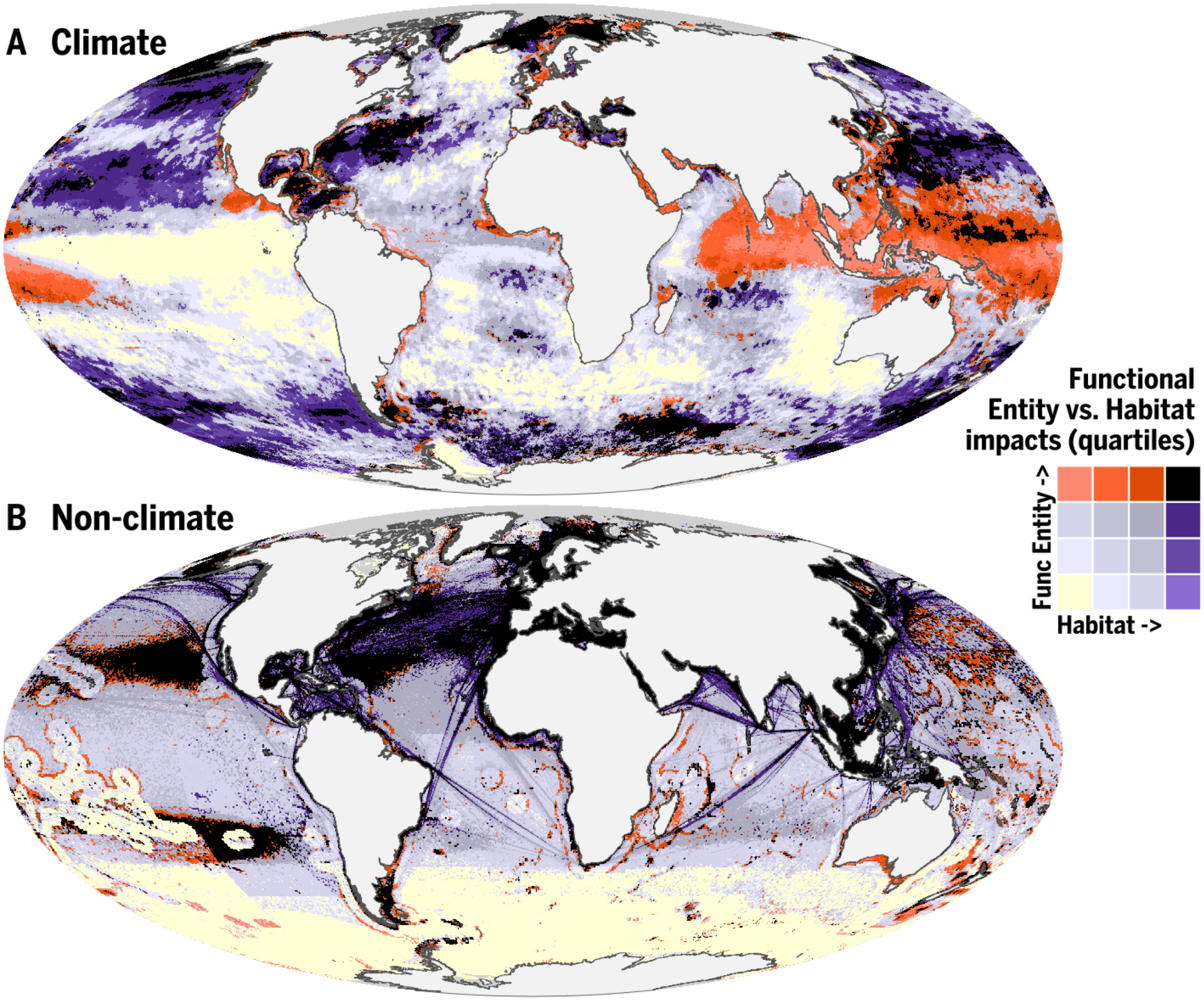

Figure 3. Comparison of mean impacts from climate and non-climate stressors on marine ecosystems based on functional entity and representative habitat methods. Overlap of quartiles of impact from (A) climate stressors and (B) non-climate stressors, highlighting top quartile according to habitat-based cumulative impact (purple tones) and functional entity-based cumulative impact (orange tones).

Impacts varied considerably by method globally and by ecological realm (37), and often diverged strongly when comparing impacts on coastal areas (≤200 m depth) vs. open oceanic areas (Fig. 4, by ecological province in Fig. S2). As expected due to concentration of human activity along coastlines, we found that on average impacts for non-climate stressors (fishing, shipping, and land-based) in coastal areas dominated those in oceanic areas globally and across all realms, with general agreement in ranking between the habitat and functional entity methods (Fig. 4C). For climate stressors, the functional entity method predicted higher impacts than the habitat method for coastal waters in all realms (e.g., all Indo-Pacific regions, Tropical Atlantic and East Pacific, Fig. 4B), often suggesting much higher levels of ecological risk to functional diversity. The intersection of elevated climate impacts and non-climate impacts in biodiverse coastal regions suggests a far higher risk to ecosystem function than previously understood from habitat-based cumulative impact methods.

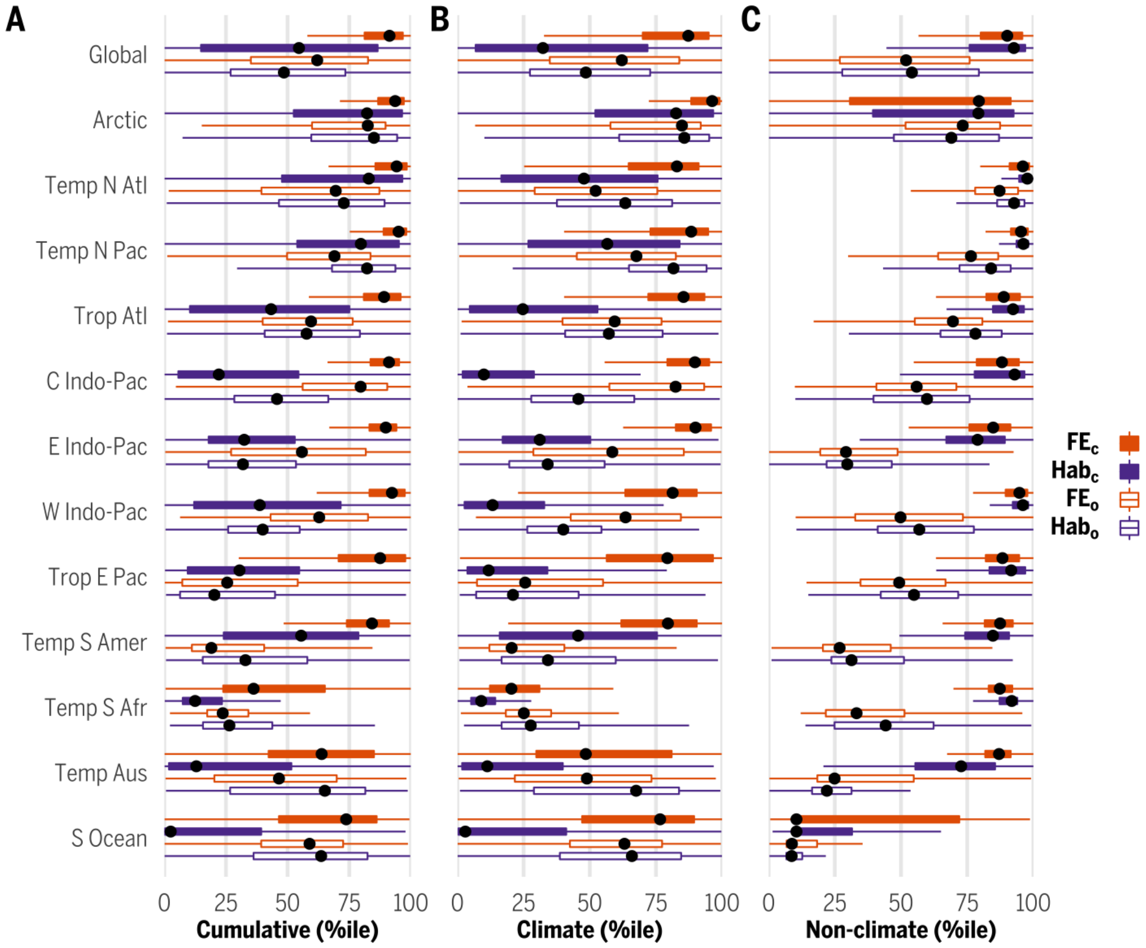

Figure 4. Comparison of cumulative, climate, and non-climate stressors by habitat and functional entity methods across 10 km resolution cells within coastal (FE_c, Hab_c) and oceanic (FE_o, Hab_o) portions of 12 representative marine ecological realms,

transformed to percentile ranks relative to global distribution within each impact category. Black point indicates median value; bars represent interquartile range (IQR, quartile Q1 to Q3); whiskers indicate observations 1.5x IQR below (above) Q1 (Q3) of bar. Outliers omitted from plots for clarity. A) Cumulative impacts by functional entity and habitat cumulative impact methods. B) Climate impacts by functional entity and habitat cumulative impact methods. C) Non-climate impacts by functional entity and habitat cumulative impact methods.

Discussion

The CBD Post-2020 Global Biodiversity Framework proposes, among other targets, that at least 30% of land and ocean areas are under some form of effective marine protection by 2030, with an emphasis on areas critical for biodiversity and its contributions to people (38). To identify such critical biodiversity areas, conservation efforts often prioritize certain species and taxa over others, as not all species are equally economically valuable, functionally unique, or at risk of extinction. Global and regional studies of marine biodiversity have implemented different aggregation methods to better communicate conservation-relevant information including population density, endemicity, extinction risk, taxonomic group, or simultaneous ecological, evolutionary, and social domains (e.g., (5, 39–43)). In all cases, the purpose of aggregation is to effectively summarize and communicate a complex and multifaceted dataset, and each aggregation method bears its own advantages and disadvantages. Our equal-weighted approach to species cumulative impact estimation is simple to calculate and understand, and accounts for the fact that the extinction of any species is likely detrimental to a functional ecosystem. Our functional entity approach integrates information about redundancy and vulnerability of ecosystem functionality to prioritize protection of ecosystem function and delivery of ecosystem services. Together these two metrics provide a more complete understanding of vulnerability, risk and impact to marine ecosystems, better informing conservation action toward the Post-2020 Global Biodiversity Framework's goal of reducing risk of extinction across taxonomic and functional diversity.

Our results show that impacts from climate-related stressors in general dominate impacts from non-climate stressors, regardless of the ecosystem element studied. This is due to broad exposure to elevated sea surface temperature and ocean acidification coupled with widespread vulnerability of species to these stressors. Even under the most optimistic emissions reduction scenarios, climate stressors are expected to increase in intensity in the near term (44–46). While local conservation policy cannot mitigate climate stressors driven by global emissions, it can reduce the intensity of stressors directly related to human activity, especially fishing, shipping, nutrient runoff, and coastal development, giving impacted species a greater chance at surviving, recovering from, or adapting to the effects of rising temperatures and declining ocean pH (47, 48). Overlapping hotspots of high climate impact between the functional entity and habitat approaches (Figs. 3, 4) indicate areas where high intensity stressors intersect with particularly vulnerable species, functional entities, and habitats, indicating ecosystems at greatest risk of biodiversity declines. Areas of overlap of high-intensity impacts from both climate and non-climate stressors should be prioritized for action to curtail human activities to reduce the risk of ecosystem collapse.

The approach to conservation differs when considering areas of high impact and areas of low impact, focusing on either reactive or proactive strategies. Areas of high impact indicate confluence of highly vulnerable ecosystem elements with high intensity of stressors, highlighting potential for reactive conservation to reduce stressors and allow the impacted ecosystem to recover. Areas of low impact on the other hand may indicate low stressor intensity, low ecosystem vulnerability, or both. Proactive conservation to prevent incursion of stressors into relatively unimpacted regions will be of lesser value if the ecosystem is not particularly vulnerable to the excluded stressors. In fact, to the extent possible, it may be beneficial to redirect harmful human activity toward lower-vulnerability areas and away from higher-vulnerability ecosystems, e.g., by rerouting shipping traffic or by encouraging fishing farther offshore and away from fragile inshore ecosystems.

Because the stressor layers used to estimate impacts by each method are largely identical, substantial differences in predicted impact among methods generally result from differences in underlying vulnerability of the ecosystem elements of interest. One important addition to the species/functional entity approach is the inclusion of mean SST as a stressor based on species' thermal tolerances, in addition to the SST extremes stressor (i.e., marine heat waves) included in both species-based and habitat-based cumulative impact assessment methods. In regions where the habitat approach predicts higher impacts than the functional entity approach, the species and functions within the ecosystem may be individually quite robust to the stressors present, but the broader processes and interactions that govern ecosystem health, or taxa not included in the species-based approach, may be adversely affected. In such cases, such as Hawai'i's oceanic waters in the Eastern Indo-Pacific realm, blanket protections such as the fully protected Papahānaumokuākea Marine National Monument can exclude human activity to protect ecosystem services (47, 49) and increase resilience to system-wide climate impacts (48).

Conversely, where the functional entity approach predicts higher impacts than the habitat approach, the general structure of the ecosystem may be robust to the stressors present, but the region may be home to one or more functionally critical and highly impacted species, posing greater risk of loss of ecosystem function. In these cases, targeted policies to reduce impacts on that subset of functionally critical species may be ecologically effective while remaining more politically and economically attractive than full exclusion. For example, the Andaman Islands in the West Indo-Pacific realm (Fig. 4 Western Indo-Pacific, SI) did not experience substantial SST extreme events during the years of our data, resulting in a low score by the habitat method – but annual mean SST has risen such that many species in vulnerable functional entities are near the top of their thermal tolerances, elevating risk of extirpation. This includes several species of mullet harvested in small-scale gillnet fisheries, as well as many benthic molluscs and polychaetes subject to bottom trawl impacts, so targeted gear restrictions could potentially reduce fishing pressure on these climate-stressed species without requiring full closure.

For several reasons, our results may be conservative. First, the anthropogenic stressors included in this analysis are by no means the only ways in which humans impose adverse effects on marine ecosystems (8, 14); however, while vulnerability estimates may be available for a broader suite of stressors (14, 18), our analysis was necessarily limited to stressors whose human-driven deviations from natural levels have been mapped globally. Second, interactions among multiple simultaneous stressors may result in synergistic impacts rather than the simple additive model we have incorporated here (50, 51), though such synergies remain an area of high uncertainty (8). Finally, it is likely that population- and community-level responses to stressors may include thresholds and nonlinearities leading to accelerating marginal risk (51, 52).

While effective and equitable conservation efforts must be well grounded in local and regional knowledge and values, global scale assessments such as this are necessary to inform the global biodiversity conservation agenda, provide broader context for local decision-making, and understand ecological and political synergies and tradeoffs across scales (53). The methods presented here however can readily be adapted to local and regional scales, incorporating finer-resolution data on species ranges, stressors, and species traits to better inform local conservation decisions.

Looking forward, rising sea surface temperatures in particular are predicted to impose substantial impacts on species as mean temperatures on warm/equator-ward range limits rise and exceed species thermal preferences, especially for tropical species as many have evolved narrow thermal ranges due to relatively stable year-round temperatures (54). Climate-driven shifts in species ranges are likely to shift patterns of vulnerability and impact over the next decades, potentially driving vulnerable but currently unexposed species into the path of higher-intensity stressors or opening up new habitat that provides refuge for highly impacted species from current stressors. Understanding future patterns of vulnerability in conjunction with expected changes in anthropogenic stressors must be a key concern for designing effective and lasting conservation strategies (8). The present analysis does not account for expected climate-driven range shifts, though the impacts predicted from SST rise reflect a major mechanism driving poleward retreats of warm trailing range edges. Future research could incorporate projections of climate-driven species range shifts (e.g., (7, 55, 56)) with forward-looking models or simulations to account for uncertainty, reference conditions, and dynamic changes in disturbance regimes (31) to predict impacts on novel range as species cold leading range edges expand into ever more temperate poleward waters.

Conservation is ultimately about balancing the social, cultural, and economic benefits and costs of conservation to improve or maximize overall utility for humans, including sustainable provision of natural resources or gainful employment, long-term delivery of ecosystem services at the local or global scale, and protecting nature to ensure its continued existence for future generations to enjoy (2). As we strive to protect 30% or more of our ocean by 2030, we must apply a holistic approach to conservation to prevent the loss of critical ecosystems, protect the functional diversity that underpins resilience and ecosystem services, slow or halt species declines and extinctions, and maintain genetic diversity essential for long-term adaptation (11).

This is especially important as climate impacts are already disrupting ecosystems and will continue to increase for decades, even under the most ambitious emissions reduction scenarios (44, 45), necessitating conservation action to mitigate non-climate stressors to allow for improved ecosystem resilience to climate change (47, 48). While well-enforced no-take marine protected areas are an effective conservation tool that can provide multiple co-benefits (47, 57–59), in certain cases, sustainable-use MPAs with targeted exclusions may provide substantial ecological benefit at lower social cost (60). Consideration of human impacts across lenses of species, function, and habitat provides a richer understanding of marine ecosystems to help conservation decision-makers determine strategies and locations for conservation that may be more politically feasible, economically efficient, and socially equitable, ultimately ensuring the greatest conservation benefit to nature and people.

Methods

Analysis grid

All spatial analyses were calculated on a gridded global map using a Mollweide equal-area projection coordinate reference system (CRS), gridded to 10 km x 10 km resolution. An ocean base map was prepared by rasterizing the vector ocean polygon features of the Natural Earth (https://www.naturalearthdata.com/) Oceans 1:10m dataset to a 1 km x 1 km Mollweide projection, then aggregating by a factor of 10 to approximate percentage of ocean within each cell. The resulting 10 km Mollweide ocean raster was used as the master raster for projecting all other datasets, and was used to mask out non-ocean cells from reprojected data.

Species distributions

Species distribution data were taken from AquaMaps (32) (n = 15,033) and IUCN species distribution maps (33, 34) (n = 6,234). For both datasets, synonymous scientific binomials and slight differences in nomenclature were resolved by comparing names against accepted names of marine species in the World Register of Marine Species (WoRMS, (61)) using the taxize package (62, 63). For species appearing in both distribution map datasets, the IUCN distribution map was preferred to distinguish subpopulations where available.

The 21,267 species (including subpopulations) included in this assessment represent only a small subset of the >240,000 marine species identified in the World Register of Marine Species (47), limited to those animal species with data on spatial distribution as well as sufficient trait data to estimate vulnerability and assign species to functional entities. However, this subset includes most known marine mammals, marine reptiles, seabirds, and cartilaginous fishes, as well as about half of marine bony fishes and warm-water corals. Together these species represent top predators, many mid-trophic species, and ecologically critical habitat-forming species. A smaller proportion of other invertebrates were included, as most lacked spatial data, trait data, or both.

The AquaMaps dataset computes species ranges as "probability of occurrence" in 0.5° cells based on relative environmental suitability across multiple environmental variables including temperature, salinity, depth, sea ice concentration, primary production, and in some cases oxygen level and distance to shore (32). To determine the distribution for each species, we converted gradient proabilities into binary presence/absence using a threshold of ≥ 0.5 probability of occurrence to represent "presence" of a given species. These results were then reprojected in raster form to the Mollweide CRS at 10 km resolution.

The IUCN dataset presents species ranges as polygons representing the historical, present and possible distribution of a taxon's occurrences (33). For each species, we excluded polygons with a "presence" value of 5 indicating "extinct" portions of a range, reprojected the remaining polygon features to the Mollweide CRS then rasterized the results to the 10 km analysis grid. For coastal and neritic species from both datasets, we masked the resulting presence maps to cells with a minimum depth of 200 m or less using GEBCO bathymetry data (64), and masked using the ocean area raster to exclude non-ocean cells.

Vulnerability estimates

Vulnerability weights, i.e., relative effect of stressor j on the fitness/health of the local population of species i, were determined using a framework that estimates species' sensitivity and adaptive capacity to that stressor based on relevant physiological and life history traits (18). Briefly, that study estimated vulnerability of species i to stressor j based on presence of certain traits that are likely to increase the species' physiological sensitivity to the stressor S_{ij}, other traits that affect the species' ability to adapt to that specific stressor, i.e., stressor-specific adaptive capacity A_{ij}, and life history and population-level traits that affect the population's ability to adapt to or recover from disturbances in general, i.e., general adaptive capacity A_i. An additional exposure modifier was included to account for possibility of exposure $E_{ij} \in \{0,1\}$ of species i to stressor j, e.g., a mesopelagic species (depth below 200 m) will not be exposed to ship strikes, so $E_{ij} = 0$. These metrics were combined to produce a vulnerability score $V_{ij} \in [0,1]$:

$$V_{ij} = \frac{S_{ij}/S_{ij,max}}{1 + A_{ij}/A_{ij,max} + G_i/G_{i,max}} \times E_{ij}$$

For the present study, we updated some aspects of methodology to improve imputation of species vulnerability for species with partial trait sets. First, for species with no traits available in the trait set assembled by Butt et al. (18), certain traits (i.e., body length, fecundity, generation time, temperature tolerances, and depth preferences) were filled using data from FishBase/SealifeBase (65, 66), while extent of occurrence was determined from the species' distribution map as described above. While these traits are only a fraction of the traits scored for species in the original study, they represent key traits for vulnerability. Second, rather than calculate vulnerability score for species groups then impute missing values based on the distribution of vulnerability scores, we first imputed missing trait values based on frequency within the species' taxonomic neighbors, then scored the vulnerability from the combination of partial traits (from FishBase and SeaLifeBase) and those imputed traits.

The updated trait-based vulnerability methods and results can be found at https://github.com/mapping-marine-spp-vuln/spp_vuln_framework.

Stressor distributions

Uniform exposure stressors

For most of the included stressors, exposure does not depend on species identity (though vulnerability to the stressor certainly might) and therefore exposure is uniform across all species. For these stressors, a single map of relative stressor intensity was created from gridded data using the following general process:

- We reprojected raw intensity to Mollweide CRS at 10 km resolution
- For stressors where marginal impact is expected to be decreasing with intensity (e.g., the hundredth hour of trawling in an area likely overlaps habitat already destroyed by the first hour of trawling), we applied a log transformation to the raw data.
- For stressors whose distribution contains a small number of extreme outliers, we identified a reference point based on the 99.9th percentile; otherwise we assigned a reference point based on the maximum observed value.
- Finally, we rescaled the data using the reference point to result in a distribution of stressor intensity ranging between zero and one.

Information on the data source, transformation, and reference point used for each stressor layer can be found in Table S1.

Bycatch stressor

The degree to which species are exposed to bycatch is dependent on their position in the water column. Pelagic species are unlikely to be swept up in a bottom trawl, while demersal species are unlikely to be swept up in a midwater trawl or purse seine. We prepared three bycatch layers, summing industrial and nonindustrial discards based on gear type listed by Watson (67) and Watson et al. (68):

- Benthic bycatch (affects species identified as benthic), based on gear types: trawl, dredge, and trap
- Pelagic bycatch (affects species identified as pelagic), based on gear types: line (tuna and non-tuna), longline (tuna and non-tuna), midwater trawl, seine, purse seine (tuna and non-tuna), gillnet, other
- Both (affects species identified as benthopelagic or reef-associated): the average of benthic and pelagic bycatch layers.

Catch estimates in Watson (67) and Watson et al. (68) provide data on discards (industrial/non-industrial) by gear type, presented in 0.5° cells. The discard values were summed across benthic or pelagic gear types, then the totals were normalized by cell ocean area resulting in an intensity of discarded catch, i.e., tonnes of bycatch per square kilometer. These intensity rasters were reprojected to the 10 km Mollweide CRS analysis grid. The intensity rasters were then adjusted by dividing by log(NPP) according to water column position, to indicate that bycatch in a high productivity area is less problematic than the same amount of bycatch in a low productivity area.

Surface NPP data were taken from Bio-ORACLE (69, 70), mean sea surface net primary productivity (NPP) of carbon, $g/m^3/day$.

Benthic NPP combine productivity at bottom depth and export flux (e.g., "marine snow") from the surface to bottom depth. Bottom NPP data were taken from Bio-ORACLE (69, 70), mean NPP of carbon at mean bottom depth, g/m^3/day. Export flux from surface to bottom depth were calculated based on an exponential decay model for export flux at depth d:

$$f(d) = f_0 \times (1 - r)^{d^\theta}$$

Applying non-linear least squares using data from Table 1 (control) in Gt C a^{-1} (globally integrated) in Yool et al (71), we identified best fit parameters $r = 0.341, \theta = .288$.

Finally, the resulting surface and benthic NPP layers were rescaled from 0 to 1, using a reference point based on the 99.9%ile of observed cell values.

Targeted fishing stressor

In addition to discards, Watson (67) and Watson et al. (68) report targeted catch for industrial and non-industrial fisheries at 0.5° cells, across multiple gear types and taxonomic groups. While any species might be vulnerable to targeted fishing, not all species are targeted, and so the targeted fishing stressor layer is distinct for every targeted species (and nonexistent for non-targeted species), thus a targeted fishing stressor layer was calculated separately for each species with non-zero catch in the Watson dataset.

Taxon names were compared to accepted names per WoRMS (61) using the taxize package (62, 63) to resolve synonyms and differences in spelling. Total catch for each taxon was summed across pelagic gears and benthic gears separately, then divided by cell ocean area resulting in intensity, i.e., tonnes of catch per km^2. Catch reported at the species level was attributed directly to that species. Catch in a given cell but reported at higher ranks (e.g., genus, family) was divided equally among all local species (per species distributions) in that genus or family. In many cases, a given species would be attributed catch at multiple levels in the same cell, in which case catch from all levels was summed for that species to create a cell total catch intensity, though still separated into pelagic and benthic. The pelagic and benthic catch intensities were reprojected to the 10 km Mollweide CRS analysis grid, and then normalized by log(NPP), either surface or benthic as appropriate, to account for the fact that a unit of catch in a highly productive region imposes less stress on an ecosystem than the same unit of catch in a low-productivity region. The pelagic and benthic NPP-normalized catch were then summed for each cell for the species.

Reference points to rescale the targeted fishing stressor layers are species specific. A global maximum reference point was set by first calculating the 90th percentile of NPP-normalized catch for each species across its entire distribution, then selecting the score of the species with the highest 90th percentile value: *Engraulis ringens*, Peruvian anchoveta, at C_{ref} = 2,170 tonnes of NPP-normalized catch. This global reference point was used to rescale (from 0 to 1) any species whose 99.9th percentile of NPP-normalized catch exceeded this value (15 species total). For species whose 99.9th percentile catch across its range falls below this reference point, we used the 99.9th percentile of that species' catch across its range as its own reference point. The reference catch for species i is therefore:

$$C_{ref}^{i} = \min\left(C_{ref}, C_{99.9\%}^{i}\right)$$

The NPP-normalized catch was then rescaled using the appropriate reference point, with values capped at 1.0, resulting in a gridded map of stressor values from 0 to 1 for every species with non-zero targeted catch.

SST rise stressor

We included two stressors related to ocean temperature: sea surface temperature extremes, representing impacts from short-lived (weeks to months) high temperature events, i.e., marine heat waves; and rise in annual mean sea surface temperature representing long-term (years to decades) changes in sea surface temperature relative to a historic baseline. The SST extremes stressor is described above in the uniform-exposure stressors. Exposure to long-term SST rise estimates the impact to a species when mean annual temperatures risk exceeding the physiological tolerance of the species due to the climatic shift from historic norms in a given location. For species included in the AquaMaps dataset, we used the thermal preference envelope used to generate species distributions; for species included in IUCN but not AquaMaps, we generated thermal preference envelopes (absolute and preferred minimum and maximum temperatures) in a manner similar to that used to generate envelopes for AquaMaps, using observed mean annual temperature in cells across the species distribution according to IUCN distribution maps:

- T^a_{min} = (25th percentile - 1.5 × interquartile) or absolute minimum mean annual temperature (whichever is lesser)
- T^a_{max} = 75th percentile + 1.5 × interquartile or absolute maximum mean annual temperature (whichever is greater)
- T^p_{min} = 10th percentile of observed variation in mean annual temperature
- T^p_{max} = 90th percentile of observed variation in mean annual temperature

We modeled physiological thermal stressor intensity s_T for each species based on the local mean annual temperature $\bar{T}$ relative to its preferred and absolute thermal range:

$$s_T = \begin{cases} 0 & \text{where } \bar{T} \leq T^p_{max} \\ \dfrac{\bar{T} - T^p_{max}}{T^a_{max} - T^p_{max}} & \text{where } T^p_{max} < \bar{T} < T^a_{max} \\ 1 & \text{where } \bar{T} \geq T^p_{max} \end{cases}$$

For each species, mean annual temperature from (72) in each pixel across its distribution was compared to the thermal preferences according to the above formula to generate a species-specific map of thermal stressor intensity. Note that species whose minimum depth preference was deeper than 200 meters (i.e., not epipelagic) were assigned a value of zero for this stressor.

Functional entities

We assigned species to functional entities based on categorical values of four traits (body size, adult mobility, water column position, trophic level) that roughly gather species into similar niche space, following Mouillot et al. (20). Out of 512 possible functional entities (8 body size categories × 4 adult mobility categories × 4 water column position × 4 trophic level categories = 512 unique combinations of trait values), 339 contained at least one species within our set (min: 1 species; max: 1034 species; mean: 63.59; median: 19). Due to limited trait data available across a broad range of taxa, our analysis relied on a smaller set of traits for assignment of functional entity than Mouillot et al. (5), which results in fewer but more populous functional entities and therefore a more conservative estimate of functional vulnerability.

Trait values were gleaned from (18, 65, 66); missing values were imputed using Multiple Imputation by Chained Equation (MICE) in the R package mice (73) using all other traits plus fecundity (where available), generation time (where available), order, and family. Categorical values used for each trait:

Body size

Values (in cm) were determined from sources: (18, 65, 66)

- Tiny: (0, 1.5]
- Very small: (1.5, 7.0]
- Small: (7, 15]
- Medium: (15, 30]
- Medium large: (30, 50]
- Large: (50, 80]
- Very large: (80, 150]
- Huge: (150, …)

For categorizing body size, we largely relied on the same values as Mouillot et al. (20), adding a bin on either end ("tiny" and "huge") to capture the wider range of values possible in our set of species.

Adult mobility

Values were determined from sources: (18)

- Sessile
- Sedentary
- Mobile resident
- Migratory/nomadic

Water column position

Values were determined from sources: (18, 65, 66)

- Benthic
- Benthopelagic
- Pelagic
- Reef-associated

Trophic level

Values were determined from sources: (65, 66)

- Primary consumer: (1, 2]
- Secondary consumer: (2, 3]
- Tertiary consumer: (3, 4]
- Apex consumer: (4, …)

Cumulative impacts: Species and Functional Entity Methods

Estimating impact at species level per grid cell

We modeled the impact on species i of stressor $j \in 1{:}J$ in a given location (i.e., grid cell) as the product of stressor intensity s_j and vulnerability of that species to that stressor v_{ij}:

$$I_i^j = v_{ij} s_j$$

Cumulative impact on species i in a given location was determined by summing impacts across all stressors (or subset, e.g., climate vs. non-climate stressors) in that location:

$$I_i^{cml} = \sum_{j=1}^{J} v_{ij}\, s_j$$

Estimating species-level mean cumulative impact across species range

For each species i, we calculated a cumulative impact score X accounting for impacts across its entire range as a weighted average of per-grid-cell impacts (either individually or summed) for all cells c in the species' range R_i, weighting by NPP as a rough proxy for local abundance or ecological importance to the species. For a single stressor j:

$$X_i^j = \frac{1}{\sum_{c \in R_i} NPP_c} \sum_{c \in R_i} I_{ic}^j\, NPP_c$$

The cumulative impact score across multiple stressors was determined as the sum of single-stressor impact scores.

Estimating impact at functional entity level per grid cell

For each functional entity $k \in 1{:}K$ consisting of some subset of species in a particular location, the impact of stressor j on the functional entity is simply the mean impact across all species in that functional entity in that location:

$$I_k^j = \frac{1}{N_{FE}} \sum_{i=1}^{N_{FE}} I_i^j$$

Cumulative impact of all stressors on this functional entity in this location is the sum of impacts across all stressors (or a subset).

Estimating impact across species per grid cell

The species-mean method for calculating the impact score for stressor j in a given location was determined by taking an unweighted mean across all N species present (or a taxonomic subset, e.g., all elasmobranchs):

$$I_{spp}^j = \frac{1}{N} \sum_{i=1}^{N} v_{ij}\, s_j$$

and the cumulative impact is the sum of impacts across all (or a subset of) stressors within that cell.

Estimating impact across functional entities per grid cell

The functional entity method for calculating the impact score for stressor j in a given location was determined by taking a weighted mean across all K functional entities present. Weighting for each functional entity was based on the functional vulnerability, *sensu* Mouillot et al. (20) with a slight modification (see below).

$$I_{FE}^j = \frac{1}{\sum_{k=1}^{K} F\,V_k} \sum_{k=1}^{K} F\,V_k I_k^j$$

In the Mouillot et al. (20) study, vulnerability of a functional entity was scored as 1 if that entity was represented by a single species and 0 otherwise; here we calculated functional vulnerability based on an inverse exponential of the number of species that represent that functional entity in that location, where functional vulnerability of entity k was calculated as

$FV_k = \left(\frac{1}{2}\right)^{N_k - 1}$, accounting for low-membership entities but rapidly approaching zero as membership increases.

As for the species-based approach, the cumulative impact is the sum of impacts across all (or a subset of) stressors within that cell.

Cumulative impacts: Habitat Method

To compare the results of our species-based cumulative impact approach to those of a habitat-based approach (e.g., Halpern et al. 2008, 2019), we recreated habitat maps at the same resolution and projection as the species-based analysis, and applied habitat vulnerability weights from Halpern et al. (2019) to determine impacts based on largely the same stressor data sources used for the species-based assessment.

Habitat maps prepared for Halpern et al. (9), at 934 m resolution in a Mollweide equal area coordinate reference system, were aggregated by a factor of 11 (to identify habitat density at approximately 10 km resolution) then reprojected to match our analysis grid. Corals and seagrass layers were based on habitat maps updated for Berger et al. (74). Kelp and saltmarsh layers were based on maps updated for the Ocean Health Index 2021.

To identify vulnerability of each habitat to various stressors we used a matrix of habitat vulnerability from Halpern et al. (9).

Stressor layers were for the most part identical to the uniform-exposure stressors used for the species and functional entity methods (see above, Table S1). Species-specific stressor layers (SST rise stressor based on species thermal tolerance, targeted fishing based on species identity, benthic and pelagic bycatch based on water column position) could not be included in the same manner as for the species approach. However, fisheries pressures (targeted and bycatch) were accounted for by creating layers from the same source, i.e., Watson (67), in the same manner as described in Halpern et al. (9). These new layers were aggregated by method, depth, and scale:

commercial pelagic and demersal low bycatch, commercial pelagic high bycatch, commercial demersal destructive, and artisanal/small scale fishing. For all these categories, overall fishing intensity (catch per km^2) was normalized by log(NPP), then rescaled to the 99.9%ile across all years for that catch category, resulting in stressor scores from 0 to 1.

Per-grid-cell habitat impact scores for each stressor j were created as the product of habitat vulnerability for each habitat $h \in 1{:}H$ and intensity of stressor j, averaged over the proportional inclusion of that habitat p_h in a given cell:

$$I_{hab}^{j} = \sum_{h=1}^{H} p_h \, v_{hj}$$

Cumulative impact per pixel is the sum of habitat-based impacts across all (or subset) of stressors.

Data availability

All analysis was performed in R statistical software, version 4.0.4 (75), relying primarily on packages tidyverse (76), terra (77), sf (78), taxize (62, 63), rfishbase (79).

All data used as inputs for this assessment are freely available from original sources. Detailed methods, code, intermediate data, and output data for this analysis are freely available at https://github.com/mapping-marine-spp-vuln/spp_vuln_mapping.

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Supporting Materials

Cumulative human impacts on global marine fauna highlight risk to fragile functional diversity of marine ecosystems

Supporting Figures

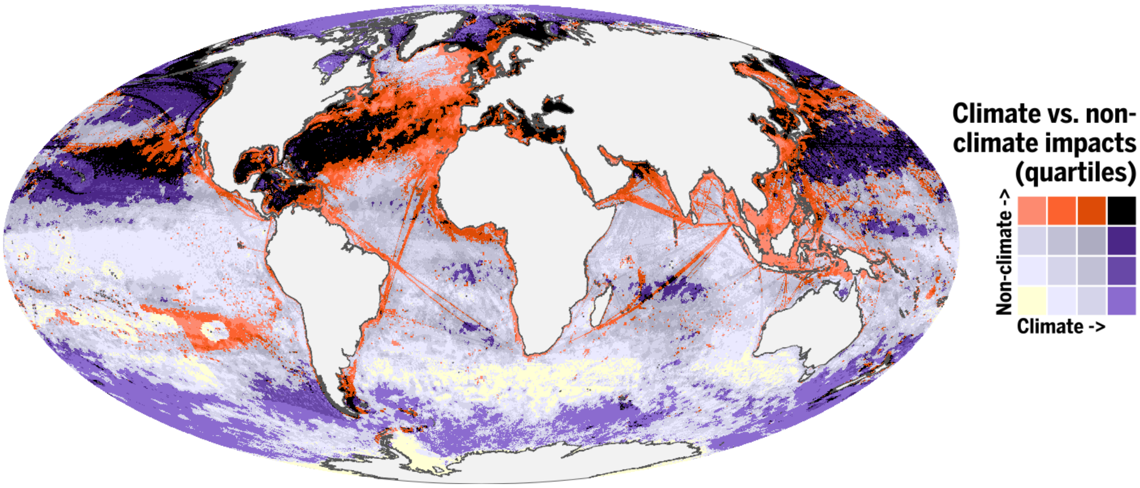
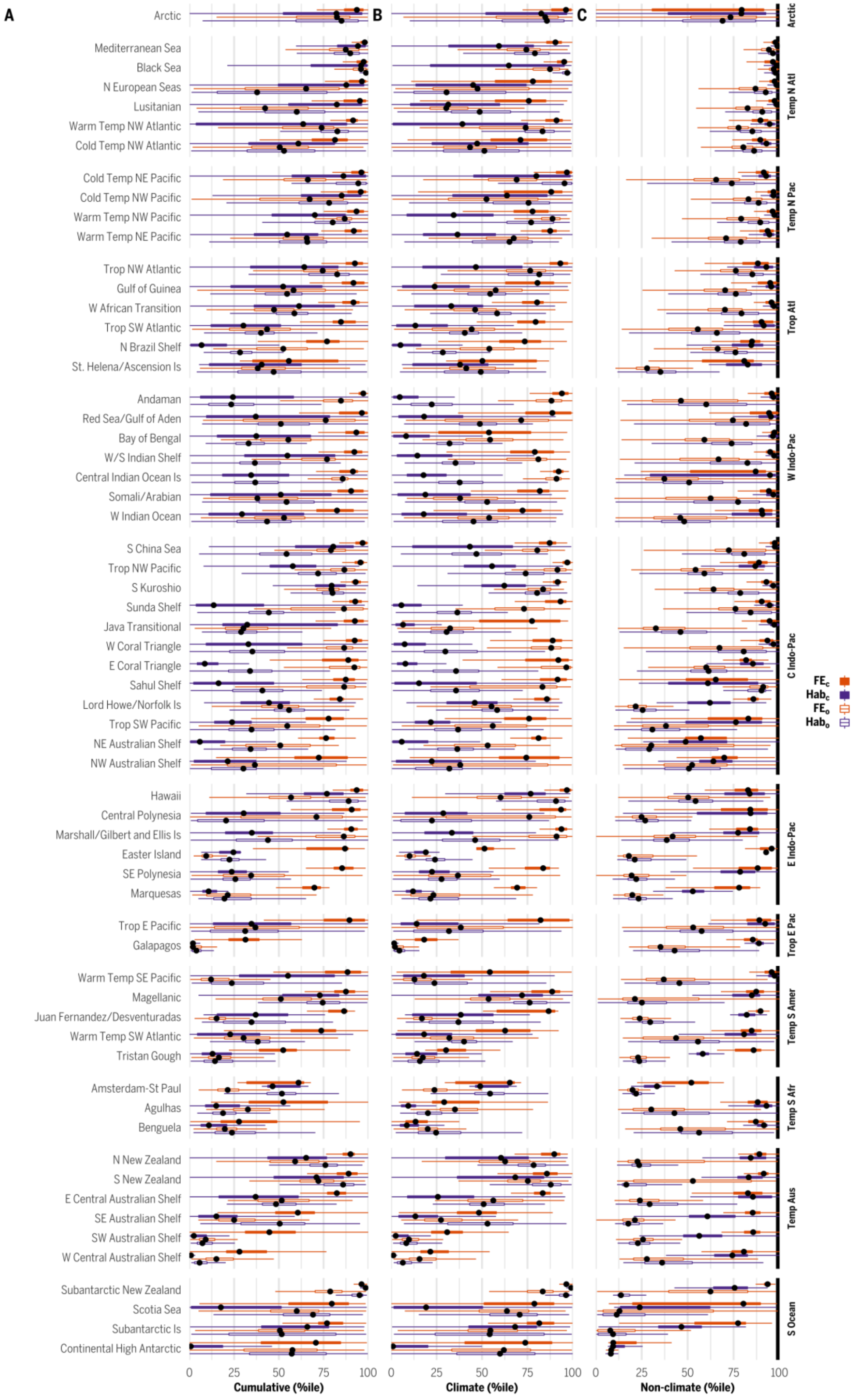


Figure S1. Comparison of mean impacts on representative habitats from climate and non-climate stressors. Biscale plot shows overlap of top quartile of impact from climate (purple tones) and non-climate (orange tones) stressors.


A
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C
Arctic
Mediterranean Sea
Black Sea
N European Seas
Lusitanian
Warm Temp NW Atlantic
Cold Temp NW Atlantic
Cold Temp NE Pacific
Cold Temp NW Pacific
Warm Temp NW Pacific
Warm Temp NE Pacific
Trop NW Atlantic
Gulf of Guinea
W African Transition
Trop SW Atlantic
N Brazil Shelf
St. Helena/Ascension Is
Andaman
Red Sea/Gulf of Aden
Bay of Bengal
W/S Indian Shelf
Central Indian Ocean Is
Somali/Arabian
W Indian Ocean
S China Sea
Trop NW Pacific
S Kuroshio
Sunda Shelf
Java Transitional
W Coral Triangle
E Coral Triangle
Sahul Shelf
Lord Howe/Norfolk Is
Trop SW Pacific
NE Australian Shelf
NW Australian Shelf
Hawaii
Central Polynesia
Marshall/Gilbert and Ellis Is
Easter Island
SE Polynesia
Marquesas
Trop E Pacific
Galapagos
Warm Temp SE Pacific
Magellanic
Juan Fernandez/Desventuradas
Warm Temp SW Atlantic
Tristan Gough
Amsterdam-St Paul
Agulhas
Benguela
N New Zealand
S New Zealand
E Central Australian Shelf
SE Australian Shelf
SW Australian Shelf
W Central Australian Shelf
Subantarctic New Zealand
Scotia Sea
Subantarctic Is
Continental High Antarctic
0
25
50
75
100
Cumulative (%ile)
Climate (%ile)
Non-climate (%ile)
Arctic
Temp N Atl
Temp N Pac
Trop Atl
W Indo-Pac
C Indo-Pac
E Indo-Pac
Trop E Pac
Temp S Amer
Temp S Afr
Temp Aus
S Ocean
FE_c
Hab_c
FE_o
Hab_o

Figure S2. Comparison of cumulative, climate, and non-climate stressors by habitat and functional entity methods across 10 km resolution cells within coastal (FE_c, Hab_c) and oceanic (FE_o, Hab_o) portions of 62 representative marine ecological provinces, transformed to percentile ranks relative to global distribution within each impact category. Filled point indicates median value; bars represent interquartile range (IQR, quartile Q1 to Q3); whiskers indicate observations 1.5x IQR below (above) Q1 (Q3) of bar. Outliers omitted from plots for clarity. A) Cumulative impacts by functional entity and habitat cumulative impact methods. B) Climate impacts by functional entity and habitat cumulative impact methods. C) Non-climate impacts by functional entity and habitat cumulative impact methods.

Supporting Tables

Table S1: Overview of methods and data sources to generate stressor distribution maps. All stressors projected to 10 km Mollweide coordinate reference system.

Stressor	Category	Exposure	Preparing data	Transform	Rescaling (0 to 1)	Potential species-level impacts	Data citation
Sea surface temperature extremes	Climate	Uniform across all species	Number of extreme SST weeks during a five-year period (2016-2020) . An extreme week was defined as a weekly anomaly (weekly SST - weekly climatological SST) exceeding the 90th quantile of anomalies calculated across 1985-2015 for that week.	NA	Number of extreme weeks divided by the total possible extreme events	Physiological stress or mortality	(1)
Sea surface temperature rise	Climate	Per species	Average SST from 2016-2020.	NA	Rescaled relative to each species's historical thermal tolerance.	Physiological stress or mortality	(1)
Ocean acidification	Climate	Uniform	Monthly aragonite saturation values (Ω) averaged to obtain annual estimate for 2017.	NA	Cell stressor score = 1 when Ω ≤ 1; otherwise, stressor score = (Ω_current - Ω_ref) / (1 - Ω_ref) where Ω_ref = average from 1880-1889	Disruption of calcium structure formation, physiological stress or mortality	(2)
Ultraviolet radiation	Climate	Uniform	Number of extreme weekly events occurring from 2016-2020 minus the extreme events from a reference period from 2005-2009. An extreme event is defined as a week that exceeds the mean UV + 1sd calculated for each week from 2004-2016.	NA	Normalized by raster value corresponding 99.9th quantile across all years	Planktonic larval mortality	(3)
Sea level rise	Climate	Uniform	Monthly anomalies averaged to obtain annual mean sea level anomaly. 5 year mean of annual data, 2015 to 2019 used to smooth large yearly variation.	NA	Normalized by raster value corresponding 99.9th quantile across all years	Flooding, habitat disruption	(4)
Nutrient pollution (runoff)	Non-climate (land-based)	Uniform	Intensity (tonnes/km2) of pollution from 2017 values of land-based nitrogen effluent from synthetic fertilizer and manure, human wastewater, and aquaculture.	NA	Normalized by raster value corresponding 99.9th quantile	Eutrophication, harmful algal blooms, physiological stress or mortality	(5–7)

Stressor	Category	Exposure	Preparing data	Transform	Rescaling (0 to 1)	Potential species-level impacts	Data citation
Direct human disturbance	Non-climate (land-based)	Uniform	Total human population living within 25 km of the shoreline for 2020 For each raster cell, coastal human population summed for a 25 km radius. Data cropped to include only cells 3nm from the coast.	ln(x') where x' = x + max(x)/100	Normalized by raster value corresponding 99.9th quantile across all years	Intertidal habitat destruction, coastal development, habitat fragmentation	(8)
Light pollution	Non-climate (land-based)	Uniform	Harmonized DMSP/VIIRS nighttime light data, using minimum value between 2017 and 2018 layers and dropping values below 10 (of 63) to reduce artifacts.	NA	Normalized by raster value corresponding 99.9th quantile across all years (excluding zero values)	Disruption of navigation	(9)
Shipping	Non-climate (ocean-based)	Uniform	Ship tracks in 2020 from AIS transponders at 0.005 degree resolution. Summed commercial, passenger, and oil/gas ship tracks and transformed to 10 km Mollweide analysis grid.	none	Normalized by raster value corresponding 99.9th quantile	Ship strikes, noise pollution, chemical pollution	(10)
Benthic structures	Non-climate (ocean-based)	Uniform	Oil/gas rigs in 2020 from AIS transponders at 0.005 degree resolution with at least 5 pings in the same position. Global offshore wind turbines identified from Sentinel-1 SAR. Modeled rig benthic footprint.	ln(x')	NA	Benthic habitat disruption or conversion	(10, 11)
Biomass removal (targeted fishing)	Non-climate (fishing)	Per species	Total tonnes of catch from nonindustrial fisheries calculated for 2015-2017 (0.5° resolution). Catch divided by Net Primary Productivity to standardize by region's productivity.	NPP ln(x'), catch not transformed	NA	Biomass removal	(12–15)
Fishing: demersal destructive	Non-climate (fishing)	Uniform	Hours of fishing effort per raster cell using destructive fishing gear in 2017.	NPP ln(x'), catch not transformed	Normalized by raster value corresponding 99.9th quantile across all years	Habitat destruction	(12, 13, 16)
Bycatch (pelagic)	Non-climate (fishing)	Position in water column	Total tonnes of discards for industrial and non-industrial fishing from 2015-2017. Pelagic bycatch based on non-demersal to standardize by local productivity.	NPP ln(x'), catch not transformed	Normalized by raster value corresponding 99.9th quantile	Biomass removal	(12–15)
Bycatch (benthic)	Non-climate (fishing)	Position in water column	Total tonnes of discards for industrial and non-industrial fishing from 2015-2017. Benthic bycatch based on demersal gear types and normalized by bottom NPP, sum of mean bottom NPP and exponential decay of surface NPP to estimate benthic nutrients from marine snow.	NPP ln(x'), catch not transformed	Normalized by raster value corresponding 99.9th quantile	Biomass removal	(12–15)

Table S2: Species inclusion by phylum

Phylum	Class	Number of species	Subpops/ synonyms
Annelida	Polychaeta	568	-
Arthropoda	Malacostraca	2957	3
Arthropoda	Pycnogonida	234	-
Chordata	Actinopterygii	10223	11
Chordata	Elasmobranchii	1118	9
Chordata	Aves	310	2
Chordata	Mammalia	121	25
Chordata	Reptilia	81	17
Chordata	Myxini	74	2
Cnidaria	Anthozoa	997	43
Echinodermata	Ophiuroidea	300	-
Echinodermata	Asteroidea	276	-
Echinodermata	Echinoidea	165	-
Echinodermata	Holothuroidea	159	-
Echinodermata	Crinoidea	65	-
Mollusca	Gastropoda	2691	29
Mollusca	Bivalvia	198	-
Mollusca	Cephalopoda	176	-
Porifera	Demospongiae	413	-

Table S3: Vertebrate species inclusion by class

Class	Order	Species in class	Species in order	Subpops/ synonyms
Actinopterygii	Perciformes	10223	1573	2
Actinopterygii	Eupercaria incertae sedis	10223	1344	2
Actinopterygii	Blenniiformes	10223	910	1
Actinopterygii	Gobiiformes	10223	625	-
Actinopterygii	Anguilliformes	10223	442	-
Actinopterygii	Pleuronectiformes	10223	436	-
Actinopterygii	Ovalentaria incertae sedis	10223	410	-
Actinopterygii	Acanthuriformes	10223	380	-
Actinopterygii	Tetraodontiformes	10223	337	-
Actinopterygii	Gadiformes	10223	324	-
Actinopterygii	Clupeiformes	10223	301	6
Actinopterygii	Syngnathiformes	10223	279	-
Actinopterygii	Stomiiformes	10223	249	-
Actinopterygii	Kurtiformes	10223	229	-
Actinopterygii	Myctophiformes	10223	216	-
Actinopterygii	Ophidiiformes	10223	210	-
Actinopterygii	Lophiiformes	10223	191	-
Actinopterygii	Scombriformes	10223	182	-
Actinopterygii	Aulopiformes	10223	175	-
Actinopterygii	Carangiformes	10223	161	-
Actinopterygii	Beloniformes	10223	130	-
Actinopterygii	Acropomatiformes	10223	120	-
Actinopterygii	Centrarchiformes	10223	107	-
Actinopterygii	Callionymiformes	10223	83	-
Actinopterygii	Alepocephaliformes	10223	69	-
Actinopterygii	Holocentriformes	10223	61	-
Actinopterygii	Carangaria incertae sedis	10223	59	-
Actinopterygii	Mulliformes	10223	58	-
Actinopterygii	Siluriformes	10223	56	-
Actinopterygii	Beryciformes	10223	55	-
Actinopterygii	Gobiesociformes	10223	53	-
Actinopterygii	Argentiniformes	10223	52	-
Actinopterygii	Other actinopt.	10223	346	-
Elasmobranchii	Rajiformes	1118	281	2
Elasmobranchii	Carcharhiniformes	1118	280	-
Elasmobranchii	Myliobatiformes	1118	181	1
Elasmobranchii	Squaliformes	1118	136	1

Class	**Order**	**Species in class**	**Species in order**	**Subpops/ synonyms**
Elasmobranchii	Rhinopristiformes	1118	72	4
Elasmobranchii	Torpediniformes	1118	61	-
Elasmobranchii	Orectolobiformes	1118	45	1
Elasmobranchii	Squatiniformes	1118	21	-
Elasmobranchii	Lamniformes	1118	15	-
Elasmobranchii	Heterodontiformes	1118	9	-
Elasmobranchii	Pristiophoriformes	1118	9	-
Elasmobranchii	Hexanchiformes	1118	6	-
Elasmobranchii	Echinorhiniformes	1118	2	-
Aves	Charadriiformes	310	115	-
Aves	Procellariiformes	310	115	2
Aves	Pelecaniformes	310	35	-
Aves	Anseriformes	310	18	-
Aves	Sphenisciformes	310	18	-
Aves	Gaviiformes	310	5	-
Aves	Podicipediformes	310	4	-
Mammalia	Cetartiodactyla	121	84	22
Mammalia	Carnivora	121	34	2
Mammalia	Sirenia	121	3	1
Reptilia	Squamata	81	71	-
Reptilia	Testudines	81	7	17
Reptilia	Crocodilia	81	2	-
Reptilia	Sauria	81	1	-
Myxini	Myxiniformes	74	74	2

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Improving value of conservation status predictions using a value of information framework

Casey O'Hara

1 Introduction

Systematic extinction risk assessments such as the IUCN Red List of Threatened Species [1] and NatureServe [2] help identify and quantify the number of imperiled species, and this information is often used to inform ecologically, socially, and economically cost effective conservation management [3–6]. However, such assessments require substantial investments of time, resources, and data, resulting in a slow pace of assessment, spatial and taxonomic bias, and many species categorized as data deficient [7]. Machine learning (ML) techniques show promise to predict conservation status and extinction risk based on incomplete information [7–11], in a rapidly and cost-effective manner [12]. These techniques face their own uncertainty inherent to such predictions, increasing the risk of inefficient or incorrect management decisions.

To reduce uncertainty in these predictive models of species conservation status, we need improved information on predictors of extinction risk and/or additional formal threat assessments, both of which are costly and time consuming [12]. Ideally, decisions on whether to invest in acquiring such information should be based on the degree to which such information improves the quality of conservation decisions made to protect threatened species. In other words, what type of information (and how much) will improve our assessment of species' status in a way that would change our management decisions to be more efficient and effective? To address this need, we apply a value of information framework [13] to a simplified model of conservation management under uncertainty to better understand the value of ML models for automated estimation of ecological threatened status.

We build and explore this framework in five steps, First, in Section 2 we explore potential types and sources of data that could be valuable to build or improve performance of a machine learning model to predict extinction risk. In Section 3 we develop a simplified framework of conservation management under uncertainty to account for elements of cost, benefit, and uncertainty in accuracy of ML estimates, then in Section 4, we use this framework to identify the factors that determine when the accuracy of an automated assessment is sufficient to justify acting on the results of the assessment. In Section 5, we explore the level of formal assessment required to inform a ML model that achieves a minimum level of accuracy given that formal assessment is costly. In Section 6, we describe several extensions to the model that account for more realistic conservation decision-making scenarios. We conclude with a discussion of several caveats to this approach, additional applications beyond predicting species extinction risk, and implications for conservation.

2 Data needs

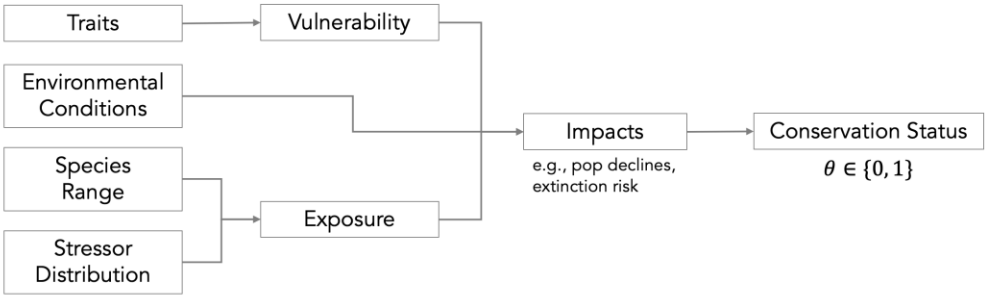

Fig. 1. Conceptual diagram of factors that influence species conservation status.

A variety of types of data can be used to inform a species' conservation status (Fig. 1). Mechanistically, we can use physiological, morphological, and life history traits to inform our understanding of a species' vulnerability to various anthropogenic stressors from climate change and human activity [14]. A vulnerable species exposed to such a stressor may suffer impacts to physiological fitness, reproductive capacity, or mortality [14], driving declines in population, changes in community structure, and loss of biodiversity [15]. Alternatively, IUCN Red List species assessments seek to quantify population-level impacts directly, applying expert knowledge of population size and trends, geographic range size and trends, and/or population modeling results against well-defined criteria to establish the risk of extinction of the species within a short time horizon [16]. Finally, species-based cumulative human impact assessments (e.g., [17,18]) predict threats by intersecting species ranges with vulnerability-weighted stressor distributions to estimate exposure and potential for population-level impact. In each of these cases, one or more factors shown in Figure 1 is used to infer or estimate extinction risk.

Certain data types may be useful for inference beyond their immediate observation. Species traits are likely to remain relatively stable over time, allowing for inference of conservation status in future time periods with little change in uncertainty. However, such traits are not likely to hold valid for other species far beyond the taxonomic neighborhood of the observed species, constraining their value for inference across taxa. Conversely, data on stressor distributions is likely to prove valuable for conservation status predictions across a wide range of taxa affected by the stressor, though because of their time varying nature, current stressor distributions are likely to provide little predictive value for conservation status far into the future.

Machine learning algorithms can be effective ways to fill gaps in data. They can identify patterns in a dataset that associate predictor variable values with an outcome variable. First, a model is trained using a subset of observations with known outcomes to identify characteristic patterns in the predictor variables. This trained model is then tested against a different subset with known outcomes to assess its accuracy. After developing a suite of possible models, a selection process identifies the model with the best predictive accuracy. ML conservation status prediction models are typically developed by training the model using a binary “threatened” vs. “non-threatened” classification (e.g., [7–9,11,19]) and/or ordinal extinction risk categories (e.g., [9,20]) based on formal IUCN Red List assessments. As predictor variables, these studies include some combination of species range size or location, species life history traits, and environmental or climatic conditions, with spatially heterogeneous information aggregated into summary statistics. Most studies, but not all (e.g., [9]), include some indication of human impact (e.g., Human Footprint Index, population density) or socioeconomic pressure (e.g., GDP, HDI) as additional predictors.

ML predictive models inherently bear some level of uncertainty; but given sufficient information as input, they can be quite cost-effective in understanding extinction risk and guiding management action [12]. For well studied taxa, life history traits are likely available in various trait databases, and geographic information may be available through OBIS and GBIF. However, for species or taxa that are rare or endemic to remote locations, such data may require investments in field work. Data on human activity and socioeconomic conditions may be critical to understanding threats, but may be even more complicated and expensive. Remote observation techniques make some environmental conditions and stressors accessible, e.g., sea level rise, sea surface temperature, or land use change; even data on fishing effort is increasingly available through remote sensing [21]. Even discounting the sunk-cost investment in putting remote observation satellites in orbit, it is costly to develop the models that convert raw satellite-based data to useful conservation inputs. More importantly, ML models cannot be effectively trained without some base knowledge of outcome, i.e., known threatened status - but such knowledge requires costly and time-consuming formal assessment. The optimal investment in sampling additional input information through field studies and remote observation data thus depends on weighing the costs of improving model accuracy against the improved quality of conservation decisions that result.

3 Model development

A value of information framework [13], or more specifically, expected value of sample information [22], is a method for weighing the costs and benefits of additional information when making a decision under uncertainty. In this case, we wish to preserve a benefit (e.g., ecosystem services) stemming from a healthy species by making an informed decision about management action based on our prediction of a species' conservation status (e.g., threatened or not threatened according to the IUCN Red List). For formally assessed species, we consider conservation status as a known value, i.e., perfect information; for as-yet unassessed species, we can use imperfect information from additional sampling and machine learning techniques to predict conservation status but with some level of uncertainty.

Consider a decision process with three phases: prediction, in which a species' threatened status is predicted using a ML model; decision, in which a manager decides whether to manage or not manage the species to maintain ecosystem service benefits based on the predicted conservation status; and realization, in which the outcome is determined.

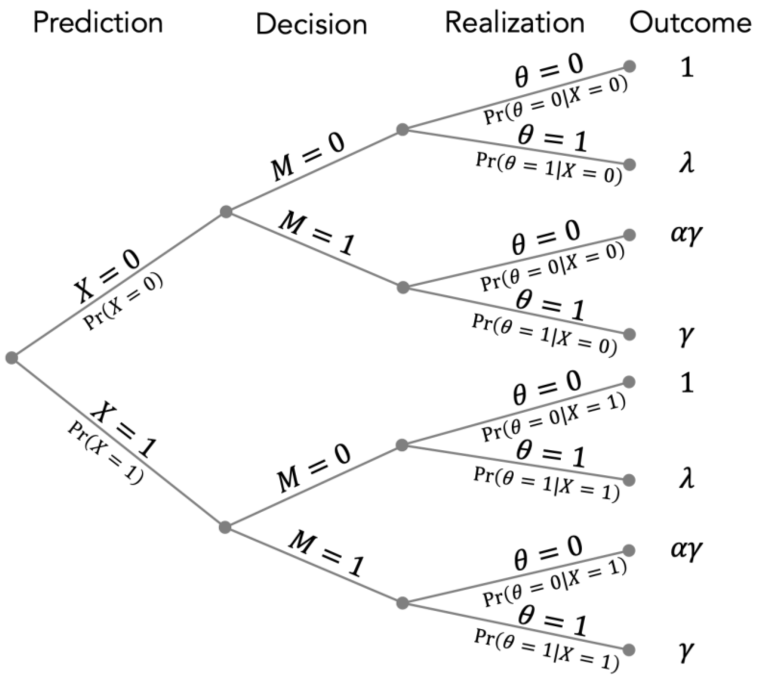

Fig. 2. Three-phase decision tree. In prediction phase, a machine learning model predicts threatened status X as either threatened ($X = 1$) or not threatened ($X = 0$). In management phase, manager decides whether to manage ($M = 1$) or not manage ($M = 0$) based on prediction of status. In realization phase, result of management is observed, revealing true conservation status ($\theta = 1$ for threatened, $\theta = 0$ for non-threatened).

Prediction phase

Assume for simplicity that the conservation status for each species in a given taxon is either truly threatened (in need of conservation action to maintain its ecosystem benefits) or truly not threatened (not in need of conservation action), but this status is unknown without further study. Each species has some latent/unobserved type θ, where $\theta = 1$ indicates truly threatened and $\theta = 0$ indicates not threatened. We further assume that this status can be perfectly determined by a formal assessment, e.g., IUCN Red List assessment. A predictive extinction risk model attempts to identify the level of latent risk X of unassessed species, with some level of uncertainty. The result of the prediction is an estimated value of θ, i.e., $X = \hat{\theta}$, with a value of 1 or 0 for *predicted* threatened or non-threatened respectively.

The probability that a predictive model would identify a randomly selected species as threatened ($X = 1$) includes true positives, in which a truly threatened species is correctly predicted ($X = 1|\theta = 1$), and false positives, in which a truly non-threatened species is incorrectly predicted as threatened ($X = 1|\theta = 0$). The same is true for a predictive model that identifies a species as not threatened ($X = 0$).

$$\begin{aligned}\Pr(X = 1) &= \Pr(X = 1|\theta = 1)\Pr(\theta = 1)\\ &\quad+\Pr(X = 1|\theta = 0)\Pr(\theta = 0)\\ \Pr(X = 0) &= \Pr(X = 0|\theta = 0)\Pr(\theta = 0)\\ &\quad+\Pr(X = 0|\theta = 1)\Pr(\theta = 1)\end{aligned}$$

Possible outcomes of assessment

Let r_+ indicate the *sensitivity* of the assessment instrument - the detection rate of true positives, i.e., $r_+ = \Pr(X = 1|\theta = 1)$. Let r_- indicate the *specificity* of the instrument, the detection rate of true negatives, i.e., $\Pr(X = 0|\theta = 0)$. The false positive term $\Pr(X = 1|\theta = 0)$ then becomes $1 - r_-$ and the false negative term $\Pr(X = 0|\theta = 1) = 1 - r_+$. Let $p_t \in (0,1)$ indicate the probability of a randomly chosen species being threatened, or the proportion of species in the set that are threatened: $\Pr(\theta = 1)$; therefore $\Pr(\theta = 0) = \Pr(\theta \neq 1) = (1 - p_t) \in (0,1)$. To simplify notation, here we've defined u_{ij} as the four possible outcomes $X = i \in \{0,1\} \times \theta = j \in \{0,1\}$:

Table 3.1: Assessment outcome matrix.

	$\theta = 0$	$\theta = 1$
$X = 0$	$u_{00} = r_-(1 - p_t)$	$u_{01} = (1 - r_+)p_t$
$X = 1$	$u_{10} = (1 - r_-)(1 - p_t)$	$u_{11} = r_+p_t$

From this matrix we formalize the intuition that the probability of a positive prediction (i.e., $X = 1$) must account both true positives and false positives, or true/false negatives for a negative prediction. Similarly, the probability of a true threatened status (i.e., $\theta = 1$) must account for both true positives and false negatives, while probability of a true non-threatened status must account for both true negatives and false positives.

Decision phase

In this phase, the manager must decide whether or not to manage a given species based on the outcome of the assessment. There are four possible outcomes for assessment: true positive, true negative, false positive, and false negative, though the manager does not know the true state of θ thus only sees X. For each individual species, the management decision should logically depend on the expected value of management based on the outcome of the assessment phase. For that, we must know the values of management or non-management for each possible outcome.

Possible values of management

As a reference point, we will use the sitation where a non-threatened species is accurately identified (i.e., $\theta = 0|X = 0$), is not managed, and delivers some ecosystem service benefit, which we will assign a value of 1. All other situations shift the balance of this benefit:

- Appropriate management ($\theta = 1|X = 1$): Managing a threatened species ensures continuation of the ecosystem service, but with a management cost, e.g., cost of monitoring and enforcement. Assume cost is proportional to benefit, and let $\gamma \in (0,1)$ represent the resulting benefit less cost.
- Over-management ($\theta = 0|X = 1$): Managing a non-threatened species maintains continuation of the benefit, and perhaps even accentuates the benefit, i.e., benefit $\geq$ 1. Let $\alpha \geq 1$ represent a potential benefit multiplier. However, cost still accrues as in appropriate management. The resulting overall outcome is thus $\alpha \times \gamma$, or augemented benefit less cost.

- Under-management ($\theta = 1 | X = 0$): Failing to identify and manage a threatened species results in reduction of benefit, though incurs no management cost. Let $\lambda \in [0,1)$ represent the proportion of overall benefit remaining after loss.

Table 3.2: Management value matrix.

	$\theta = 0$	$\theta = 1$
$M = 0$	$v_{00} = 1$	$v_{01} = \lambda$
$M = 1$	$v_{10} = \alpha\gamma$	$v_{11} = \gamma$

Again to simplify notation, here we've defined v_{ij} as the value for management in four possible situations: $X = i \in \{0,1\} \times \theta = j \in \{0,1\}$.

Logically, $\gamma > \lambda$, otherwise benefit for under-management exceeds benefit from appropriate management (i.e., cost of management exceeds the benefit) and management will never be preferred over non-management. Additionally, let us forestall the case where management of an otherwise unthreatened species provides such a boost to benefits that it more than accounts for the costs, i.e., while $\alpha \geq 1$, the product $\alpha\gamma < 1$; otherwise, management will always be preferred over non-management. Therefore, for challenging decision contexts: $\gamma^{-1} > \alpha \geq 1 > \alpha\gamma > \gamma > \lambda \geq 0$.

Using this value of information framework, we will examine several questions in the following sections:

- At high enough uncertainty in predicted conservation status and costs relative to benefits, there may be situations in which a prediction of "threatened" status does not justify a costly management action. In Section 4, we calculate the level of predictive accuracy, relative to potential costs and benefits, that is necessary to ensure a clear management decision.

- For a poorly studied taxonomic group, with few or no formal assessments, machine learning methods may not have sufficient labeled outcomes to train a model with adequate predictive accuracy. However, additional formal assessments are costly. In Section 5, we explore the optimal level of formal assessment to achieve adequate predictive accuracy, relative to estimated costs and benefits of management and cost of formal assessment.
- In Section 6, we explore several applications and extensions of this model to inform more complex cases of conservation decisionmaking.

4 Minimum required accuracy

Predictions of conservation status are only valuable insofar as they provide actionable information for management decisions. If the prediction is too uncertain and/or the costs of mismanagement are too high relative to the potential benefits, it may be wiser to hold off on taking an action (for an uncertain diagnosis of "threatened") or proactively acting (for an uncertain diagnosis of "not threatened"). Comparing the expected value of management vs. non-management for different values of predicted conservation status, we can identify the predictive accuracy (both sensitivity r_+ and specificity r_-) required for a confident management decision, based on the potential costs and benefits of management or mismanagement.

Expected value of management

Management vs. non-management when $X = 1$

For the overall set of ecosystem elements, the distribution of elements into various bins is driven by true and false positives and negatives, and tied to the underlying proportion of threatened elements in the set, i.e., $\mathbb{E}[M|X]$, which is driven by the conditional probability of θ with respect to X. Define q_{ij} as conditional probability that $\theta = j$ given $X = i$:

$$q_{ij} = Pr(\theta = j|X = i) = \frac{u_{ij}}{u_{ii} + u_{ij}}$$

Then the expected value of management ($M = 1$) when predicted (with uncertainty) as threatened ($X = 1$), i.e., $\mathbb{E}[M = 1|X = 1]$, can be expressed as the potential outcomes $\mathbb{E}[M = 1|\theta = j \in \{0,1\}] = v_{1j}$ weighted by the conditional probabilities $\Pr(\theta = j|X = 1) = q_{1j}$.

$$\begin{aligned}
\mathbb{E}[M = 1|X = 1] &= \mathbb{E}[M = 1|\theta = 1]Pr(\theta = 1|X = 1) + \\
&\qquad \mathbb{E}[M = 1|\theta = 0]Pr(\theta = 0|X = 1) \\
&= v_{11}q_{11} + v_{10}q_{10}
\end{aligned}$$

Substituting with values of p_t, r_+, r_- and γ, α:

$$\begin{aligned}
\mathbb{E}[M = 1|X = 1] &= v_{11}q_{11} + v_{10}q_{10} \\
&= \gamma \frac{u_{11}}{u_{11} + u_{10}} + \alpha\gamma \frac{u_{10}}{u_{11} + u_{10}} \\
&= \frac{\gamma r_+ p_t + \alpha\gamma(1 - r_-)(1 - p_t)}{(1 - r_-)(1 - p_t) + r_+ p_t}
\end{aligned}$$

Compare this to the expected value of *not* managing ($M = 0$) when predicted as threatened ($X = 1$):

$$\begin{aligned}
\mathbb{E}[M = 0|X = 1] &= \mathbb{E}[M = 0|\theta = 1]Pr(\theta = 1|X = 1) + \\
&\qquad \mathbb{E}[M = 0|\theta = 0]Pr(\theta = 0|X = 1) \\
&= v_{01}q_{11} + v_{00}q_{10} \\
&= \lambda \frac{u_{11}}{u_{11} + u_{10}} + 1 \frac{u_{10}}{u_{11} + u_{10}} \\
&= \frac{\lambda r_+ p_t + (1 - r_-)(1 - p_t)}{(1 - r_-)(1 - p_t) + r_+ p_t}
\end{aligned}$$

Note the denominators are identical (i.e., $\Pr(X = 1)$), so when a species is predicted as threatened, management is an appropriate decision when

$$\begin{aligned}
\mathbb{E}[M = 1|X = 1] &> \mathbb{E}[M = 0|X = 1] \\
\Rightarrow \quad \gamma r_+ p_t + \alpha\gamma(1 - r_-)(1 - p_t) &> \lambda r_+ p_t + (1 - r_-)(1 - p_t) \\
\Rightarrow \quad (\gamma - \lambda) r_+ p_t &> (1 - \alpha\gamma)(1 - r_-)(1 - p_t) \\
\Rightarrow \quad \frac{\gamma - \lambda}{1 - \alpha\gamma} &> \frac{(1 - r_-)(1 - p_t)}{r_+ p_t}
\end{aligned}$$

This can be thought of as:

$$\text{Manage when:} \quad \frac{\text{Net benefit of managing threatened}}{\text{Net benefit of NOT managing NOT threatened}} > \frac{\text{false positives}}{\text{true positives}}$$

When this inequality does not hold, the quality of the prediction is poor; the risk of mismanagement due to uncertainty is too costly relative to the potential benefits. By increasing sensitivity r_+ and/or specificity r_-, we improve our ability to more accurately predict threatened status, i.e., reducing false positives and increasing true positives, and thus reducing the ratio on the righthand side. Improving predictive accuracy will increase confidence in management decisions given increasingly higher management costs (i.e., lower γ) and/or lower potential losses due to undermanagement (i.e., higher λ).

Note that under perfect information, $r_+ = r_- = 1$. The positives ratio drops to zero, while the benefits ratio is necessarily greater than zero under the conditions for γ, λ, α stipulated earlier, so the inequality holds true. Therefore, under perfect information, management will always be the rational response to a species formally assessed as threatened.

Management vs. non-management when $X = 0$

In the situation of a species or ecosystem element predicted (with uncertainty) as not threatened, we can also consider the decision to manage by comparing expected values, i.e., $\mathbb{E}[M = 1|X = 0]$ vs. $\mathbb{E}[M = 0|X = 0]$. Expected value of management ($M = 1$) when predicted as not threatened ($X = 0$):

$$\begin{aligned}
\mathbb{E}[M = 1|X = 0] &= \mathbb{E}[M = 1|\theta = 1]Pr(\theta = 1|X = 0) + \\
&\quad \mathbb{E}[M = 1|\theta = 0]Pr(\theta = 0|X = 0) \\
&= v_{11}q_{01} + v_{10}q_{00} \\
&= \gamma \frac{u_{01}}{u_{01} + u_{00}} + \alpha\gamma \frac{u_{00}}{u_{01} + u_{00}} \\
&= \frac{\gamma(1 - r_+)p_t + \alpha\gamma r_-(1 - p_t)}{r_-(1 - p_t) + (1 - r_+)p_t}
\end{aligned}$$

And expected value of *not* managing ($M = 0$) when predicted as not threatened ($X = 0$) becomes:

$$\begin{aligned}\mathbb{E}[M = 0|X = 0] \quad &= \mathbb{E}[M = 0|\theta = 1]Pr(\theta = 1|X = 0) + \\ &\qquad \mathbb{E}[M = 0|\theta = 0]Pr(\theta = 0|X = 0) \\ &= v_{01}q_{01} + v_{00}q_{00} \\ &= \lambda\frac{u_{01}}{u_{01} + u_{00}} + 1\frac{u_{00}}{u_{01} + u_{00}} \\ &= \frac{\lambda(1 - r_+)p_t + r_-(1 - p_t)}{r_-(1 - p_t) + (1 - r_+)p_t}\end{aligned}$$

Note again the denominators are identical (i.e., $\Pr(X = 0)$), so when an ecosystem element is predicted as *not* threatened, i.e., $X = 0$, management is an appropriate decision when

$$\begin{aligned}\mathbb{E}[M = 1|X = 0] \quad &> \mathbb{E}[M = 0|X = 0] \\ \Rightarrow \quad \gamma(1 - r_+)p_t + \alpha\gamma r_-(1 - p_t) \quad &> \lambda(1 - r_+)p_t + r_-(1 - p_t) \\ \Rightarrow \quad (\gamma - \lambda)(1 - r_+)p_t \quad &> (1 - \alpha\gamma)r_-(1 - p_t) \\ \Rightarrow \quad \frac{\gamma - \lambda}{1 - \alpha\gamma} \quad &> \frac{r_-(1 - p_t)}{(1 - r_+)p_t}\end{aligned}$$

Similar to the case when status was predicted to be threatened, this can be thought of as:

$$\text{Manage when:} \quad \frac{\text{Net benefit of managing when threatened}}{\text{Net benefit of NOT managing when NOT threatened}} > \frac{\text{true negatives}}{\text{false negatives}}$$

Here, by improving prediction accuracy, we reduce false negatives and increase true negatives, thereby *increasing* the ratio on the right-hand side. In the case of a negative prediction, improving prediction accuracy will indicate *non*-management, avoiding increasingly higher management costs (i.e., lower γ) and/or lower potential losses due to undermanagement (i.e., higher λ).

Under perfect information, when $r_- \to 1$ and $r_+ \to 1$, then $\frac{r_-(1-p_t)}{(1-r_+)p_t} \to \infty$, always indicating non-management as the rational choice when status is predicted to be non-threatened.

Realization phase

Once an assessment or prediction has been performed and a management decision has been made, then the outcome would be realized, with benefits delivered based on preservation of the species, and costs accrued based on the decision to manage or not.

For a situation in which predictive accuracy and relative costs dictate that a prediction of "threatened" indicates management and "not threatened" indicates non-management, we can calculate an overall expected value by summing the product of the outcome probability matrix and the value of each outcome:

$$\mathbb{E}[outcome] = (1 - p_t)r_- + (1 - p_t)(1 - r_-)\alpha\gamma + p_t(1 - r_+)\lambda + p_t r_+ \gamma$$

We can examine the relative effects of r_+, r_-, p_t by taking partial derivatives of the expected outcome:

$$\begin{aligned}\frac{\partial \mathbb{E}}{\partial r_+} &= -\lambda p_t + \gamma p_t = p_t(\gamma - \lambda)\\ \frac{\partial \mathbb{E}}{\partial r_-} &= (1 - p_t) - \alpha\gamma(1 - p_t) = (1 - p_t)(1 - \alpha\gamma)\\ \frac{\partial \mathbb{E}}{\partial p_t} &= -r_- - \alpha\gamma(1 - r_-) + \lambda(1 - r_+) + \gamma r_+\end{aligned}$$

From these formulas, several ideas become clear. First, note that if α, γ, λ are constant and p_t is fixed for a given set of species, the marginal contributions of r_+, r_- are constant and positive. Second, as defined earlier, $\gamma > \lambda$ and $\alpha\gamma < 1$, ensuring the partials of r_+, r_- are positive. Therefore, improving sensitivity (r_+) and specificity (r_-) of our predictive methodology will increase expected value, as should be expected. Third, the marginal value of r_+ is proportional to p_t; as more species are expected to be threatened, a marginal increase in r_+ will become more valuable. Fourth, the greater the difference between γ and λ, the greater the marginal value of improving r_+. Since γ is net benefit after cost of management (i.e., benefit - cost of management), lower management cost improves marginal value of r_+; similarly, since λ is net benefit after loss of a threatened species (i.e., benefit - loss due to under-management), higher potential losses due to under-management will increase the marginal value of r_+. Fifth, the marginal value of r_- is proportional to $1 - p_t$; as *fewer* species are expected to be threatened, a marginal increase in r_- will prove increasingly valuable. And finally, lower values for product $\alpha\gamma$ increase marginal value of r_-; this corresponds to higher management costs (lower γ) and lower enhancement of value from managing non-threatened elements (lower α). Lower scores for these parameters indicate higher penalties for over-management of non-threatened elements.

Edge cases

Several edge cases outline the bounds of possible outcomes: (1) A perfect information case, in which prevalence of threat within the set is known, and sufficient information (e.g., traits and/or stressor exposure) is available to predict threatened status of a given species with 100% accuracy. (2) A prevalence-only case, in which the prevalence of threatened status within the set of species can be estimated, though no information is available to help inform an accurate predictive model. In this case, prediction is a random guess, weighted by the (known or estimated) prevalence of threatened status - e.g., if it is estimated that 30% of species are threatened, then any given species is given a 30% chance of being classified as threatened. (3) A prevalence-informed zero rule case, similar to above, except that all species are assigned the status of the most prevalent case. For example, if it is estimated that 30% of species are threatened, then all species are classified as non-threatened (the more prevalent status).

Perfect information

Under perfect information, prediction of conservation status of a species is perfectly accurate, i.e., $r_+ = r_- = 1$.

For the set of all species perfectly assessed, based on underlying prevalence of threatened status, the outcomes matrix becomes:

Table 4.1: Outcome matrix for perfect information.

	$\theta = 0$	$\theta = 1$
$X = 0$	$1 - p_t$	0
$X = 1$	0	$p_t\gamma$

Summing across the matrix, expected value becomes:

$$\mathbb{E}[PI] = 1 - p_t + p_t\gamma = 1 - (1 - \gamma)p_t$$

where the $1 - \gamma$ term represents basically the cost of management. This outcome represents an upper bound of predictive accuracy (i.e., 100% accuracy).

Prevalence-informed random guess

Two common methods are typically used to set lower bound reference points of predictive accuracy for comparison of model predictive power. In the case where we have some estimate of prevalence $\hat{p}_t$ of threatened status within our set of species, we can use this prevalence value to inform random assignment of species to bins of threatened vs. non-threatened. We have no information on our predictive ability beyond this random assignment, so specificity and sensitivity are basically a coin flip: $\hat{r}_+ = \hat{r}_- = 0.50$.

Table 4.2: Outcome matrix for prevalence-informed random guess.

	$\theta = 0$	$\theta = 1$
$X = 0$	$\frac{1 - \hat{p}_t}{2}$	$\frac{\hat{p}_t\lambda}{2}$
$X = 1$	$\frac{(1 - \hat{p}_t)\alpha\gamma}{2}$	$\frac{\hat{p}_t\gamma}{2}$

Summing the matrix results in expected value of:

$$\mathbb{E}[PIRG] = \frac{(1 - \hat{p}_t)(1 + \alpha\gamma) + \hat{p}_t(\lambda + \gamma)}{2}$$

This lower bound of predictive accuracy is often used to calculate $kappa$, $\kappa \in [0,1]$, a metric of a model's predictive ability:

$$\kappa = \frac{\text{model accuracy} - \mathbb{E}[PIRG]}{1 - \mathbb{E}[PIRG]}$$

A κ near zero indicates a model offering very little value in its predictive performance, while as $\kappa \to 1$ the model approaches perfect performance.

Prevalence-informed zero rule

For the “zero rule”, we assign to all elements the most prevalent status (threatened or not threatened) found in the set (and *zero* elements to the less prevalent status). Per exsting IUCN assessments, for most taxa, there are more non-threatened elements than threatened, i.e., $\hat{p}_t < (1 - \hat{p}_t) \Rightarrow \hat{p}_t < 0.5$; in this case, all negatives will be detected ($r_- = 1$) but no positives will be detected ($r_+ = 0$). If $\hat{p}_t \geq 0.5$ the prediction results just flip.

Table 4.3: Outcome matrix for prevalence-informed zero rule for $p_t < 0.5$.

	$\theta = 0$	$\theta = 1$
$X = 0$	$1 - \hat{p}_t$	$\hat{p}_t\lambda$
$X = 1$	0	0

Summing across the matrix:

$$\mathbb{E}[PIZR, \hat{p}_t < 0.5] = (1 - \hat{p}_t) + \hat{p}_t\lambda = 1 - (1 - \lambda)\hat{p}_t$$

where the $1 - \lambda$ term represents lost benefits due to not managing threatened species. If $\hat{p}_t \geq 0.5$ then assign all to $X = 1$, thus $r_- = 0, r_+ = 1$ and the predicted results just flip:

Table 4.4: Outcome matrix for prevalence-informed zero rule for $p_t > 0.5$.

	$\theta = 0$	$\theta = 1$
$X = 0$	0	0
$X = 1$	$(1 - \hat{p}_t)\alpha\gamma$	$\hat{p}_t\gamma$

Summing across the matrix:

$$\mathbb{E}[PIZR, \hat{p}_t > .5] = (1 - \hat{p}_t)\alpha\gamma + \hat{p}_t\gamma$$

This value will always outperform $\mathbb{E}[PIRG]$ and therefore is a more conservative metric of comparison for model assessment.

4.4 Improving accuracy by improving predictor data

By definition, increasing sensitivity r_+ and specificity r_- will increase predictive value, leading to greater confidence in management decisions and thus greater expected benefit of management decisions across a given set of species. Depending on estimates of potential costs, benefits, and proportion of threatened species, there may be greater net benefit in improving specificity over sensitivity or vice versa, but any improvement will provide value on balance.

For our conservation status predictive model, we can improve predictive performance by (a) increasing the pool of observations with known outcome variables on which to train the model, and/or (b) increasing the number or quality of the predictor variables upon which the model can act. Given a set of species, a subset of which has been formally assessed (and thus θ is known), the number of observations with known outcomes is fixed. Therefore we must invest in including additional predictor variables into both our training and prediction datasets.

For each additional variable built into our predictive model, such as a physiological trait or metric of exposure to a stressor, we expect that the marginal contribution to improving r_+ and/or r_- is increasing and concave, asymptotically approaching some limit ≤ 1.0. Increasing predictive value in turn increases expected value of management decisions based on the predictive model. However, the additional data required comes at a cost. Optimal investment occurs when marginal benefit of additional data meets marginal cost of acquisition (Fig. 3, point X).

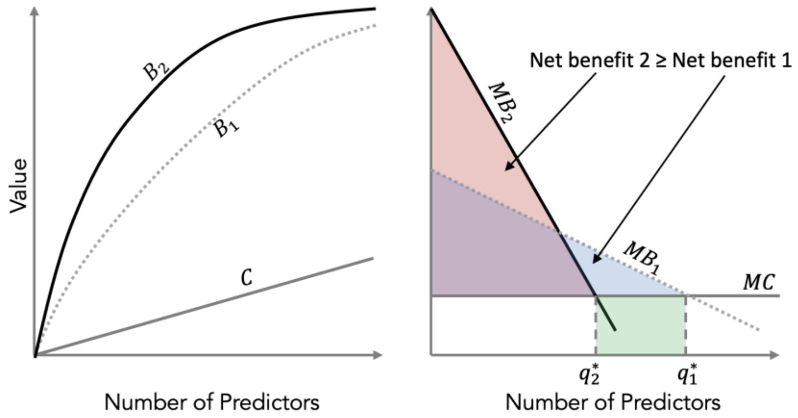

Fig. 3. Conceptual model of benefits and costs of acquiring data to inform additional predictors. B_1 and MB_1 represent benefit and marginal benefit, respectively, of predictors chosen at random; B_2 and MB_2 represent benefit and marginal benefit, respectively, of selecting from high-quality predictors identified through expert knowledge. High-quality predictors require fewer predictors to achieve equal or better performance, resulting in cost savings represented by the green box.

Not all predictors are likely to be equally valuable in increasing predictive ability of a model, or equally costly to acquire. Consultation with taxonomic experts is likely to identify traits that are particularly associated with vulnerability to certain stressors of concern [14]; focusing on these high value predictors would result in more rapid increases in predictive power (Fig. 3), with optimal investment achieving higher benefits with fewer additional predictors, resulting in lower overall costs. Beyond this, it is reasonable to assume that values for some predictors may be more readily observed than others, requiring lower acquisition costs; focusing on these lower-cost predictors enables a greater quantity of additional predictors for a given budget. For example, body length of a species can be measured easily by fishers, surveyors, or through remote visual surveys, while age at first reproduction requires far more intense field work. Similarly, distributions of some stressors, e.g., sea surface temperature or land use change, are increasingly available from satellite imagery, while distributions of other stressors, e.g., excess nitrogen pollution or marine microplastics, require intensive modeling and/or survey data. A small amount of planning and up-front research to identify high-value and/or low-cost candidates for additional predictor variables would certainly pay off in expected benefits of higher-quality conservation management decisions.

5 Formal assessments as input

Any predictive model, regardless of method, must be trained using observations "labeled" with accurate values of the desired outcome variable. A model to predict conservation status requires some set of formal (non-data-deficient) assessments, e.g., IUCN Red List assessments, to identify "known" cases of threatened and non-threatened status. For data-poor taxa with few formal assessments, then, training a reasonably accurate conservation status prediction model becomes challenging or impossible [23,24]. As additional formal assessments become available for training, the predictive accuracy of the model will increase until eventually the accuracy is sufficient to guide effective conservation decisions (as in Section 4).

For a given taxon with few formally assessed species, what proportion of species should be formally assessed to maximize the value of applying predictive models to estimate threatened status across a whole taxon? Bland et al. [12] examined the cost effectiveness of investing in a strategy of formal assessments coupled with modeled predictions relative to the same investment in formal asssessments alone to determine prevalence of threatened status across multiple taxa. In all cases, a coupled formal assessment plus modeling approach was significantly more cost effective than formal assessment on its own. But by focusing on the prevalence of threat status across a data-deficient subset of species, rather predictions of threat status of particular species, it is difficult to map their results to species-specific conservation action. Here we apply the value of information framework from Section 3 to identify the optimal level of formal threatened status assessment that maximizes overall expected benefits of management decisions, based on uncertain threatened status predictions of the remaining (modeled) species.

For a taxon represented by N species, we wish to find some number of species m whose formal assessment maximizes overall expected benefits of threat-based management decisions across all N species. For each species i, let unimpacted ecosystem service value be β_i; let net benefit ratio (1 - proportional cost) of management be γ_i; let net loss ratio of undermanagement be λ_i; and let augmented benefit ratio of overmanagement be α_i.

For those m species with formal assessments, the overall expected value is based on management under perfect information less the cost of performing the assessment, summed across all m species to be assessed:

$$\mathbb{E}[assessed] = \sum_{i=1}^{m} \beta_i \left(1 - (1 - \gamma_i)p_t\right) - c_i$$

For the remaining $N - m$ species, predictive models will be used to determine management decisions under uncertainty, with r_- and r_+ increasing as the number of assessed species m increases. Assuming the use of pre-existing predictor data, cost of modeling would be negligible (<< 1%) relative to formal assessments [12] (note: for collection of new prediction data, see Section 4 for a model to optimize costs against benefits). If we balance the ML probability threshold for categorization such that $r_- \approx r_+$, we can approximate both as a concave increasing function of m, i.e., $r(m)$ such that $r'(m) > 0$ and $r''(m) < 0$. Let us simplify by assuming costs and benefits are such that threatened status dictates management and the converse.

$$\mathbb{E}[estimated] = \sum_{j=m+1}^{N} \beta_j \Big((1 - p_t)r(m) + (1 - p_t)\big(1 - r(m)\big)\alpha_j\gamma_j + p_t\big(1 - r(m)\big)\lambda_j + p_t\gamma_j r(m)\Big)$$

The total taxa-wide expected value of a strategy to formally assess threatened status of m species (with perfect information) to inform ML estimation of threatened status of the remaining $N-m$ species (with uncertainty) is the sum of expected values of these two subsets. The optimal number of species for formal assessment m is the value that maximizes this combined expected value.

To further simplify notation for analytical tractability and conceptual understanding, let all parameters $\beta, \gamma, \lambda, \alpha$ be an average value rather than species specific values.

$$\begin{aligned}
\mathbb{E}[tot] &= \mathbb{E}[assessed] + \mathbb{E}[estimated] \\
&= m(\beta(1-(1-\gamma)p_t) - c) + \\
&\qquad (N-m)\beta\Big((1-p_t)r(m) + (1-p_t)\big(1-r(m)\big)\alpha_j\gamma_j + p_t\big(1-r(m)\big)\lambda_j + p_t\gamma_j r(m)\Big) \\
&= m(\beta(1-(1-\gamma)p_t) - c) + \\
&\qquad (N-m)\beta\big[r(m)\big((1-p_t)(1-\alpha\gamma) + p_t(\gamma-\lambda)\big) + (1-p_t)\alpha\gamma + p_t\lambda\big]
\end{aligned}$$

Taking the derivative of $\mathbb{E}[tot]$ with respect to m and setting to zero should result in the optimal number of species to assess, based on average values of other parameters:

$$\begin{aligned}
\frac{\partial \mathbb{E}[tot]}{\partial m} = 0 \quad &= \beta[1-(1-\gamma)p_t] - c + \\
&\qquad \beta\frac{\partial}{\partial m}(N-m)r(m)[(1-p_t)(1-\alpha\gamma) + p_t(\gamma-\lambda)] + \\
&\qquad (-\beta)[(1-p_t)\alpha\gamma + p_t\lambda] \\
&= \beta[1-(1-\gamma)p_t] - c + \\
&\qquad \beta r'(m)[(1-p_t)(1-\alpha\gamma) + p_t(\gamma-\lambda)] + \\
&\qquad (-\beta)[(1-p_t)(1-\alpha\gamma) + p_t(\gamma-\lambda)]\frac{\partial\big(mr(m)\big)}{\partial m} + \\
&\qquad (-\beta)[(1-p_t)\alpha\gamma + p_t\lambda] \\
&= \beta[1-(1-\gamma)p_t] - c + \\
&\qquad \beta r'(m)[(1-p_t)(1-\alpha\gamma) + p_t(\gamma-\lambda)] + \\
&\qquad (-\beta)[(1-p_t)(1-\alpha\gamma) + p_t(\gamma-\lambda)][r(m) + mr'(m)] + \\
&\qquad (-\beta)[(1-p_t)\alpha\gamma + p_t\lambda]
\end{aligned}$$

Rearranging terms we find the optimal value of $m^* = f(r(m), r'(m), \gamma, \lambda, \alpha, \beta, c, p_t)$:

$$m^* = \frac{1}{r'(m)}\left[1 - (1-\gamma)p_t - (1-p_t)\alpha\gamma - p_t\lambda - \frac{c}{\beta} + r'(m) - r(m)\right]$$

Note that $r(m), r'(m)$ are the relationship, for a given set of predictors, between the number of known observations m and the predictive accuracy of the model r, and as such are independent of parameters $\gamma, \lambda, \alpha, \beta, c$. If r is balanced such that $r_{-} \approx r_{+}$ then $r(m)$ should be independent of p_t. Examining partial differentials of m with respect to various parameters, and recalling that $r'(m) > 0$, we find:

$$\begin{aligned}
\frac{\partial m^*}{\partial c} &= -\frac{1}{\beta} < 0 \\
\frac{\partial m^*}{\partial \beta} &= \frac{1}{r'(m)} \frac{c}{\beta^2} > 0 \\
\frac{\partial m^*}{\partial \lambda} &= \frac{-p_t}{r'(m)} < 0 \\
\frac{\partial m^*}{\partial \gamma} &= \frac{1}{r'(m)} p_t(1+\alpha) > 0 \\
\frac{\partial m^*}{\partial \alpha} &= \frac{p_t \gamma}{r'(m)} > 0 \\
\frac{\partial m^*}{\partial p_t} &= \frac{1}{r'(m)} (\gamma + \alpha\gamma - \lambda) > 0
\end{aligned}$$

These results formalize intuitions around changes in marginal cost and benefit of additional formal assessments. As cost of formal assessment c increases, the optimal number of formal assessments decreases, as the elevated cost exceeds the marginal benefit of additional assessements. Similarly, a decrease in the potential loss due to undermanagement (i.e., 1-λ) reduces marginal benefit and thus the optimal number of assessments. As the value of ecosystem service β increases, or potential ecosystem service enhancement due to overmanagement (i.e., α increases, or cost of management (i.e., $1-\gamma$) decreases, so too does the marginal benefit of improved conservation decisions, and thus the optimal number of formal assessments increases. Finally, as the proportion of threatened species p_t rises, risk of undermanagement in the face of uncertainty rises, driving up the optimal number of formal assessments.

Note that this analysis requires some idea of the shape of $r(m)$ for a given set of predictor data, which is likely to be a logistic curve based on the above formula for m^*. While the logistic parameters may be difficult to assess ahead of time for a poorly studied taxa, some small sample of species could be selected and formally assessed to understand the beginning of the logistic curve, and better predict the overall shape. Note also that the subset of m species chosen for formal assessment must be representative of the broader taxa - a biased sample will inevitably result in a biased estimate of p_t, r_+, r_-, leading to biased estimates of conservation status, and inevitably a biased estimate of the expected value of conservation decisions based upon flawed predictions.

6 Model extensions

The model as developed up to this point generally considers expanding knowledge of conservation status to inform conservation decisions for species individually. However, many environmental management decisions involve more complex situations: policies or protected areas that affect multiple species simultaneously, both threatened and non-threatened; dynamic situations involving periodic decisions over time; making decisions while grappling with uncertainty around costs and benefits of action. But first, is cost-effective conservation compatible with a philosophy of zero tolerance for extinction?

Extinction as unacceptable

Extinction of any species is without a doubt a tragedy; some might say it is a tragedy that should be avoided at all costs. If extinction of a species is entirely unacceptable, our framework for understanding the value of conservation status predictions becomes uninformative: in drawing a red line at extinction, we effectively assign infinite value for the continuation of the species, and the cost of extinction becomes $\infty \times (1 - \lambda) = \infty$. Avoiding this infinite cost for a given species requires perfect knowledge of the species' conservation status combined with perfect action. Per our stated model assumptions, perfect knowledge of conservation status can only be achieved through formal assessment, leaving no room for modeling.

Even with perfect information on conservation status, a no-extinction red line also indicates that no cost is too high to conserve a threatened species - i.e., cost of conservation is $\infty \times (1 - \gamma) = \infty$, which is simply not realistic. Note that while our model assumes formal assessments to indicate "Truth," in the real world, even such formal assessments bear some uncertainty. Extinction of even the meanest of species is indeed a tragedy, and while a no-extinction red line may be a laudable goal, it is not a realistic approach to inform conservation policy.

Scenario analysis

IUCN extinction risk assessments implicitly integrate information on traits, species ranges, current and expected stressors, and explicit integration of population assessments and models to predict near-term extinction risk. There may be great potential in using ML models of extinction risk to evaluate benefits of conservation action, e.g., the reduction in extinction risk due to reduction of shipping traffic, curtailing of agriculture-based nutrient pollution, or establishment of a no-take marine protected area. However, to be responsive to changes in stressor distribution and/or intensity due to conservation action, the ML model must necessarily be initially trained on predictors that include detailed stressor data, particularly stressors that may conceivably be managed by spatial protections or sectoral management.

Most of the studies we examined that applied machine learning to model conservation status included one or more metrics of exposure to stressors, e.g., land use change [7,20], human population density [7,8,11], Human Footprint Index [7,8,19], and/or marine cumulative human impact [7]. Not all studies included information on stressors (e.g., [9]). Of studies that included data from the Human Footprint Index, only Borgelt et al. [7] disaggregated the component stressors to any degree. To allow for scenario analysis, future applications of ML methods must incorporate detailed summary statistics of impacts attributable to distinct and manageable human activities.

The benefits of persistent area-based protection, e.g., terrestrial or marine protected areas, would accrue to more than just a species targeted for direct protection. To fully account for benefits across all species enclosed in a protected area would require some method of spatial aggregation of conservation benefit across many species, some threatened, some not threatened. Such a scenario analysis might estimate the net benefit of establishing a marine protected area by estimating the reduction in stressor intensity relative to a counterfactual of existing stressors, then using this updated stressor layer to repredict conservation status. The optimal level of protection (e.g., MPA area) would balance the net benefit of protection (across all species affected) against the cost of protection (e.g., monitoring and enforcement), which could be amortized across all species present.

In some cases, management decisions may be periodic rather than permanent. Scenario assessment for time-varying management decisions (e.g., dynamic closures or total allowable catch) would need to account for costs and benefits of conservation decisions in each (discounted) time step looking forward, which may in turn influence future assessments of conservation status. A dynamic programming model could be used to maximize net present value of a series of expected conservation decisions made in each period t, based on conservation status predictions driven by expected stressor values in time t. Such an approach could enhance analysis of management scenarios, but would require projections of stressor information into the future.

Uncertainty in cost and benefit parameters

In our examination of expected value of information, we modeled costs and benefits as fractions of the benefit from unmanaged/unthreatened status. However, benefits and costs of management or mismanagement surely bear some level of uncertainty as well. These uncertainties are likely to change the thresholds of required precision accuracy (Section 4) or number of required formal assessments (section 5), as well as previous model extensions presented in this section. Probabilistic approaches such as Bayesian analysis or Monte Carlo simulation could incorporate distribution information for cost and benefit estimates to provide insights in the effects of uncertainty.

7 Discussion and conclusion

In the above analysis and exploration, we have assumed that (a) each species falls into a conservation status of either threatened or non-threatened, and (b) formal assessment of a species, e.g., the IUCN Red List, can identify the species' conservation status perfectly. Regarding assumption (a), it is clear that conservation status should be more accurately considered along a curriculum, with some species at far greater risk of extinction than others. This is clear in the IUCN's more nuanced (though still discrete) categories of conservation status denoting ever-increasing risk of extinction, which are sometimes applied as ordinal outcomes (e.g., [9,20]) rather than a binary threatened/non-threatened status. Regarding assumption (b), no assessment of conservation status can be 100% certain, as even the best formal assessment is still based on data, observations, and assumptions that can only approximate the "truth." However, IUCN Red List assessments are widely recognized as the gold standard for understanding species extinction risk, and thus represent the best available information for training predictive models.

The IUCN Red List strives to avoid within-taxon bias, e.g., singling out particularly endangered species within a taxon for assessment, by encouraging use of comprehensively-assessed taxa (i.e., 90% or more species within the taxon have been formally assessed) in analysis. Even comprehensively assessed taxa generally contain some subset of species classified as data deficient; predicting the conservation status of these data-deficient species within otherwise comprehensively assessed taxa has been the focus of previous predictive models. However, while this comprehensively-assessed taxon approach reduces within-taxon bias, there is considerable bias among the taxa slated for formal assessment - particularly toward vertebrate species rather than invertebrates. For poorly assessed taxa, the hybrid assessment/prediction model discussed in Section 5 (and in [12]) would be particularly valuable to quickly and cost-effectively expand our understanding of threatened biodiversity before any more species are lost to extinction.

Here we have focused on species conservation status as the key question in our value of information and decision framework. However, this framework can readily be applied to other conservation contexts, by defining as "threatened" any ecosystem element whose value is at risk of loss if no conservation action is taken. This could be an entire ecosystem identified as threatened by the IUCN Red List of Ecosystems [25,26], or more informally, fishery value of a locally threatened population of an otherwise globally unthreatened species, storm surge protection of a vibrant coral reef, cultural importance of a traditionally important rain forest, or phylogenetic diversity of a biodiverse prairie.

Conservation efforts around the globe rely on accurate, up-to-date understanding of species conservation status to design effective strategies to reduce extinction risk, and data deficient or otherwise unassessed species are at risk of being lost before we have sufficient formal knowledge to identify them as threatened. Machine learning methods applied to predicting conservation status show great promise to rapidly update our understanding of extinction risk, and may enable scenario analysis of proposed conservation actions. Improving the accuracy of ML predictions of conservation status will require investment in new data and/or additional formal assessments, but weighing the value of such information against the value of avoided loss of ecosystem services, the costs of new investment will be more than compensated by the quality of conservation decisions that result.

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