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Improving Marine Conservation Planning in a Time of Global Change

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Abstract

Despite substantial growth in marine conservation efforts over the past two decades, biodiversity continues to decline. This is due to human activities impacting biodiversity almost everywhere in the ocean, combined with a failure to address the full range of stressors to marine biodiversity. These stressors fall into three broad categories – ocean-based stressors such as fishing, land-based stressors such as nutrient runoff, and anthropogenic climate change stressors such as increasing temperatures.

To date, marine conservation efforts have primarily focused on stopping ocean-based stressors, primarily by using marine protected areas (MPAs) which have grown ten-fold since the year 2000. While this growth is promising, effective marine conservation requires not only further expansion of the global MPA estate, but also other measures aimed at ameliorating land-based stressors and climate change. To secure marine biodiversity into the future, these measures must be used as part of a multi-faceted strategy that secures imperilled species, facilitates recovery of already degraded ecosystems, and preserves places free from intense human activity. This thesis draws on decision science to provide scientific guidance and planning methods for this type of multi-faceted marine conservation strategy that addresses the full range of stressors to biodiversity.

Given the severe impact climate change is already having on biodiversity, it is crucial that marine conservation approaches consider and plan for the impacts of climate change, now and into the future. Despite this imperative, there have been no assessments of how climate change is being incorporated into conservation planning. In **Chapter 2** I address this gap by reviewing conservation planning approaches to assess if and how they incorporate climate change. I discover that the vast majority of approaches do not consider climate change at all, and those that do often rely on uncertain forecasts of future climate or species distributions. By summarising the benefits and weaknesses of various approaches, this review highlights future research needs to improve marine conservation action in the face of multiple threats including climate change.

Chapter 2 showed that an important approach for incorporating climate change into conservation planning is to identify and protect those places or ecosystems that will be most

resilient to change. Due to their intact nature, marine 'wilderness areas' (those places free from intense human impacts) are well-placed to resist and recover from the impacts of climate change, yet there has been no systematic identification of these areas in the ocean. In **chapter 3** I present a global assessment of marine wilderness and discover that only 13.2% of the ocean remains as wilderness, with most located at extreme latitudes. I also show that most of these wilderness areas are unprotected, highlighting the need for future conservation agreements to recognise the unique values of wilderness and set targets for their retention.

While conserving wilderness is a crucial conservation goal, most marine species remain poorly represented in conservation areas, making it clear that future MPA expansion is also vital to conserve marine biodiversity. In **chapter 4** I identify priority areas for marine conservation action to meet current representation targets for ~23,000 marine species and complement existing conservation areas. I discover that representing 10% of all mapped marine species ranges will require an additional 8.5 million km^2 of conservation areas, an expansion of the existing MPA estate by one-third. To guide conservation action, I then determine if the threats to these priority areas are ocean-based or land-based. Securing these areas through marine and terrestrial management will help protect marine biodiversity and provide a solid foundation for ambitious future conservation goals.

Given widespread degradation of the ocean, facilitating ecosystem recovery will be an essential future conservation goal. Using a model of reef fish biomass recovery in the Western Indian Ocean, in **chapter 5** I develop conservation planning methods to facilitate rapid recovery of degraded coral reef fisheries, which will help to increase sustainable fisheries yields and increase reef resilience to acute stressors. The results demonstrate that aiming to minimise reef recovery time substantially changes management priorities compared to other common prioritisation approaches. Changing priorities to minimise reef recovery time is likely to require a trade-off against other fishery management and conservation objectives.

In **chapter 6** I synthesize the findings of this thesis, highlight their implications for conservation practice and policy, and identify priorities for future research. Given the unparalleled scale and severity of human impacts to the ocean, it is clear that increases in the scope of global conservation strategies are needed to avoid widespread biodiversity declines and maintain ecosystem services. This thesis helps to advance the science needed to develop such strategies and ensure that marine biodiversity, along with the vast suite of benefits humanity derives from it, is preserved in perpetuity.

Declaration by author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

I have clearly stated the contribution of others to my thesis as a whole, including statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, financial support and any other original research work used or reported in my thesis. The content of my thesis is the result of work I have carried out since the commencement of my higher degree by research candidature and does not include a substantial part of work that has been submitted to qualify for the award of any other degree or diploma in any university or other tertiary institution. I have clearly stated which parts of my thesis, if any, have been submitted to qualify for another award.

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<u>Publications included in this thesis</u>

1. Jones, KR, Watson, JEM, Possingham, HP, Klein, CJ. 2016. Incorporating climate change into spatial conservation prioritisation: A review. *Biological Conservation* 194, 121-130.

2. Jones, KR, Klein, C, Halpern, BS, Venter, O, Grantham, H, Kuempel, C, Shumway, N, Friedlander, AM, Possingham, HP, Watson, JEM. The location and protection status of Earth's diminishing marine wilderness. *Current Biology* 28, 1-7.

3. Jones, KR, Maina, JM, Kark, S, McClanahan, TM, Klein, CJ, Beger M. Incorporating feasibility and collaboration into regional management planning for recovery of coral reef fisheries. *Marine Ecology Progress Series* 604, 211-212.

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Allan, JR, Venter, O, Maxwell, S, Bertzky, B, **Jones, KR**, Shi, Y, Watson, JEM. 2017. Recent increases in human pressure and forest loss threaten many Natural World Heritage Sites. *Biological Conservation*. 206, 47 – 55.

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Contributions by others to the thesis

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No works submitted towards another degree have been included in this thesis.

Research Involving Human or Animal Subjects

No animal or human subjects were involved in this research

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List of Abbreviations

CBD	Convention on Biological Diversity
EEZ	Exclusive Economic Zone
FAO	United Nations Food and Agriculture Organization
IUCN	International Union for the Conservation of Nature
KBA	Key Biodiversity Area
MPA	Marine Protected Area
OECM	Other Effective Area-Based Conservation Measure
PA	Protected Area
PU	Planning Unit
RFMO	Regional Fisheries Management Organisation
SDM	Species Distribution Model
Tr	Time to Recovery
WDPA	World Database on Protected Areas
WIO	Western Indian Ocean

Chapter 1 – Introduction

As NASA's Voyager I spacecraft hurtled past Pluto in 1989, on the cusp of becoming the first human object ever to leave our solar system, astronomer Carl Sagan pleaded with the imaging team to turn the camera around for one last look at Earth before entering interstellar space. The image it beamed back from 6 billion kilometres away, showing Earth as a mote of dust suspended in an immense sunbeam, became known as "The Pale Blue Dot", and Sagan had this to say of the photo:

> *Consider again that dot. That's here. That's home. That's us…. Our planet is a lonely speck in the great enveloping cosmic dark. In our obscurity, in all this vastness, there is no hint that help will come from elsewhere to save us from ourselves. Like it or not, for the moment the Earth is where we make our stand.*

So, how are we faring as custodians of this pale blue dot? Unfortunately, given our seemingly unbounded ability to destroy other life on Earth, the answer seems to be very poorly. Our appetite for flesh, fibre and fuel is now responsible for species extinctions occurring at a rate up to 1000 times greater than normal (Pimm et al. 1995). Even in the ocean, where large-scale human access was limited until the industrial revolution, we have already depleted 90% of commercially or functionally important species and destroyed 65% of seagrasses and wetlands (Lotze et al. 2006). Our insatiable appetite for energy means we are now also impacting every organism on Earth, including those that we are not hunting or harvesting, by warming the atmosphere and acidifying the oceans (IPCC 2014).

Humanity is now faced with a question - will we take a stand to preserve the diversity of life on Earth, the only planet we know to harbour it? Or will biodiversity continue to decline until we are threatened with our own extinction, forced into action by a collapsing biosphere? This thesis contributes to a growing body of conservation research aimed at ensuring humanity acts to halt threats to biodiversity using effective and efficient conservation strategies. Focusing on the ~70% of our planet covered by the oceans, this thesis provides scientific guidance and planning methods to help develop marine conservation approaches which consider the full range of threats to marine biodiversity.

The Marine Realm

The ocean is the most widespread ecosystem on Earth, covering more than 70% of the planet. It harbours a diverse range of environments, from semi-terrestrial mangroves through to shallow-water seagrasses and coral reefs, and all the way down to deep trenches where life persists without sunlight. These habitats support around 2.2 million known eukaryotic species, but given that less than 5% of the ocean has been explored, roughly 91% of marine species remain undescribed (Mora et al. 2011b). The ocean is also responsible for around half of Earth's primary productivity (Field et al. 1998), and produces almost three-quarters of total atmospheric oxygen (Sekerci & Petrovskii 2015).

Given the diversity and productivity of marine environments, it is unsurprising that humans have an intimate connection with the ocean. Human population density is roughly three times higher in coastal areas than inland (Small & Nicholls 2003), and coastal migration is constantly increasing (Neumann et al. 2015). This relationship is based primarily around harvesting marine biodiversity for food, and each year humanity catches around 20kg of fish for every single one of the 6.8 billion people on Earth (FAO 2016). Over 2.8 billion people rely on this catch as an important source of protein, and millions rely on fishing for their livelihoods, especially in developing regions (FAO 2016). Beyond fishing for food and employment, humans also use the ocean for the vast majority of global trade (Curtis 2009), for natural resource extraction (Sandrea & Sandrea 2007), and as a source of recreation (Pearson 2016). As such, the ocean is crowded with a variety of human activities and no area is totally free from human impacts (Halpern et al. 2008, 2015).

Human stressors on the ocean have driven massive declines in marine biodiversity worldwide, especially in biodiverse coastal regions. Populations of locally and commercially fished species have fallen by half since 1970 (Tanzer et al. 2015), intense fishing has driven range contractions in almost 90% of large pelagic fishes (Worm & Tittensor 2011), and one in four shark species is currently threatened with extinction (Dulvy et al. 2014). There are numerous places in the Caribbean named after sea turtles whose populations have dropped from tens of millions to tens of thousands (Jackson 1997; Jackson et al. 2001). Even in areas with world-class fisheries management, such as the Great Barrier Reef in Australia, land-based runoff is 5-10 times higher than historical levels (McCulloch et al. 2003), contributing to reduced coral recruitment and diversity, replacement of corals by macroalgae and filter feeders, and more frequent crown-of-thorns starfish outbreaks (Kroon et al. 2012).

Despite widespread impacts to the ocean, and a long history of overexploitation of marine resources, current trends and future prospects of marine biodiversity remain controversial (Worm et al. 2009). In many studied fisheries the average exploitation rate is now at or below the level predicted to achieve a long-term sustainable yield (Worm et al. 2009), and in some developed countries (e.g. USA, Australia, New Zealand) fisheries management systems appear to be working to achieve sustainable fisheries management (Hilborn 2007a). However, in many other regions such as Africa and Asia, the institutions required to achieve sustainable fisheries simply do not exist (Hilborn 2007b). Regardless of the success of fisheries management in some areas, effective controls on exploitation rates are still lacking in vast areas of the ocean (Worm et al. 2009), and it remains clear that humans have profoundly altered the marine environment (McCauley et al. 2015).

While human activities impact marine biodiversity in many different ways, they can generally be split into three categories: ocean-based stressors, land-based stressors, and climate change stressors. Ocean-based stressors include commercial fishing, which has a spatial extent four times that of agriculture (Kroodsma et al. 2018); and habitat alteration driven by destructive fishing methods (Halpern et al. 2008), resource extraction (Mengerink et al. 2014), energy generation (Gill 2005) and aquaculture (Klinger & Naylor 2012). Land-based stressors consist mainly of sediment and nutrient runoff driven by deforestation and agriculture (Smith et al. 2003; Fabricius 2005). Climate change stressors, including increased temperatures and ocean acidification, impact biodiversity directly by causing mass coral bleaching (Hughes et al. 2003) or shifts in species ranges (Parmesan & Yohe 2003); and indirectly, through human responses to climate change (e.g. seawall construction to combat sea-level rise; Grantham et al. 2011). While these stressors have different sources, they do not occur independently from one another, and they often interact synergistically – where the simultaneous impacts of multiple stressors have a greater total impact than the sum of individual stressor impacts alone (Brook et al. 2008). However, it is useful to separate them when considering possible conservation responses as all require different management actions to address.

Global Marine Conservation

In response to widespread human stressors driving persistent biodiversity declines, the international community has developed a number of conservation agreements. The most prominent of these is the Convention on Biological Diversity (CBD), an international treaty which sets out a global strategy for the conservation and sustainable use of biological diversity. The 196 signatories to the CBD create National Biodiversity Strategies and Action Plans, aiming to implement the goals of the CBD at the national scale and meet 20 time-bound, measurable targets by 2020 (the “Aichi Biodiversity Targets”; Convention on Biological Diversity (CBD) 2014). Aichi Target 11, which mandates protection of at least 17% of terrestrial and 10% of marine environments by 2020, has led to a doubling of the protected area estate since 1992 (UNEP-WCMC & IUCN 2018a). Marine protected areas (MPAs) now cover 7.26% of the ocean (26 million square kilometres), with many nations set to meet their 10% protection goal under Aichi target 11.

Despite considerable progress towards 2020 marine protection commitments, recent global assessments show no sign of the biodiversity crisis being abated (Collen et al. 2009; Dirzo et al. 2014; Tittensor et al. 2014). Aggregated population data shows historical abundance declines of around 22% in marine mammals, 38% in marine fish, and 90% in some whale species (McCauley et al. 2015). Human activities are also destroying the habitats on which species depend, with tropical coral reefs losing over half their reef-building corals over the last 30 years (Hoegh-Guldberg 2015), and 20% of global mangrove cover being lost since 1980 (Tanzer et al. 2015). While the rapid growth in MPAs is no doubt encouraging, as they can be one of the most effective tools for conserving marine biodiversity (Edgar et al. 2014), it is clear that they are currently insufficient to halt marine biodiversity declines.

One reason that biodiversity continues to decline despite increasing MPA coverage – beyond the fact that MPAs poorly represent most species (Klein et al. 2015) – may be a failure to address the full range of stressors to the environment. Marine conservation efforts generally aim to reduce ocean-based stressors such as over-harvesting or destructive fishing methods (Beck 2003; Lester & Halpern 2008; Klein et al. 2010), and this is achieved through MPA designation or fishery management. Conservation planning – a systematic approach to locating and designing conservation actions (Margules & Pressey 2000) – is now commonly used to design MPA networks to deal with ocean-based stressors, but it has historically overlooked the land-based and climate change stressors that also impact marine biodiversity (Álvarez-Romero et al. 2011). Despite the impacts of runoff to the ocean being recognised as early as the 1950's (Hutner & McLaughlin 1958), land-based stressors have only recently been incorporated into marine conservation planning (Klein et al. 2012, 2014; Tulloch et al. 2016). Similarly, several mandates for considering climate change in conservation planning have emerged over the past decade (UNFCCC 2011; Cross et al. 2012b; Stein et al. 2014), but there have been no assessments of how climate change is actually being incorporated into conservation planning approaches.

Given that marine ecosystems are affected by a combination of threats from multiple sources, some of which are unstoppable using local conservation action, it is now clear that effective marine conservation will require a multi-faceted approach. First, active conservation efforts (e.g. MPAs, runoff management) must be used to stop imminent biodiversity loss by securing endangered biodiversity and irreplaceable sites. Second, where biodiversity loss and ecosystem degradation has already occurred, conservation efforts should facilitate ecosystem recovery, as this can increase resilience to global stressors such as climate change (Carilli et al. 2009a). Third, places that are still intact and functioning unimpeded by large-scale human activities must also be preserved, as they are likely more resilient to the threats that MPAs are unable to stop (e.g. climate change; Martin & Watson 2016). It is now crucial that marine conservation science provides the guidance and decision-making approaches needed to develop and implement these multi-faceted conservation plans.

Conservation research and policy recognises the importance of securing endangered biodiversity and irreplaceable sites, and the techniques for efficiently designating conservation actions to do so first emerged over three decades ago (Kirkpatrick et al. 1983; Kirkpatrick 1983). However, much less attention has been placed on identifying areas where human impact is relatively low - often termed wilderness. These areas act as vital refugia for biodiversity (Kormos et al. 2016; Watson et al. 2016b); contain high genetic diversity (Smith et al. 1991; Epps et al. 2005; Pinsky & Palumbi 2014); and maintain high levels of ecological and evolutionary connectivity (Jones et al. 2007; Grober-Dunsmore et al. 2009; Haddad et al. 2015), giving them high resilience to climate change (Prugh et al. 2008; Rudnick et al. 2012; Martin & Watson 2016). On land, devastating declines in wilderness have recently been documented (Watson et al. 2016b; Allan et al. 2017b), leading to several calls for conservation of the remaining areas (Kormos et al. 2016; Allan et al. 2017a). In the ocean however, few studies have assessed large unmodified areas despite several calls to do so (Craig 2003; Graham & McClanahan 2013; D'agata et al. 2016). Wilderness areas present a substantial opportunity for marine conservation, as they are relatively free of the ocean and land-based stressors which impact biodiversity, and may also be more resilient to climate change stressors which local management cannot address (Prugh et al. 2008; Carilli et al. 2009b; Graham et al. 2013; Martin & Watson 2016).

In an era of widespread biodiversity declines and shifting baselines, intact wilderness areas also act as reference points to inform restoration and recovery of degraded areas (Graham & McClanahan 2013; Watson et al. 2016b). When marine ecosystems are overexploited or degraded, biodiversity and ecosystem function declines (Jackson et al. 2001; Hughes et al. 2003; Pandolfi et al. 2003; McCauley et al. 2015) and these areas can also become less resilient to acute stressors such as climate change (Hughes et al. 2003; Carilli et al. 2009b; Côté & Darling 2010; Mumby et al. 2015). In those ecosystems that are heavily impacted by fishing or other human activities, facilitating ecosystem recovery will be essential to preserve the full range of biodiversity and can also increase resilience to acute stressors. Ecosystem recovery can be achieved by limiting human access and activities in certain areas (e.g. MPAs), or through other approaches such as active restoration (e.g. planting seagrass), or fishery regulations (e.g. gear restrictions, catch quotas).

A growing body of research is now calling for the broad-scale thinking and action needed to achieve global plans for nature conservation by expanding the MPA estate to secure imperilled species and ecosystems, identifying and protecting intact ecosystems, and restoring degraded areas (Lovejoy 2016; Dinerstein et al. 2017; Watson & Venter 2017). Identifying the most important places for achieving these goals, and assessing the actions required to address threats facing those places, is a crucial future question for conservation decision science.

Conservation Decision Science

Each of the major research agendas undertaken in this thesis either directly uses tools from decision science or develops methods and results that can inform the application of such tools. Broadly speaking, decision science is used in conservation to help choose between actions in places. This stems from necessity: there are limited resources available to conserve biodiversity and using decision science tools can increase the efficiency of conservation investments. A brief background on the use of decision science in conservation is provided here, but a more detailed presentation can be found in Moilanen et al. (2009a).

Over the past 30 years, a systematic approach to conserving biodiversity has evolved, which uses decision science to help us choose how, when and where to protect biodiversity (Margules & Pressey 2000). Known as “Systematic Conservation Planning”, this framework includes 11 well-defined stages (Table 1.1) and is more transparent, rigorous, and accountable than allocating conservation funds opportunistically (Margules & Pressey 2000; Groves et al. 2002; Pressey & Bottrill 2009). This thesis focuses mainly on spatial conservation prioritisation, a fundamental part of step 9, which is based on identifying area-based conservation measures such as MPAs (Table 1.1).

Table 1.1 Systematic conservation planning framework adapted from Pressey and Bottril (2000).

1.	Scoping and costing the planning process
2.	Identifying and involving stakeholders
3.	Identifying the context for conservation areas
4.	Identifying conservation goals
5.	Collecting socio-economic data
6.	Collecting biodiversity data
7	Setting conservation targets
8.	Reviewing target achievement in existing conservation areas
9.	**Selecting additional conservation areas**
10.	Implementing conservation actions
11.	Maintaining and monitoring established conservation areas

Spatial conservation prioritisation involves designing systems of conservation areas which aim to fulfil a set of basic principles (Moilanen et al. 2009a): *comprehensiveness* – that is including a portion of every biodiversity feature (e.g. species, ecoregions) of interest; *representativeness* – that is including representative samples of each biodiversity feature; *adequacy* – that is being adequately sized and placed to ensure persistence and continued evolution of biodiversity; and *cost-efficiency* – that is aiming to achieve the previous three principles for the lowest cost, which can be measured directly (e.g. land purchasing value) or indirectly (e.g. lost fishing opportunity within an MPA).

To help identify conservation areas which meet these principles, a number of decision support tools have been developed, such as ‘Marxan’ and ‘Zonation’ (Moilanen 2007; Watts et al. 2009). These tools use data on the distribution of biodiversity features and costs to identify priority areas of a land/seascape for conservation action. Typically, these kinds of tools solve one of two problems. First, the minimum set problem, aims to identify a set of areas which meets predetermined targets (e.g. include 30% of all species ranges) for the lowest cost. The second, the maximum set problem, aims to maximise conservation benefit for a set budget (e.g. $3,000,000 to spend on land acquisition).

Thesis Overview

This thesis aims to provide scientific guidance and planning methods to help develop marine conservation approaches which prioritise and protect threatened biodiversity, secure places that remain relatively untouched by humanity, and allow for recovery of degraded areas. In an era of massive global change driven by human population growth and carbon emissions, these approaches are crucial to help marine biodiversity survive the impacts of ocean-based, land-based and climate change stressors.

Chapter 2 is a systematic review of how spatial conservation prioritisation approaches incorporate climate change. I assess whether climate change is considered, the types of climate impacts considered; the biological units, spatial scale, and timeframe assessed; and the goal of each prioritisation approach (i.e. how did approaches plan to deal with climate impacts). By categorising approaches into broad groups and summarising their benefits and weaknesses, this review informs parts of **chapters 3-5**, identifying research gaps and highlighting future research needs to improve marine conservation action in the face of multiple threats including climate change.

In **chapter 3** I present the first systematic global identification of marine wilderness by mapping marine areas devoid of ocean-based, land-based, and climate change stressors. Recognising that human influence differs substantially across the ocean, I also develop regionally downscaled maps of marine wilderness, identifying the lowest impact areas of each ocean realm. Finally, I assess the extent of wilderness across marine ecosystems (e.g. coral reefs, soft-bottom shelf), and the level of wilderness protection in the global MPA estate.

Chapter 4 is a global analysis identifying current marine conservation priorities. I first evaluate representation of ~23,000 marine species within protected areas (MPAs), key biodiversity areas (KBAs), and marine wilderness areas (from **chapter 3**) because all can offer conservation benefits through direct protection or a lack of threats to species. For species which are not adequately represented (<10% of range protected), I use integer linear programming to identify additional conservation priorities to achieve 10% representation for all species while minimising the total area required. To assess the actions needed to protect species in these conservation priorities, I then map the intensity of ocean-based (e.g. fishing) and land-based (e.g. run-off) stressors across them.

In **Chapter 5** I present a regional case study which develops conservation planning methods to facilitate rapid recovery of degraded coral reef ecosystems. Coral reefs are overharvested in many regions across the globe, leading to loss of biodiversity and ecosystem functions (Dulvy et al. 2004; Mora et al. 2011a; McClanahan et al. 2011; Bellwood et al. 2011), and decreased resilience to acute stressors such as climate change. With the appropriate conservation actions these areas can recover, but recovery rates depend on degradation level, local demography, and management conditions. Using the Western Indian Ocean as a case study, this chapter identifies spatial priorities to minimise coral reef recovery time and thereby maximise resilience to acute stressors such as coral bleaching or land-based runoff. I also incorporate spatial estimates of management feasibility to help ensure limited conservation and fishery management resources are used efficiently, as well as exploring the potential efficiencies to be gained through international collaboration.

In **chapter 6** I examine the major conclusions from each chapter and their significance for marine conservation. I then discuss some of the emergent conclusions from looking at this thesis as a whole, and also consider some limitations of the research. Finally, I identify important directions for future research which I believe can inform the broad-scale thinking and action needed to secure marine biodiversity in perpetuity.

This thesis was developed as a series of individual papers for publication. As such, in **chapters 2-5** I use the plural ‘we’, which is required of multi-author journal articles. Because each chapter is written in a style suitable for the journal in which it is published, or intended for publication, there are some differences in the formatting among chapters. Finally, there is some repetition among chapters in their introductions, which is necessary for each chapter to stand on its own.

Chapter 2

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Contributor	Statement of contribution
Jones, KR (Candidate)	Conception and design (50%) Analysis and interpretation (65%) Drafting and production (65%)
Watson JEM	Conception and design (20%) Analysis and interpretation (15%) Drafting and production (15%)
Possingham, HP	Conception and design (10%) Analysis and interpretation (10%) Drafting and production (5%)
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Chapter 2 – Incorporating climate change into spatial conservation prioritisation: A review

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Abstract

To ensure the long-term persistence of biodiversity, conservation strategies must account for the entire range of climate change impacts. A variety of spatial prioritisation techniques have been developed to incorporate climate change. Here, we provide the first standardised review of these approaches. Using a systematic search, we analysed peer-reviewed spatial prioritisation publications (n = 46) and found that the most common approaches (n = 41, 89%) utilised forecasts of species distributions and aimed to either protect future species habitats (n = 24, 52%) or identify climate refugia to shelter species from climate change (n = 17, 37%). Other approaches (n = 17, 37%) used well-established conservation planning principles to combat climate change, aimed at broadly increasing either connectivity (n = 11, 24%) or the degree of heterogeneity of abiotic factors captured in the planning process (n = 8, 17%), with some approaches combining multiple goals. We also find a strong terrestrial focus (n = 35, 76%), and heavy geographical bias towards North America (n = 8, 17%) and Australia (n = 11, 24%). While there is an increasing trend of incorporating climate change into spatial prioritisation, we found that serious gaps in current methodologies still exist. Future research must focus on developing methodologies that allow planners to incorporate human responses to climate change and recognise that discrete climate impacts (e.g. extreme events), which are increasing in frequency and severity, must be addressed within the spatial prioritisation framework. By identifying obvious gaps and highlighting future research needs this review will help practitioners better plan for conservation action in the face of multiple threats including climate change.

Introduction

Anthropogenic greenhouse gas emissions have caused increased temperatures, sea level rise, altered rainfall patterns and increases in the frequency and severity of extreme events (IPCC 2014). We are already witnessing a range of impacts on biodiversity including changes in species ranges (Parmesan & Yohe 2003), mass coral bleaching events (Hughes et al. 2003), changes in phenology (Lane et al. 2012), and changes in species interactions and community composition (Thomas 2010). While habitat loss, agricultural expansion, overexploitation, invasive alien species and land-use change have been the main direct drivers of biodiversity loss in recent past (Hoffmann et al. 2010), an increasing number of studies suggest that climate change is likely to become the main cause of extinction over the coming century (Thomas et al. 2004; Brook et al. 2008; Maclean & Wilson 2011; Urban 2015).

Human-forced climate change also has indirect impacts on the environment, as it is altering how and where people interact with their environment (Watson 2014). For example, significant reductions in frost occurrences are altering wheat and maize cropping systems, which is leading to increased agricultural expansion in some areas (Zwiers et al. 2011; Porter et al. 2014). Some communities are migrating away from agricultural lands entirely, because they can no longer maintain agricultural yields (Feng et al. 2010). Other human responses to climate change include the building of seawalls to protect against sea-level rise, which has a variety of ecological impacts including habitat loss (Dugan et al. 2008; Grantham et al. 2011), and the shifting of fishing grounds with changes in fish distribution (Pinsky & Fogarty 2012). As the climate continues to rapidly change, future human responses are likely to increase in magnitude and have increasing impacts on biodiversity. For example, Wetzel et al. (2012) show that relocation of urban areas and agricultural land due to future sea level rise will significantly impact Pacific island mammals, and these impacts may be more severe than the direct impacts of sea-level rise. Additionally, historical examples of adaptation (e.g. agricultural shifts) to environmental change show that it can have serious biodiversity impacts (e.g. large-scale natural vegetation losses; Henry et al. 2003). Therefore effective conservation strategies must consider all impacts of climate change, including direct (e.g. temperature change) and indirect (e.g. shifting agricultural production), as well as incorporating climate threats at different time scales, as threats may be long-term (e.g. temperature increases) or discrete (e.g. coral bleaching events, cyclones) (Chapman et al. 2014)

Several mandates for the consideration of climate change in spatial conservation prioritisation and resource management have emerged over the past decade (UNFCCC 2009; Prip et al. 2010; Cross et al. 2012b, 2012a; Stein et al. 2014). These approaches all argue that to be "climate-smart" (Stein et al. 2014) they must not only consider climate impacts, but also identify spatially-explicit priority adaptation actions (hereafter "spatial prioritisation"; Moilanen et al. 2009a). While other reviews have summarised some broad climate change adaptation approaches for conservation planning, e.g. maintaining connectivity, protecting climate refugia (Schmitz et al. 2015), or reviewed recommendations for climate adaptation measures (Heller & Zavaleta 2009) no study has reviewed the spatial prioritisation methods used to implement these adaptation approaches. Given the impact climate change is having, and is likely to have on conservation planning and actions, we provide the first formal review of the methods used to incorporate climate change into spatial prioritisation. For each publication we assessed the objectives that were considered and the impacts and actions prioritised for, and the overall methodology employed. As climate change is a continuous, dynamic threat, we also evaluated the time frames, biological units, and spatial scale considered by each prioritisation. By doing this, we were able to categorise approaches into broad groups, summarise their benefits and weaknesses, and at the same time identify obvious gaps and highlight future research needs to help practitioners better plan for conservation action in the face of multiple threats including climate change.

Assessing different approaches

In order to assess how spatial conservation prioritisation approaches are addressing climate change, we conducted a review of peer-reviewed journal articles, with no restrictions on the date of publication. We searched ISI Web of Science using the primary keywords 'Reserve Design', 'Spatial Conservation Prioriti*', 'Spatial Prioriti*', 'Systematic Conservation Planning', 'Protected Area' or 'Natura 2000'. We combined all primary keywords with the following secondary keywords 'Climate change', 'Warming', 'Temperature', 'Precipitation', 'Sea level', 'Fire', 'Coral bleaching', 'Acidification', 'Drought', 'Flood*' or 'Extreme event'. We searched using all possible combinations of the four primary keywords and each secondary keyword with the Boolean 'AND' operator, and combined the results of each search, to return 1309 results. Using the Web of Science refine function, we refined these results to the research area of "Biodiversity

Conservation”, to return 304 articles. While we acknowledge that there are many examples of spatial prioritisation approaches incorporating climate change in the grey literature (e.g. NGO or government reports), we followed previous reviews (e.g. Knight et al. 2008) and excluded it, due to the difficulties of comprehensively collating it. We also recognise that when reviews of grey literature are conducted on climate adaptation, they have identified a clear pattern showing that the methods employed are almost always from the published literature (Seimon et al. 2011).

For each article we assessed whether spatial prioritisation was conducted, following the definition in Wilson et al. (2009), where to satisfy our criteria methods needed to spatially identify (i.e. map) priority locations using a quantitative method. Non-quantitative approaches to prioritisation, such as expert opinion or intuition were not included. Similarly, articles that only provided recommendations were excluded from analysis (e.g. Araújo, (2009); who reviewed potential methods to incorporate climate change into spatial prioritisation, but did not conduct an analysis). To fit our criteria, articles also needed to mention that they were specifically planning for climate change. Those which used methods that could potentially be used to deal with climate change (e.g. increasing connectivity) but did not specify that their purpose was to plan for climate change, were excluded. We found 46 articles meeting our criteria, with publication dates ranging from 2004 to 2015, though most were published during or after 2010 (n = 37, 80%). There was a strong focus on terrestrial ecosystems (n = 34, 74%), and heavy geographical bias of studies being conducted within Australia (n = 11, 24%) and North America (n = 8, 18%; Figure 2.1).

It is important to note that the number of spatial prioritisation publications incorporating climate change is still relatively very low (n = 46), given that > 1100 spatial prioritisation articles had been published by May 2008 (Moilanen et al., 2009). The earliest article in our review was published in 2004 (Araújo et al. 2004), despite recommendations that climate change be incorporated into conservation planning coming as early as 1985 (Peters & Darling 1985), and the first assessments of species vulnerability to climate change being published at the latest by 1994 (Grabherr et al. 1994).

Figure 2.1 Approximate location of study areas in articles fitting our search criteria, and the ecosystem they focused on. Two global terrestrial studies are not shown.

Direct versus indirect impacts of climate change

To determine the aspects of climate change that are being incorporated into spatial prioritisation, we examined the methodological details from articles that met our criteria. We first analysed how different climate impacts were considered in the prioritisation by classifying the impacts into two classes: direct and indirect. Following Chapman et al. (2014), direct impacts were defined as those impacts caused directly by changes in climatic variables (e.g. temperature, precipitation etc). Examples of direct impacts include changes in species distributions due to a shift in their climatic niche (Parmesan & Yohe 2003), or ocean acidification reducing the ability of marine organisms to produce calcareous skeletal structures (Fabry et al. 2008). Indirect impacts were defined as those caused by human responses to climate change, such as shifting agricultural patterns or the building of seawalls.

All but one article (n = 45, 98%) focused on direct impacts, while one article considered both direct and indirect impacts of climate change. While some articles incorporated human activities such as land-use change, we only considered these as indirect impacts if climate change was driving those activities, or used in predicting them.

Discrete versus continuous impacts of climate change

The impacts of human-forced climate change not only include continuous, gradual changes in temperature and precipitation regimes, but also changes in the frequency and severity of extreme events, and changes in the magnitude and timing of seasonal events (IPCC 2014). We therefore analysed the form of climate change impact considered in each prioritisation by classifying articles based on their consideration of continuous, gradual impacts such as temperature and precipitation change, and discrete impacts such as coral bleaching events or extreme floods. All but one article (n = 44, 98%) focused only on continuous impacts while one article considered continuous and discrete impacts. We also assessed the timeframe of impacts considered in each approach, by classifying them into 3 groups: short (present to 2030), mid-range (2031–2050), and long (beyond 2051). Long-term impacts were most considered (n = 43, 43%) although short (n = 31, 31%) and mid-range (n = 26, 26%) predictions were also frequently used (Table 2.1).

Biological units and spatial scale

Because prioritisation goals sometimes depend on the natural history of the conservation feature (e.g. species or ecosystem), we assessed the biological units and spatial scale considered in each approach. We separated the biological units into three categories: single species, multiple species, or entire ecosystem. Approaches were classed as entire ecosystem when they did not identify priorities for individual species (regardless of the number of species), but instead used non-species based data to identify priorities, such as temperature, geodiversity etc. The majority of approaches focused on multiple species (n = 38, 60%) or entire ecosystems (n = 19, 31%), with very few prioritising for single species (n = 6, 9%). We assessed the spatial scale of each approach by categorizing sites into 5 categories, adapted from Forman and Collinge (1996): individual site, landscape, region, nation, multi-nation/global. Most approaches conducted prioritisation at the regional (n = 22, 35%) national (n = 19, 30%) or multi-national/global level (n = 17, 27%). Only 5 studies (8%) conducted prioritisation at a landscape scale, while no studies used an individual site (Table 2.1).

Table 2.1. Timeframe, biological units and spatial scale considered by approaches used to identify spatial priorities for conservation actions while incorporating the effects of climate change. Note that numbers differ from Table A.1 (see online material) as some publications used more than one prioritisation approach.

	Timeframe considered			**Biological units considered**			**Spatial Scale**				
	Short (now to 2030)	Mid-range (2031-2050)	Long (beyond 2051)	Single species	Multiple species	Entire ecosystem	Individual Site	Landscape	Region	Nation	Multi-nation/Global
Prioritising for future distribution	13	14	17	3	19	2	0	1	8	8	7
Representing refugial habitats	9	2	13	2	10	7	0	4	4	4	7
Increasing connectivity	5	6	7	1	5	5	0	0	4	5	2
Increasing heterogeneity	4	3	6	0	3	5	0	0	6	1	1
Incorporating indirect effects	0	1	0	0	1	0	0	0	0	1	0
All Studies	31	26	43	6	38	19	0	5	22	19	17

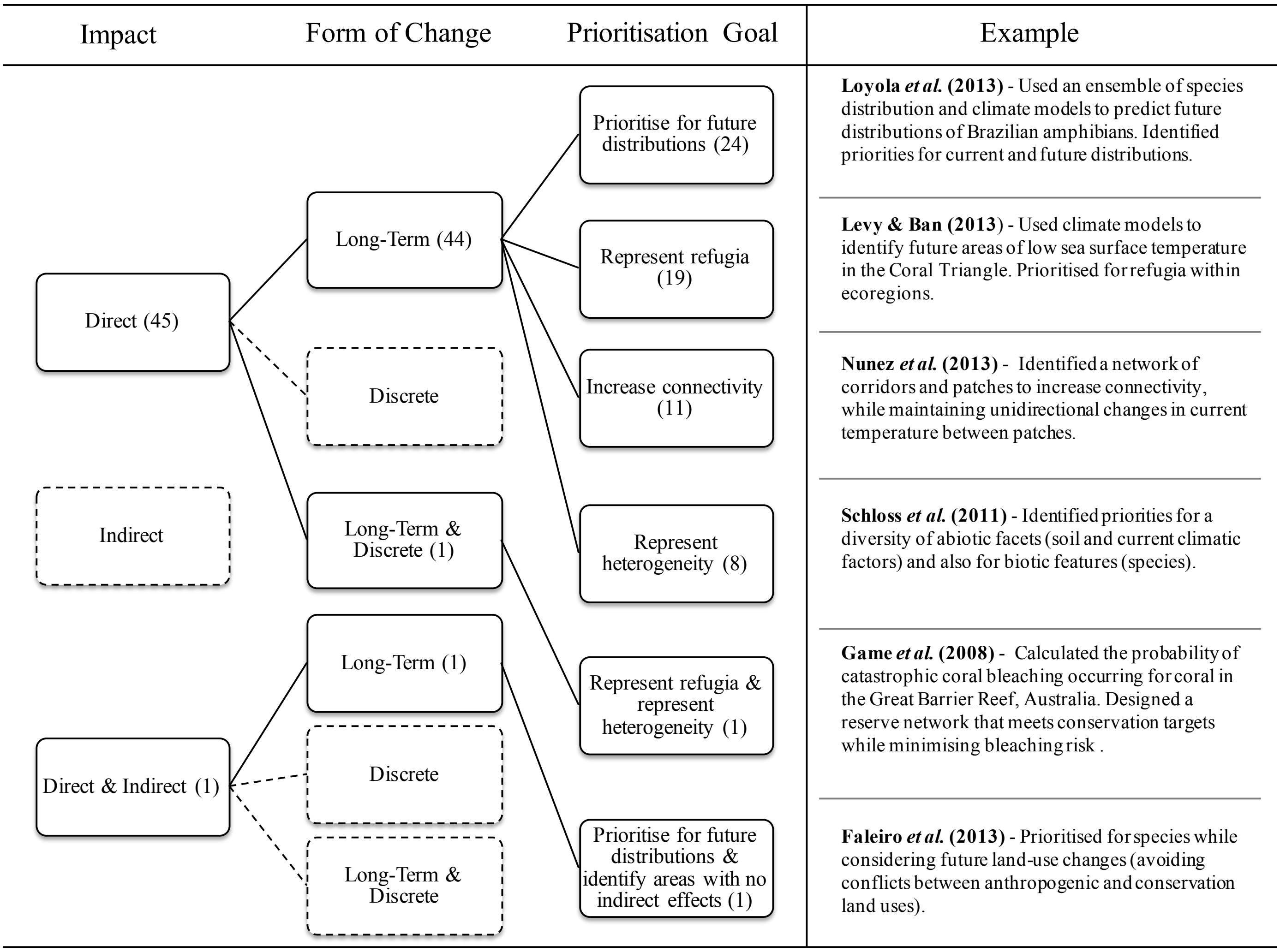

Figure 2.2 Classification of prioritisation goals of articles that incorporate climate change into spatial prioritisation. The number of publications is shown in brackets, and dashed boxes indicate areas where no publications were found. Classifications are as follows: 1) impact, where indirect impacts are those caused by human responses to climate change and direct impacts are all other climate impacts, 2) form of change, where discrete effects are one off extreme events such as coral bleaching or floods, and long-term effects are gradual changes brought about by climate change, such as temperature or rainfall changes, and 3) prioritisation goal, which describes the specific aim of each approach.

Uncertainty

There is a large amount of uncertainty associated with predicting climate change and species responses, so we assessed if and how each approach attempted to deal with this uncertainty. We found that just under half of the approaches (n = 22, 48%), made some attempt to deal with uncertainty (see online Table A.1). Of these approaches, all except one did so by using either a variety of methods for predicting future species distributions (ensemble approach), a variety of global climate models, a range of future emissions scenarios, or a combination of these. By combining various methods and scenarios, these approaches attempt to better reflect the range of different outputs for predicting future species distributions and climate. One approach (Mumby et al. 2011), developed a suite of evidence based hypotheses for the response of corals to climate change.

Prioritisation goal

We categorised each article based on the overall prioritisation goal, to analyse how each approach planned to deal with climate impacts. Some articles (n = 14, 30%) conducted prioritisations with more than one goal, and in these we analysed each goal separately, in order to examine the similarities and differences between methods used for each overall prioritisation goal. As such, the number of prioritisation goals is slightly higher than the number of publications (n = 63 and 46 respectively; Figure 2.2). A general overview of the strengths and limitations of each prioritisation goal is provided in Table 2.2.

Table 2.2. Strengths and limitations of the different approaches used to identify spatial priorities for conservation actions while incorporating the effects of climate change.

Planning Approach	Strengths	Limitations
Prioritise for future distributions	• Applicable to a wide range of taxa at various spatial scales (Pacifici et al. 2015). • Can be targeted to single (e.g. Adams-Hosking et al. 2015 p.) or multiple species (Struebig et al. 2015). • Species specific predictions of future distributions can inform a variety of planning strategies, such as identifying priorities for future protected areas (e.g. Nakao et al. 2013; Shen et al. 2015), or identifying where existing conservation efforts can be scaled	• Climate data are often not sufficiently fine-scaled for modelling rare species or species with small geographic distributions (Guisan & Thuiller 2005; Wiens et al. 2009; Lawler et al. 2010). • Modelling technique and ecological predictor choice can greatly influence results (Beaumont et al. 2005; Heikkinen et al. 2006). • Correlative approaches make uncertain assumptions about species biology

	back or abandoned as species move with climate change (Alagador et al. 2014).	(Bellard et al. 2012; Pacifici et al. 2015). • Mechanistic approaches require detailed data that are lacking for most species (Bellard et al. 2012; Pacifici et al. 2015). • As species respond individually to climate change, the current system of species interactions will change in the future, so predictive models based on current species interactions may be inaccurate (Pearson & Dawson 2003).
Representing refugial habitats	• Can be identified without forecasts of climate or species distributions, by using historical or current climatic factors (e.g. Hermoso et al. 2013) or landscape topography (James et al. 2013). • Useful for large-scale prioritisations (e.g. Ban et al. 2012), where predicting future distributions of many species is difficult due to data requirements and uncertain assumptions about species biology (Bellard et al. 2012; Pacifici et al. 2015).	• Difficult to define and target specific conservation features (e.g. species specific refugia). • If refugia are identified using forecasts of species distributions, the limitations in the above section also apply.
Increasing connectivity	• Not reliant on uncertain climate and species distribution forecasts. • Can be used to increase physical connectivity, to allow species to track	• General lack of understanding of exactly what types of connectivity are most important for climate change driven species movement (Cross et al. 2012b, 2012a).

	suitable habitat under climate change (e.g. Game et al. 2011), or ecological connectivity, to facilitate gene flow (Mumby et al. 2011).	• For most species, little is known about their actual movements, so it is difficult to determine an appropriate level of connectivity to aim for (Groves et al. 2012). • Not useful for species restricted to rare habitat, as there is unlikely to be a sufficient suitable habitat for species to move amongst as the climate changes (Heller & Zavaleta 2009). • Difficult to accommodate connectivity requirements of multiple species when they differ, and trade-offs among species would be required unless it is feasible to conserve a large area.
Increasing heterogeneity	• Not reliant on uncertain climate and species distribution forecasts. • Avoids Linnean and Wallacean shortfalls (Bini et al. 2006), and/or costly collection of biological data (Sutcliffe et al. 2015).	• Unlikely to retain historical assemblages of species and ecosystems as species mix under new climate regimes (Stein et al. 2014). • Conserving abiotic diversity alone likely to be insufficient to protect biodiversity under climate change, because it does not capture species responses to biodiversity (Lawler et al. 2015), and conservation plans that incorporate some form of biological information will be more effective (Sutcliffe et al. 2015).

Incorporating indirect effects	• Incorporating the full range of climate impacts is likely to be more successful, as indirect impacts can significantly alter species vulnerability to climate change (Segan et al. 2015). • Allows avoidance of maladaptation - where interventions that address climate vulnerability for biodiversity may exacerbate climate impacts to humans (Stein et al. 2014). • Some conservation actions can provide benefits to humans and biodiversity, e.g. ecosystem based adaptation (Maxwell et al. 2015b).	• Factors driving indirect impacts are often complex, and vary across regions. • Very few existing methods for forecasting indirect impacts

Prioritising 'future habitat'

The most common goal is to prioritise for areas to protect the future habitats of species by spatially forecasting where they are likely to move in the future (n = 24, 52%, Figure 2.2). By conserving areas that species may use in the future, these approaches are thought to be 'climate-smart' (IPCC, 2014; Stein et al., 2014). The most common approach is to use species distribution models (SDM's) or niche/bioclimatic modelling to forecast future species distributions, and then use a decision support tool such as Marxan (Ball et al. 2009) or Zonation (Moilanen 2007) to prioritise for those distributions. For example, Loyola et al. (2013) use an ensemble of SDM's to predict the current and future (2050) distribution of amphibians in South America, and then use Zonation (Moilanen, 2007) to prioritise for current and future representation of each species to meet range-size based conservation targets. One approach applied a sequential scheduling of priority identification, including the release of areas when they stop contributing to conservation goals as species distribution changes with climate change (Alagador et al. 2014). Approaches that prioritised for future habitat generally did so for multiple species at a spatial scale or regional or larger, and considered all timeframes equally (Table 2.1).

These prioritisation approaches are clearly limited by the variability in projections from different methodologies, along with the accuracy and reliability of predicted species distributions (Pereira et al. 2010; Table 2; Bellard et al. 2012; Porfirio et al. 2014). Bellard et al. (2012) reviewed common approaches to estimate future biodiversity ranges, incorporating variability in projection methods, biodiversity measures and socio-economic scenarios (e.g. different SRES scenarios). They found that models are extremely variable, depending on the method, taxonomic group, spatial scale and time period considered. Additionally, correlative modelling approaches often make uncertain assumptions about species biology (Pacifici et al., 2015), and ignore key ecological processes and interactions in predicting distributional changes (Kearney & Porter 2009). One way to overcome these issues is to use mechanistic or semi-mechanistic approaches, which incorporate the processes that influence the response of biodiversity to environmental change, such as dispersal, adaptation and inter-specific interactions (Mokany & Ferrier 2011). The problem with these approaches is that they require large amounts of species-specific information and are thus limited to very small numbers of well-studied species (Mokany and Ferrier, 2011). It is also important to prioritise investment toward species and ecosystems that will be most impacted by climate change, and those that will be impacted soonest. For example, the IUCN Red List assessment methods can identify species most at risk of extinction due to climate change, and can give decades of warning time, allowing for adaptation actions to be implemented for those species (Akcakaya et al. 2014; Keith et al. 2014; Stanton et al. 2015). Another potential strategy that was not considered in any approaches we found in our review is to use predictions of future habitat to identify target sites for translocation or assisted migration of species (as suggested in Schwartz & Martin 2013).

In cases where the predictability of future ranges of species is poor, there is a risk that conservation resources will be used in the wrong areas. It is therefore important to assess and attempt to deal with the uncertainty involved in species range predictions. One method for doing this is to use multiple methodologies for distribution forecasts, using a range of climate models and emissions scenarios (an “ensemble” approach; Porfirio et al. 2014). This produces a number of different species forecasts, which can be combined (by taking the mean, median etc.) in order to better reflect the range of outputs. This method was used by many of the approaches we reviewed (Kujala et al. 2013; Lung et al. 2014; see online Table A.1), however it is important to recognise that while ensemble approaches can help reduce the uncertainty associated with using a single species forecasting technique, the development of forecasting techniques with greater certainty is still required. It is also important that the climate variables used in species forecasts are biologically and ecologically relevant, as this is often not the case (Porfirio et al., 2014), and simply using all available variables can lead to over-estimates of range reduction and extinction (Beaumont et al. 2005). The emerging field of conservation value-of-information analysis (Runge et al. 2011) could be used to determine the value of resolving uncertainties in predicting species range changes, such as collecting data on species presence or dispersal ability, or gaining information about biologically relevant climate variables, and assessing whether this would lead to a more effective management strategy (Runting et al. 2013; Maxwell et al. 2015a).

Representing refugial habitats

Representing 'refugia' is also a common prioritisation goal (n = 19, 41%, Figure 2.2), and there are examples incorporating both continuous and discrete impacts. Most approaches are based on methodologies that forecast future climate and identify areas where climate change will have little effect. For example, Levy and Ban (2013) identify refugia by forecasting sea surface temperature to 2100, and using Marxan to prioritise for areas that continually hold temperatures < 1 °C above maximum temperatures that have not caused coral bleaching. Approaches like these generally prioritise for entire ecosystems, such as coral reef systems or ecoregions (Table 2.1). Another common approach is to model future species distributions and prioritise for areas where current and future distributions overlap or are in close proximity. To be clear, refugia identified using future species distributions are different from all future habitat, in that they are areas which currently contain a species, and will contain the same species in the future. For example, Terribile et al. (2012) use ecological niche models to predict South American tree distributions in three time periods (last glacial maximum, present day, and 2080–100), and prioritise for areas which contain a large proportion of species throughout all time periods. There are two approaches which do not predict future climate but instead identify refugia based on current or historical conditions. Hermoso et al. (2013) identify refugia for freshwater shrimp by prioritising for ephemeral streams which retain water for long periods relative to other streams, while Ban et al. (2012) identify coral reef refugia by analysing historical temperatures. Representing refugia is also the only approach that has been used to incorporate discrete impacts of climate change. Game et al. (2008) do this by calculating the probability of catastrophic coral bleaching due to climate change, and identifying areas to minimise this risk (bleaching refugia).

Given that most refugia are currently identified using climate forecasts and predicted species distributions, the accuracy and uncertainty of these predictions is a limiting factor. Therefore the criticisms directed at approaches that prioritise for future habitats also apply to those that prioritise for refugia. The use of “ensemble” approaches that better reflect the range of species distribution predictions, along with the use of ecologically relevant climate variables will lead to more robust identification of refugia. Additionally, because most of the approaches that prioritise for refugia do so at the regional level or above (Table 2.1), it is likely that these coarse predictions lack the biological realism of smaller scale models (Bellard et al. 2012). For more robust refugia identification, fine-scale prioritisation could be used within the priority areas identified using broad-scale predictions. There are also methods for identifying refugia which do not rely on uncertain future predictions, such as using landscape topography (James et al. 2013) to identify areas which are likely to undergo little change in the future. These non-predictive refugia identification approaches could easily be used in spatial prioritisation (similar to Hermoso et al., 2013), where prioritisation that occurs after refugia are identified, based on some ecological measure such as the biodiversity each refugial area contains, or their connectivity with existing protected areas.

Increasing connectivity

Other articles aimed to increase physical connectivity (n = 11, 24%, Figure 2.2), so species can track suitable habitat as the climate changes. For example, Game et al. (2011) use Marxan to identify priorities that meet conservation targets for Papua New Guinean herptiles and mammals, while ensuring that the reserve network has high levels of connectivity between different environments. There is one unique approach which aims to increase ecological connectivity, by identifying optimal reserve networks based on larval dispersal and coral reef responses to thermal stress, in order to allow for gene flow between reefs from desirable thermal stress regimes (Mumby et al. 2011). All approaches which aimed to increase connectivity were conducted at the state/country level or above (Table 2.1).

A protected area network with high connectivity can allow species to adapt to climate change by facilitating the protection of habitat that will enable them to track their climatic niche (Heller & Zavaleta 2009). However, given that the current protected area system is doing poorly at conserving most aspects of biodiversity (Watson et al. 2014), increasing connectivity by simply considering physical elements such as vegetation corridors is unlikely to effectively conserve all biodiversity under climate change. Additionally, all approaches in this study focused on increasing connectivity at large spatial scales (Table 2.1) which is unlikely to aid dispersal-limited species, or those restricted to rare habitat, in adapting to climate change (Heller and Zavaleta, 2009). A lack of understanding of the types, locations, and amounts of connectivity necessary for species to adapt to climate change also makes explicitly incorporating connectivity targets into prioritisation difficult. (Table 2.2; Cross et al., 2012a, 2012b, Groves et al., 2012). We found some approaches which combined increasing connectivity with other prioritisation aims, such as Wan et al. (2014), who prioritise for current and future distributions of an endangered East-Asian tree species, while ensuring connectivity between these priority areas in order to facilitate gene flow. Approaches such as these, which combine connectivity with other prioritisation goals, are more likely to effectively conserve a large proportion of biodiversity.

Increasing heterogeneity

Another common goal is to prioritise for a set of abiotically or bioclimatically diverse areas, which will support a variety of ecological systems in the future (n = 8, 17%, Figure 2.2). When this concept – also known as conserving the “stage” on which biodiversity “plays” (Anderson & Ferree 2010; Beier et al. 2015; Lawler et al. 2015) – is used, the goal is almost always to represent a heterogeneous system of current conditions. For example, Schloss et al. (2011) use Marxan to identify priorities to represent the diversity of soils, topographies and current climates of the Columbia Plateau in the North-Western US. Only three analyses (6%) aimed to represent a heterogeneous system of future bioclimatic conditions. For example, Pyke et al. (2005) predicts future climate, assesses how bioclimatically heterogeneous the current reserve system will be in the future, and prioritises for new areas based on their potential for improving this bioclimatic representation.

Representing heterogeneity is a useful prioritisation goal as it is based on evidence from many climatic regimes which shows that different geophysical settings can maintain distinct ecological communities under a wide range of climates (Rosenzweig 1995). Another advantage is that this goal does not rely on uncertain forecasts of species distribution and future climate. Spatially explicit predictions of how climate change will affect biodiversity are limited by a lack of knowledge on the current distributions of many species (the Wallacean shortfall; Lomolino & Heaney 2004). Similarly, the spatial detail and magnitude of climate predictions are of low confidence in sparsely sampled areas such as Antarctica and the tropics (Hartmann et al. 2013). Increasing abiotic heterogeneity is therefore very useful where climatic information is lacking and/or where species data is poor. In a heterogeneous reserve network, connectivity between areas can also allow for adaptation to climate change (Schloss et al. 2011). Additionally, it is important to recognise that representing heterogeneity is unlikely to retain historical assemblages of species and ecosystems (Stein et al., 2014). It is difficult to use this approach to target conservation efforts towards specific species or aspects of biodiversity that are most threatened by climate change. Therefore coarse filter approaches such as representing heterogeneity, which conserve the “stage”, should be complemented by fine filter approaches which will ideally incorporate biological information (Sutcliffe et al. 2015) to conserve the “actors” (e.g. individual species; Tingley et al. 2014).

Incorporating the human response

Only one approach incorporated indirect effects (2%, Figure 2.2). Faleiro et al. (2013) use SDM's to predict future distributions of Brazilian mammal species, and generate a future land use model based on climate and anthropogenic variables. They then use the spatial prioritisation tool Zonation (Moilanen, 2007) to identify priorities that conserve future species distributions while minimising the impacts of future land use change. Approaches such as this, which incorporate both direct and indirect impacts of climate change, are likely to be more successful than approaches that focus on only direct impacts.

Accounting for indirect impacts requires forecasts of human responses to climate change, including land use change, displacement, and altered resource utilisation patterns (Turner et al. 2010). The factors driving these changes are extremely complex and vary across countries and regions, so there are very few tools and approaches that can forecast indirect impacts, and these forecasts are even more uncertain than climate change and species responses. One example of the few existing tools is the IMAGE model (Bouwman et al. 2007), which uses predicted changes in demography, resource utilisation and climate change to forecast future land cover. Tools such as IMAGE can easily feed into spatial prioritisation analyses by allowing for the identification of priority areas that minimise the impacts of future human responses, while simultaneously achieving aims to combat direct impacts, such as increasing heterogeneity or representing refugia. However, given that there are so few methods for predicting indirect impacts, an intensive focus on developing methods and tools to do so is urgently needed.

Future research needs

We found few prioritisations that incorporate multiple goals, and none that incorporate the full range of climate impacts and forms of change. It is essential that future research develops truly integrative approaches which incorporate the direct and indirect impacts of climate change at all timeframes. These prioritisation approaches need to incorporate adaptation actions which strengthen current conservation efforts, and also anticipate and respond to future conditions (Schmitz et al. 2015). Most actions which strengthen current conservation efforts (e.g. increasing the size and effectiveness of protected areas, reducing poaching pressure) will likely be good actions to take, even if climate change plays out differently than projected (Groves et al. 2012). Anticipating and responding to future conditions is hampered by uncertain climate predictions, but the impacts of climate change will be so great that there is no option but to accept this uncertainty and continue planning regardless. It is important to note that uncertainties can be reduced using sensitivity analyses, or scenario analyses that explore a range of outcomes (Galatowitsch et al. 10; Glick et al. 2010), and incorporating these methods into spatial planning is crucial. For the development of approaches that incorporate all impacts of climate change, there are two research needs that, if addressed, could significantly move the climate oriented prioritisation field forward.

Methods that incorporate the human response to climate change

In concordance with an equivalent review of climate change vulnerability assessments (Chapman et al. 2014), this review has shown that the human response to climate change is largely being ignored or overlooked in the spatial prioritisation literature. There is no doubt that the indirect impacts of climate change on biodiversity are likely to be as serious, if not more serious, than direct impacts (Paterson et al. 2008; Turner et al. 2010; Wetzel et al. 2012) so ignoring these indirect impacts may lead to a serious underestimation of the risk climate change poses.

While indirect effects are being largely overlooked, they are – somewhat paradoxically – often the threats that conservation planners and practitioners are most capable in dealing with. For example, one of the most common strategies for protecting marine biodiversity is to identify and designate marine protected areas (MPA's) that deal with issues such as over-fishing and habitat destruction (Lubchenco et al. 2003). However MPA's are unable to prevent direct impacts such as temperature increase, so they can only help biodiversity cope with climate change by reducing other stressors such as fishing and habitat destruction (Hughes et al. 2003; McLeod et al. 2012; Selig et al. 2014). As fish distributions and fishing efforts are shifting with climate change (Perry et al. 2005; Pinsky & Fogarty 2012), effective marine conservation may be better achieved by reducing fishing pressure on current distributions, or protecting areas that are likely to be fished into the future, rather than simply protecting areas threatened by the direct impacts that are not possible to prevent.

Some studies have identified the potential for conflict between human adaptation activities, and conservation (Dugan et al. 2008; Paterson et al. 2008; Bond et al. 2008). Bradley et al. (2012) found that 328 protected areas in South Africa are likely to be exploited for food and fuel in the future as climate change alters crop suitability and increases food scarcity. When human adaptation responses are likely to impact biodiversity, conservation planners can either try to shield biodiversity from these impacts, or can work with communities to facilitate adaptation while minimising impacts to biodiversity. This can be done by using the process of ecosystem-based adaptation (Jones et al. 2012), or payments for ecosystem services (Manzo-Delgado et al. 2014). Some examples include restoring and conserving mangrove forests to increase resilience to flooding and storm surges (Alongi 2008), restoring forest around primary water sources to ensure potable water supply (Birdlife International 2010), or protecting forest to stop landslides and avalanches (UNFCCC 2011).

Although it is crucial to incorporate indirect impacts of climate change, modelling the human response to climate change is still extremely difficult (Turner et al. 2010). The development of socio-ecological models which link climate, human behaviour and land/seascapes, has proven useful for modelling how human responses to climate change will impact species (Holdo et al. 2010; Ban et al. 2013). However, these models are rare and require significant data, so in situations where such models are unavailable, a simpler approach that could make prioritisation exercises more robust is to include indirect impacts as a risk factor to conservation efforts. For example, Ramankutty et al. (2002) identified a global area of almost 7 million km2 which will become suitable for agriculture by 2080, and it is likely that human food production will shift into these areas. These predictions of agricultural change could be used as an indirect risk factor, where areas of high agricultural suitability are most at risk. Spatial prioritisation tools could then be used to identify conservation priorities while minimising this risk. Klein et al. (2013) used a similar risk-factor method, prioritising for marine biodiversity features while minimising the probability that habitat was in poor condition due to multiple stressors including climate change.

Methods that deal with discrete impacts

Despite the lack of approaches incorporating discrete impacts, ignoring them is not an option, as they can have severe consequences for biodiversity (Corlett 2011) and are affecting conservation strategies (IPCC, 2014). Furthermore, the frequency and intensity of these events is expected to increase over coming decades (IPCC, 2014). For example, coral bleaching events will increase with more frequent and intense heat waves due to climate change (Hughes et al., 2003), and forest ecosystems will be affected by increased frequency and intensity of droughts and fires (Dale et al. 2001). The development of approaches that incorporate discrete impacts of climate change is vital, to ensure that biodiversity is not lost in the short-term while planning for the future.

Discrete impacts are, by definition, stochastic, and thus inherently difficult to predict in detail, which probably explains why few spatial prioritisation approaches incorporate them (Seneviratne et al. 2012). Although broad forecasts suggest that the intensity and frequency of extremes will increase, there is an urgent need for spatially explicit predictions of discrete impacts, at scales and timeframes relevant to conservation planners. Improved forecasts would allow for the development of spatial prioritisation approaches that identify priorities to meet conservation targets while minimising loss of biodiversity due to discrete impacts (e.g. Game et al., 2008).

Another way to incorporate discrete impacts of climate change is to prioritise for management actions that strengthen current conservation efforts in order to combat discrete impacts that have been broadly predicted. For example, it is likely that droughts will intensify in Central and North America, Southern Europe, and Southern Africa, thus creating greater potential for forest wildfires (Seneviratne et al., 2012). In these areas, spatial prioritisation could be used to identify priority areas for management actions to reduce fire risk, which might include fuel reduction or complete fuel breaks around high-value areas (Millar et al. 2007). Another example is protecting native riparian vegetation to reduce the impacts of pesticide input (Sánchez-Bayo et al. 2013) and sedimentation (Dunbar et al. 2010) from extreme precipitation events on refugia in deep freshwater pools (Bush et al. 2014).

Conclusions

We have shown that spatial prioritisation approaches focus on the more easily forecasted continuous, direct impacts of climate change while the discrete and indirect (human response) impacts are almost always completely neglected. This highlights a serious research need for the development of integrative approaches to incorporate all climate change impacts and timeframes, combining methods that strengthen current conservation efforts, and those that attempt to predict future changes. We recognise that in the absence of accurate predictions of indirect and discrete impacts, or knowledge of the vulnerability of biodiversity to these impacts, developing prioritisation approaches to combat them is extremely difficult. Thus, an intensive focus on forecasting the effects of climate change with more certainty, including discrete impacts, and predictions of the human response, is now urgently needed (Chapman et al., 2014; Watson, 2014). Only by addressing the full range of impacts will conservation plans have a real chance at effectively addressing the impacts of climate change on biodiversity.

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Chapter 3

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Chapter 3 – The location and protection status of Earth's diminishing marine wilderness

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Summary

As human activities increasingly threaten biodiversity (Halpern et al. 2008; Butchart et al. 2010), areas devoid of intense human impacts are vital refugia (Watson et al. 2016b). These wilderness areas contain high genetic diversity, unique functional traits and endemic species (Graham & McClanahan 2013; Pinsky & Palumbi 2014; Friedlander et al. 2016; D'agata et al. 2016); maintain high levels of ecological and evolutionary connectivity (Jones et al. 2007; Grober-Dunsmore et al. 2009; Haddad et al. 2015); and may be well placed to resist and recover from the impacts of climate change (Carilli et al. 2009b; Côté & Darling 2010; Martin & Watson 2016). On land, rapid declines in wilderness (Watson et al. 2016b) have led to urgent calls for its protection (Watson et al. 2016b; Allan et al. 2017a). In contrast, little is known about the extent and protection of marine wilderness (Graham & McClanahan 2013; D'agata et al. 2016). Here we systematically map marine wilderness globally by identifying areas that have both very little impact (lowest 10%) from 15 anthropogenic stressors and also a very low combined cumulative impact from these stressors. We discover that ~13% of the ocean meets this definition of global wilderness, with most located in the high seas. Recognizing that human influence differs across ocean regions, we repeat the analysis within each of the 16 ocean realms (The Nature Conservancy 2012). Realm-specific wilderness extent varies considerably, with >16 million km^2 (8.6%) in the Warm Indo-Pacific, down to <2,000 km^2 (0.5%) in Temperate Southern Africa. We also show that the marine protected area estate holds only 4.9% of global wilderness and 4.1% of realm-specific wilderness, very little of which is in high biodiversity areas such as coral reefs. Proactive retention of marine wilderness should now be incorporated into global strategies aimed at conserving biodiversity and ensuring that large scale ecological and evolutionary processes continue.

Methods

All spatial data described below were processed using ESRI ArcGIS v10 in Behrmann equal-area projection.

Marine human impact data

To map the global extent of marine wilderness we utilised data on the intensity and cumulative impact of 19 different anthropogenic stressors to marine environments globally in 2013 (Halpern et al. 2015). These data are the finest resolution marine cumulative threat maps available ($1km^2$ cells), as well as the most comprehensive, including data on land-based stressors (e.g. nutrient runoff), ocean-based stressors (e.g. fishing), and climate change. To create the map of cumulative impact on the ocean, data for each stressor is normalized (placed on a 0-1 scale), resampled to a $1km^2$ resolution, transformed by vulnerability weights that are ecosystem-specific and the values for all ecosystem-stressor combinations within each $1km^2$ cell are averaged across cells to give a final cumulative impact value (Halpern et al. 2015). We utilized both the individual stressor layers, and the cumulative impact map to identify marine wilderness.

We used the finest resolution human threat data available at a global scale, but there are some limitations which should be recognised. Given the lack of data available for the high-seas and polar regions, it is somewhat challenging to accurately determine whether low-threat regions are being identified due to a true absence of human impacts, or just an absence of data. However, it is clear that most of the human activities captured in our data occur primarily within EEZ's, because land-based impacts are concentrated in coastal waters, and most marine resources (and thus fishing catch) are located within shallower inshore areas rather than the high seas (Watson et al. 2016c). Furthermore, the most recent research available shows that for some of the individual threats used in this analysis (such as commercial fishing), polar regions and the high seas have generally low levels of impact (Watson 2017). Sensitivity analyses of the cumulative impact data we used have also shown that the maps are most robust at high and low extremes (e.g. they are accurate for identifying high and low impact areas) but are less accurate at medium levels of human impact (see supplementary materials in (Halpern et al. 2008). Given that we focus only on low impact areas in this study, and use the best available data, we have produced the most accurate marine wilderness map currently possible.

Mapping global marine wilderness

Because even relatively low levels of human activities can significantly impact vulnerable aspects of marine biodiversity (e.g. mobile top predators; (D'agata et al. 2016)), identifying wilderness requires finding those areas that have little to no impact across all human activities. We therefore identified marine wilderness by conducting a primary classification of each individual normalized stressor layer using a 10% threshold, so that cells within the bottom 10% of values for each stressor were assigned a score of zero and all other cells were assigned a score of one. By summing the values across all stressors, we identified areas within the bottom 10% across all individual stressors. In some cases, areas with a moderate cumulative impact still remained (e.g., when the impact value for multiple stressors was just below the 10% threshold). Therefore, we applied a secondary classification to identify our final map of marine wilderness, to only include areas within the bottom 10% of cumulative impact globally (Halpern et al. 2015). We conducted this analysis for 2 scenarios, one that included all 19 stressor layers in the primary stressor reclassification, and one that excluded climate change based stressors, leaving 15 stressor layers (see Table S3.1 for individual stressor layers). Both scenarios use the same layer (that includes climate change variables) for the secondary cumulative impact classification.

Mapping realm specific wilderness

We also created maps of realm specific wilderness for 2013, based loosely on the methodology used in the terrestrial realm (2002). We first followed the primary classification used to map marine wilderness, using a 10% threshold to classify each individual stressor so that cells within the bottom 10% of values for each stressor were assigned a score of zero and all other cells were assigned a score of one. By summing the values across all stressors, we identified areas within the bottom 10% for all individual stressors. We then used 2013 cumulative marine impact data (Halpern et al. 2015) to identify the 10% least impacted areas of each ocean realm (using the Marine Ecoregions and Pelagic Provinces of the world dataset (The Nature Conservancy 2012)). Finally, to identify realm specific wilderness, we identified all areas within the lowest 10% for all individual stressor layers, and within the 10% least impacted areas of each realm according to cumulative impact data. This created a different map to the global marine wilderness map because we identified the least impacted places within each marine realm, which highlights areas with higher impacts compared to when using a global threshold (as in the global marine wilderness map).

Wilderness coverage across ecosystems

To assess the distribution of marine wilderness across ecosystem types, we used the ecosystem maps developed by Halpern et al. (2008). Because global maps for most marine ecosystems are largely non-existent, these data use available distribution maps for several ecosystems, and models the distribution of many other ecosystems. We excluded all intertidal ecosystems from our analysis, along with suspension feeding reefs (mussel beds), as these ecosystem models are identical, such that all intertidal ecosystems (e.g. rocky intertidal, mudflats) occur in every cell within 1km from the shoreline. Thus, when calculating wilderness extent and protection, all intertidal ecosystems would have identical results. Excluding intertidal ecosystem data left 12 ecosystems – 5 coastal ecosystems (e.g. seagrass, coral reefs), and 7 deep-water ecosystems (e.g. soft bottom shelf, seamounts). Using our global maps of marine wilderness (not the realm-specific wilderness maps), we quantified the area of each ecosystem that overlapped with marine wilderness areas.

Wilderness protection

To assess protection of marine wilderness within MPAs we extracted data on MPA location, boundary, and year of inscription from the 2017 World Database on Protected Areas (WDPA) (UNEP-WCMC & IUCN 2017). Following similar global PA studies (Butchart et al. 2012), we extracted MPAs from the WDPA database by selecting those areas that had a status of "designated", "inscribed", or "established", and were not designated as UNESCO Man and Biosphere Reserves. We included only MPAs with detailed geographic information in the database, excluding those represented as a point only. We then used a layer of terrestrial country boundaries to clip MPA polygons to only include protected areas which have some overlap with marine area (http://datadryad.org/resource/doi:10.5061/dryad.6gb90.2). The resulting MPA data was overlaid with the global and realm specific marine wilderness maps to quantify the current level of global and realm specific wilderness protection, both across the globe and across the realms and ecosystem types used in the above analysis.

Wilderness and biodiversity

To assess overlap between marine wilderness areas and biodiversity, we first conducted an analysis using data on marine biodiversity from Aquamaps, a species distribution modelling tool that produces standardised global range maps for 22,885 aquatic species (Kaschner et al. 2016). This is the most comprehensive and highest resolution data available on the distribution of marine biodiversity globally, and includes Animalia (fishes, marine mammals, and invertebrates), Plantae (fleshy algae, seagrass), Chromista (calcifying algae) and Protozoa. The species distribution maps predict relative probabilities of species occurrence (ranging from 0.00–1.00) at a resolution of 0.5-degree cells. It is assumed that the preferred range is where probability is 1, outside the range limits is where probability is 0, and between these two thresholds the relative environmental suitability decreases linearly. As there is no recommended threshold to use, we follow previous studies and use a probability threshold of 0.5 or greater (Klein et al. 2015).We did not repeat our analysis using different thresholds, as previous studies have shown this makes very little difference to global scale analyses (Selig et al. 2014; Klein et al. 2015).

To assess coverage of marine species distributions in wilderness areas, we determined the proportion of wilderness in each 0.5-degree cell. As we do not know the exact distribution of species within each cell, we assumed that the area of a species' range contained in wilderness was equal to the area of wilderness in each cell that species was present in. Using the same species distribution data, we also calculated species richness, species range rarity, and proportional species range rarity. Species richness was calculated as the number of species within each 0.5-degree cell. Species range rarity was calculated as:

$$R = \sum_{i=1}^{N} \frac{1}{A_i} \times w$$

where for each species *i* of *N* species per 0.5 degree cell, *Ai* is the total range area for that species *i* including all areas inside and outside of the cell and *w* is the proportion of the cell which is ocean (i.e. *w = 1* if the entire cell is ocean, or *w = 0.5* if half the cell is terrestrial). When calculating *Ai* we summed the area of cells in which a species is found, rather than simply counting the number of cells, to deal with changes in cell area as cells move towards the poles (0.5 degree cells are large at the equator than the poles). Species range rarity reflects both the number of species and the size of their ranges, which is a common way to delineate priorities based on endemism as it quantifies the number of relatively range-restricted species within a cell (Selig et al. 2014).To calculate proportional species range rarity, we used the same formulation as species range rarity, but divided the value for each cell by the number of species found in that cell, to remove the confounding effect of species richness. We then calculated average species richness, range rarity and proportional range rarity for wilderness and non-wilderness areas across the marine ecoregions of the world (The Nature Conservancy 2012).

Results and Discussion

Global Marine Wilderness

Identifying marine wilderness requires finding biologically and ecologically intact seascapes that are mostly free of human disturbance (Mittermeier et al. 2003; Watson et al. 2016b). Here we do so by mapping those areas that have low impact across all human stressors, and also have a low cumulative impact, as even low levels of human activity can significantly impact some critical aspects of biodiversity (e.g. mobile top predators (D'agata et al. 2016)). To identify marine wilderness, we used the most comprehensive global data available for 19 human stressors to the ocean (detailed summary in Table S3.1), and the cumulative impact of these stressors (Halpern et al. 2015). We first identified areas within the bottom 10% for every separate human stressor (e.g. demersal fishing, fertilizer runoff; Table S3.1), and then applied a secondary classification to only include areas also within the bottom 10% of total cumulative impact at the global scale (see methods). Because the impacts of climate change are widespread and unmanageable at a local scale, there are significant variations in exposure and vulnerability across marine ecosystems (e.g. coral reefs vs deep sea), and including climate variables would result in no wilderness remaining (Figure S3.1), we excluded climate change variables (temperature and UV anomalies, ocean acidification, and sea level rise) from the individual stressor analysis but included them in the cumulative impact analysis (Table S3.1).

Our method identified 13.2% (54 million km^2) of the world's ocean as global marine wilderness (Figure 3.1), primarily located in the high seas of the southern hemisphere and at extreme latitudes. Most wilderness within EEZ's is found across the Arctic (6.9 million km^2) or Pacific island nations (2.7 million km^2; Figure 3.1), although there is substantial wilderness in the Exclusive Economic Zones (EEZ) of some other nations, such as New Zealand (25% of EEZ, 1.1 million km^2), Chile (6% of EEZ, 120,000 km^2), and Australia (4.3% of EEZ, ~350,000 km^2). This is likely due to low human populations in these areas, and in some cases, sea ice preventing human access to the ocean (Figure S3.2). However, with sea ice rapidly disappearing in the Arctic (Harris et al. 2017), some wilderness loss has already occurred in previously ice-covered areas (Figure S3.2), and this trend is likely to accelerate as sea ice continues to decline.

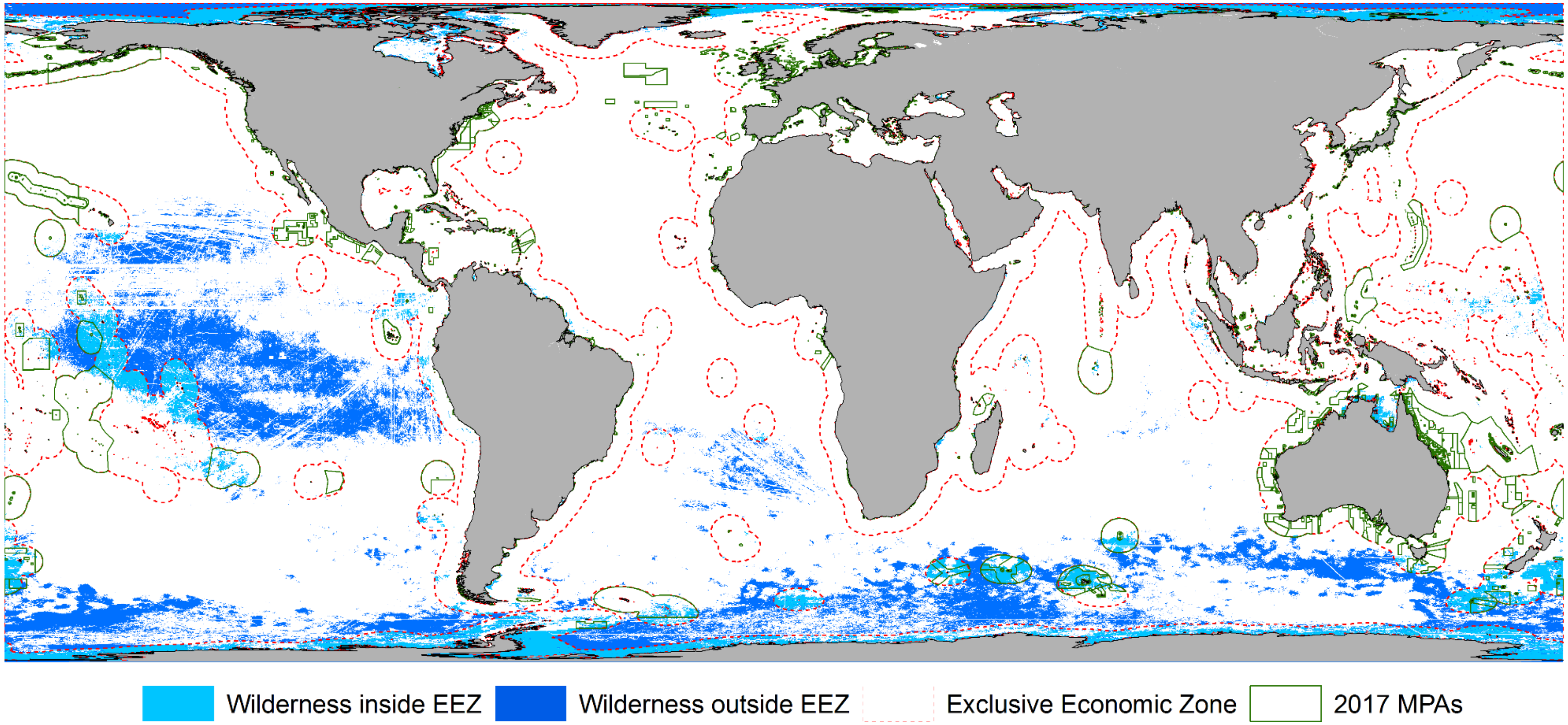

Figure 3.1. Global marine wilderness extent and protection. Marine wilderness in Exclusive Economic Zones (light blue), in areas outside national jurisdiction (dark blue), and marine protected areas (green). Waters 200 nautical miles from the Antarctic coastline, while marked here as Exclusive Economic Zones, are in fact not under jurisdiction of any single nation.

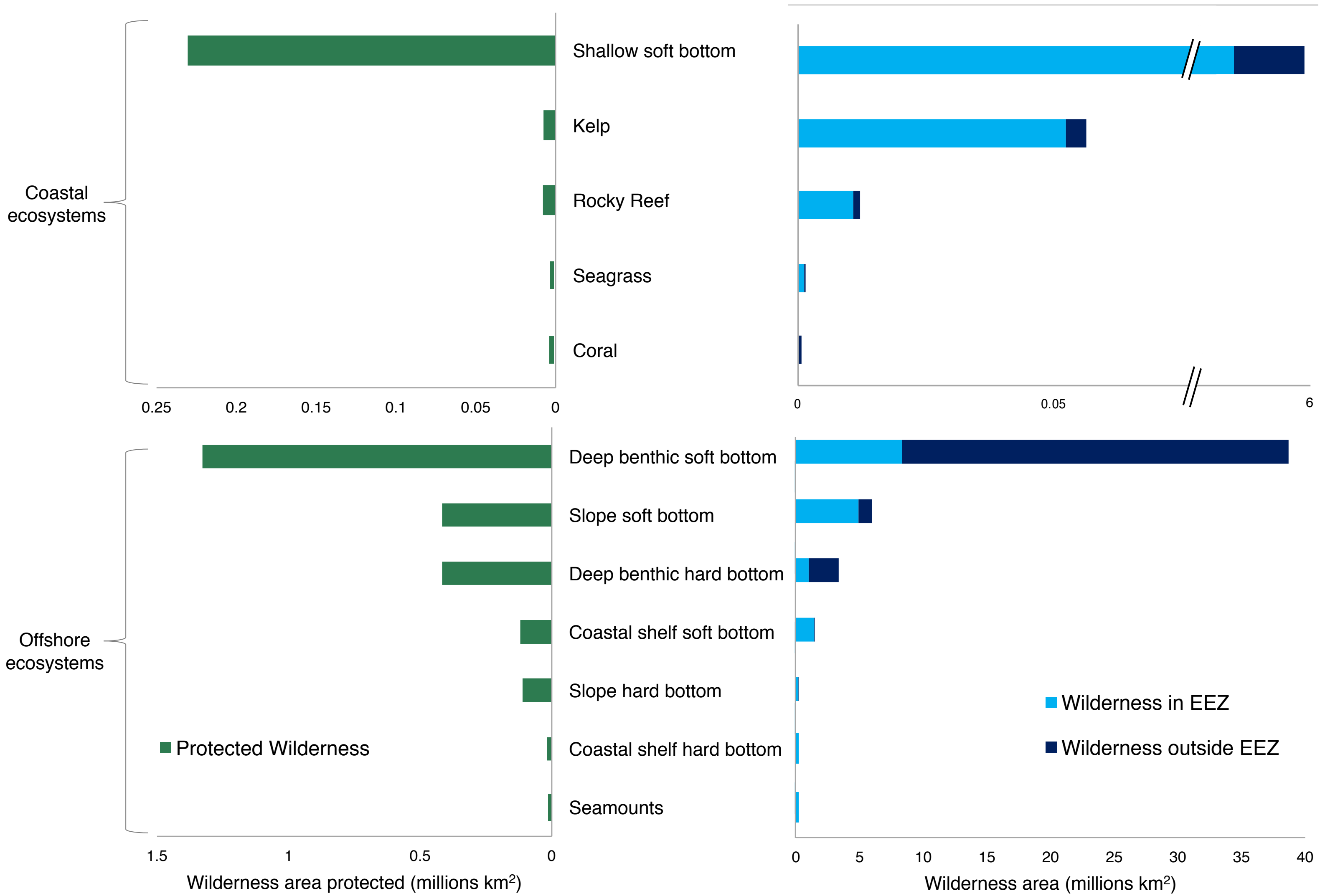

Figure 3.2. Global marine wilderness extent and protection across coastal (top) and offshore (bottom) ecosystems. Marine wilderness in Exclusive Economic Zones (light blue), in areas outside national jurisdiction (dark blue), and marine protected areas (green). See Table S3.2 for proportional ecosystem protection details.

Global wilderness extent varies considerably across the ocean, with substantial wilderness in the southern high seas, and very little in the northern hemisphere (Table 3.1). For example, 26.9% (25 million km^2) of the Southern Cold-Water realm is defined as global marine wilderness, compared to <0.3% (13,263 km^2) of the temperate North Atlantic (Table 3.1). This difference is due to significant fishing and shipping activity occurring in the waters around northern Asia, Europe and North America (Halpern et al. 2015). Global marine wilderness extent also varies across ecosystem types, and is generally much higher offshore than in coastal regions (Figure 3.2). All coastal ecosystems (except for naturally extensive soft bottom areas), have <100,000 km^2 of wilderness remaining (Figure 3.2). In contrast, almost 40 million km^2 (12%) of deep benthic soft bottom habitat is classified as wilderness, and all offshore ecosystems (except seamounts and the hard bottom coastal shelf) have retained >200,000km^2 of wilderness (Figure 3.2).

An analysis of the most comprehensive (~23,000 species) and high-resolution data on the global distribution of marine biodiversity (Kaschner et al. 2016), shows that the geographic ranges of 93% (n =21,322) of all marine species overlap with marine wilderness areas (Table S3.2). These overlaps are higher for species with large home ranges, such as marine mammals (8.4% average overlap), and lower for groups with more coastal distributions, such as reptiles (2.6% average overlap; Table S3.2). Marine wilderness overlaps with areas of high species richness, range rarity and proportional range rarity (see methods; Figure S3.3-3.4), and also with previously identified hotspots of both functional diversity, such as the Gulf of Carpentaria in Australia (Stuart-Smith et al. 2013); and of species endemism, such as the Desventuradas islands West of Chile (Friedlander et al. 2016). On average, global wilderness areas have 31% higher species richness, 40% higher range rarity and 24% higher proportional range rarity than non-wilderness areas, though this varies substantially across marine ecoregions (Table S3.3). For example, wilderness areas in the Solomon Sea have more than three times higher range rarity values than non-wilderness areas (Table S3.3). Conversely, in the Banda Sea wilderness areas have approximately three times lower species richness than non-wilderness areas (Table S3.3).

Realm-specific wilderness

A primary objective of conservation is to achieve representative protection of biodiversity (Convention on Biological Diversity (CBD) 2014). Oceanic realms and ecoregions are an increasingly important biogeographical classification for conservation planning and assessment (Butchart et al. 2015), and are important surrogates for biological representativeness when assessing global MPA coverage (UNEP-WCMC & IUCN 2018a). We therefore mapped realm-specific wilderness by identifying areas within each ocean realm (The Nature Conservancy 2012) that have little impact (bottom 10%) from 15 anthropogenic stressors and also have very low (bottom 10%) cumulative human impact (see methods and Table S3.1).

Realm-specific wilderness identifies the least impacted places within each ocean realm, meaning that the extent varies considerably, as it is dependent on the total level of human impact within realms. Consistent with global marine wilderness, most realm-specific wilderness is found in the high seas (66%; Figure 3.3). There is much more global wilderness than realm-specific wilderness overall (Table 3.1), and the location of wilderness areas differs substantially (Figures 3.1, 3.3). In highly impacted realms (e.g. Temperate Northern Atlantic) the extent of realm-specific wilderness is four times that of global wilderness (Table 3.1). Conversely, areas of low human impact (e.g. the Arctic) have far less realm specific wilderness than global wilderness (Table 3.1). Given the widespread nature of human impacts in some ocean realms (Halpern et al. 2015), realm-specific wilderness can occur in places with significant human activity, such as the Gulf of Mexico and the Persian Gulf. While these sites are under considerable human influence, they still represent some of the least impacted places within each ocean realm and are therefore important to protect.

Table 3.1 Global and realm-specific wilderness area (km^2) and protection across ocean realms

Ocean realm (area)	***Global marine wilderness area (% of realm)***	***Global marine wilderness protection (% of realm's wilderness)***	***Realm-specific wilderness area (% of realm)***	***Realm-specific wilderness protection (% of realm's wilderness area)***
Arctic (8740149)	4024686 (46.0)	282050 (7)	868845 (9.9)	63406 (7.3)
Atlantic Warm Water (69141433)	843548 (1.2)	0 (0)	4331890 (6.3)	1293 (0)
Central Indo-Pacific (6787301)	334825 (4.9)	58938 (17.6)	396728 (5.8)	65212 (16.4)
Eastern Indo-Pacific (173647)	10187 (5.9)	1183 (11.6)	9446 (5.4)	777 (8.2)
Indo-Pacific Warm Water (194431741)	15739747 (8.1)	708293 (4.5)	16711560 (8.6)	729597 (4.4)
Northern Cold Water (23320478)	6037333 (25.9)	44343 (0.7)	2377516 (10.2)	1373 (0.1)
Southern Cold Water (94049192)	25308475 (26.9)	1465581 (5.8)	9275414 (9.9)	544014 (5.9)
Southern Ocean (2697385)	2386053 (88.5)	83091 (3.5)	1551322 (57.5)	2187 (0.1)
Temperate Australasia (1178349)	33417 (2.8)	2310 (6.9)	43228 (3.7)	4861 (11.2)
Temperate Northern Atlantic (4790838)	13263 (0.3)	255 (1.9)	55012 (1.1)	7116 (12.9)
Temperate Northern Pacific (3477947)	26176 (0.8)	3022 (11.5)	58992 (1.7)	7511 (12.7)
Temperate South America (1958501)	62272 (3.2)	4341 (7)	81557 (4.2)	6147 (7.5)
Temperate Southern Africa (326680)	557 (0.2)	547 (98.2)	1744 (0.5)	793 (45.5)
Tropical Atlantic (2502305)	62932 (2.5)	6575 (10.4)	90105 (3.6)	14578 (16.2)
Tropical Eastern Pacific (293975)	4146 (1.4)	472 (11.4)	10438 (3.6)	1239 (11.9)
Western Indo-Pacific (2578128)	88248 (3.4)	14086 (16)	118313 (4.6)	17359 (14.7)
Total (416448049)	54975865 (13.2)	2675087 (4.9)	35982110 (8.6)	1467463 (4.1)

Wilderness protection

We found that only 4.9% of global marine wilderness (2.67 million km^2) is inside marine protected areas (MPAs; Table 3.1), despite 6.97% of total ocean area being under protection. This protection occurs almost exclusively within national waters, with 12% (2.65 million km^2) of global wilderness within EEZs protected, but only 0.06% (0.02 million km^2) of wilderness in high seas protected. Global wilderness protection is high in some populated regions, with 98% protected in Temperate Southern Africa, and 17% protected in the Central Indo-pacific (Table 3.1). However, these areas also have very little total wilderness left (<5%; Table 3.1), suggesting MPAs play a crucial role in preserving the small amount remaining. Wilderness protection is much lower in remote areas, such as the Southern Ocean and Northern Cold Water realms, where few MPAs are designated (Table 3.1).

Considerably more global marine wilderness remains in offshore ecosystems (49.7 million km^2) than coastal ecosystems (5.5 million km^2; Figure 3.2), but the proportion of protected wilderness is similar (4.4% and 4.8% respectively). In coastal ecosystems, the vast majority of protected wilderness (93%) is in soft bottom areas, rather than habitats such as rocky reefs or coral reefs that people depend on for food and income ((FAO 2016); Figure 3.2, Table S3.4). However, despite having low wilderness extent and areal protection, these ecosystems have high proportional levels of protection, with 66% and 26% of rocky reef and coral reef wilderness covered by MPAs, respectively (Table S3.4). A substantial amount of wilderness in these ecosystems is contained in large, remote MPAs, such as the British Indian Ocean Territory MPA (Graham & McClanahan 2013). Offshore ecosystems generally have more protected wilderness area than coastal ecosystems (Figure 3.2), but lower proportional wilderness protection (Table S3.4).

Realm-specific wilderness has much higher MPA coverage than global marine wilderness, with half of all realms having >50% wilderness protection (Table 3.1). This is likely because, when compared to global marine wilderness, there is more realm-specific wilderness in coastal waters where most MPAs are designated (UNEP-WCMC & IUCN 2018a). However, some realms have very poor wilderness coverage, with the Southern Ocean, Northern Cold Water and Atlantic Cold Water realms all having <0.1% of realm-specific wilderness protection (Table 3.1).

Implications for global conservation policy

Human pressures across the ocean are increasing rapidly and nowhere in the sea is entirely free of human impacts (Halpern et al. 2008, 2015). We show that there is very little marine wilderness in coastal areas, with most remaining wilderness relegated to extreme latitudes or the high seas (Figure 3.1). Although there are vast differences in the amount of wilderness remaining across marine ecosystems, the level of wilderness protection is low in most ecosystems (Figure 3.2). International conservation policies should now recognize the values of wilderness and target conservation actions towards reducing threats in these areas to ensure their retention.

Marine wilderness loss may impact the ability of nations to achieve global conservation goals within key multilateral environmental agreements, such as the Convention on Biological Diversity (CBD), which mandates inclusion of at least 10% of marine areas in effectively managed and ecologically representative MPAs by 2020 (Convention on Biological Diversity (CBD) 2014). Achieving a truly representative MPA network will require the protection of global and realm-specific wilderness alongside imperilled biodiversity rich areas, because wilderness areas support unique species compositions and higher biomass than populated areas (Graham & McClanahan 2013; D'agata et al. 2016). Wilderness areas can also exhibit extremely high endemism (Friedlander et al. 2016) and harbour functional traits rarely found in areas of higher impact (D'agata et al. 2016). Furthermore, while many marine wilderness areas are located in deep-water areas (Figure 3.1), recent research shows these places are not as species impoverished as once thought, as they hold significant biodiversity (Danovaro et al. 2014) and maintain crucial ecosystem processes (Danovaro et al. 2008).

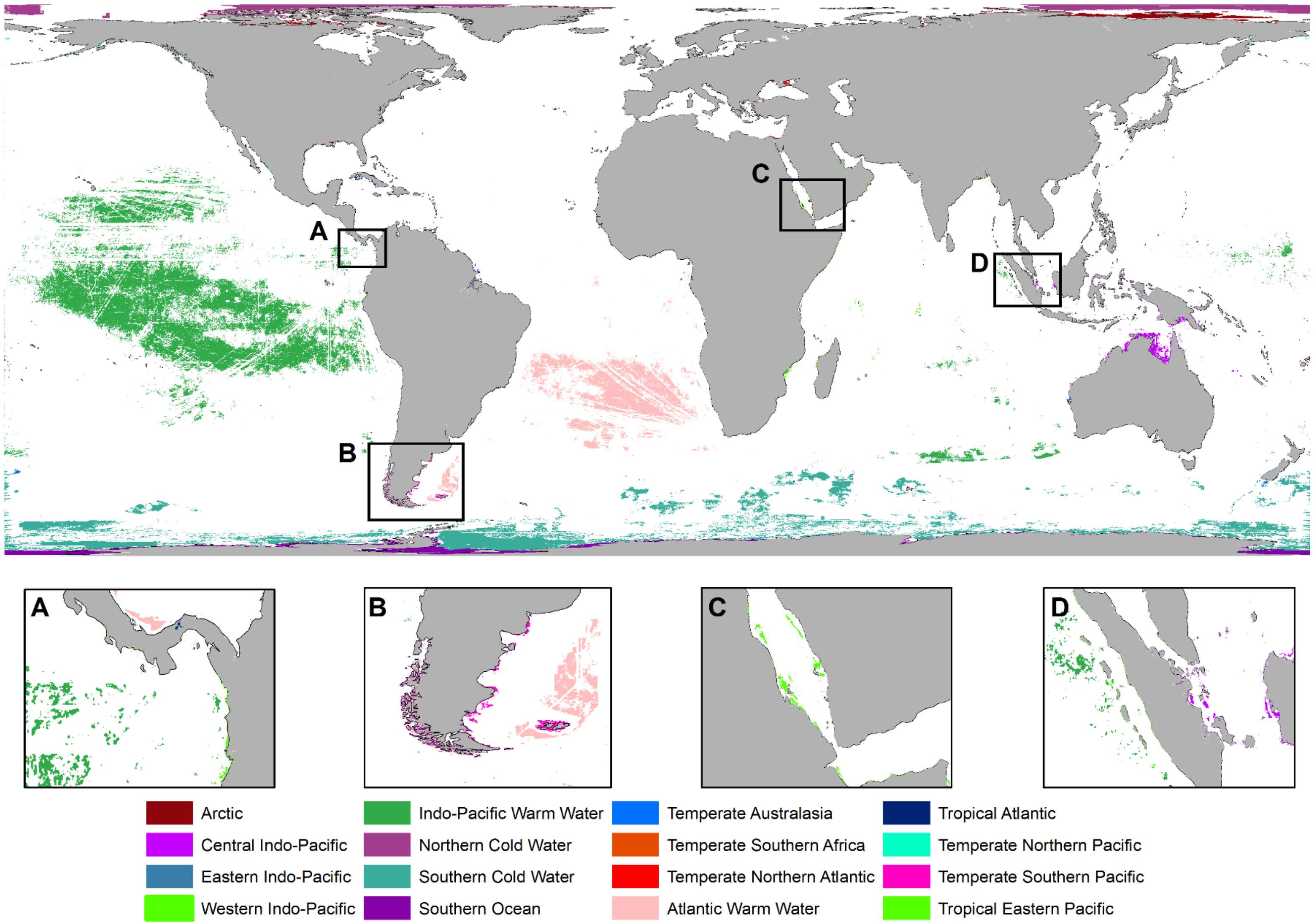

Figure 3.3. Realm-specific wilderness extent –Wilderness map showing the least impacted areas of each ocean realm.

Marine wilderness areas may also be well placed to resist and recover from the impacts of climate change, though the evidence for this is mixed (Côté & Darling 2010). There are a number of studies showing less degraded ecosystems can return more quickly to their original state following disturbances (including climate stressors) than more degraded ones (Carilli et al. 2009b; Côté & Darling 2010; Hughes et al. 2017). Furthermore, there is also some evidence that local stressors can reduce ecosystem resilience to climate change, meaning that wilderness areas may have increased climate resilience (Carilli et al. 2009b; Côté & Darling 2010). However, local stressors do not always affect susceptibility to climate change (Côté & Darling 2010), and some areas of low anthropogenic activity are already severely impacted by climate change (Hughes et al. 2017). Nevertheless, conserving wilderness areas will provide numerous biodiversity benefits including preserving unique species compositions and functional traits, and these areas may also be resilient to climate change.

Marine wilderness is often overlooked, both in global conservation policy and national conservation strategies, because these areas are assumed to be free from threatening processes and therefore not a priority for conservation efforts (Mittermeier et al. 2003). Our results follow recent terrestrial analyses which debunk the myth that wilderness is not threatened (Watson et al. 2016b), as we show only 13% of global marine wilderness remains. International policies are often blind to the benefits that flow from intact, functioning ecosystems, and there is no text within the CBD or the United Nations World Heritage Convention that recognises the importance of retaining large intact landscapes or seascapes (Watson et al. 2016b; Allan et al. 2017a). Similarly, national level conservation plans tend to focus on securing under-pressure habitats or endangered populations (Watson et al. 2009), rather than multi-faceted strategies which also focus on wilderness protection. While conservation efforts in high-biodiversity, high-pressure regions (e.g. the Coral Triangle and Caribbean) are very important, they should be complemented by proactive action to prevent human pressures eroding Earth's marine wilderness areas.

Future conservation actions

Multilateral environmental agreements should now recognize the importance of wilderness, and the increasing threats it faces, both on land and in the ocean. Such recognition will help drive large-scale actions needed to secure wilderness into the future.

These actions will vary across nations and regions, but should focus on human activities that threaten wilderness. In the ocean, this includes preventing overfishing and destructive fishing practices, minimising ocean-based mining that extensively alters habitats, and limiting runoff from land-based activities. Better enforcement of existing laws is also needed to prevent illegal, unreported and unregulated fishing, which makes up 10-30% of global catch (Agnew et al. 2009).

Along with ocean-based threats that erode wilderness, it is crucial to consider the impacts of climate change, which are already affecting marine biodiversity (Perry et al. 2005; Hughes et al. 2017). While we include climate change in our secondary cumulative impact classification, including climate variables in our individual stressor analysis resulted in almost zero marine wilderness remaining (Fig. S1, see methods). Our results must therefore be interpreted with the caveat that marine wilderness is already, and will continue to be, impacted by climate change. While considering the direct impacts of climate change (e.g. temperature increases) is crucial, it is also important to predict and counter threatening human responses to climate change, such as shifting fishing grounds (Pinsky & Fogarty 2012) or the opening of previously ice covered areas for shipping and fishing (Harris et al. 2017). Given the devastating recent impacts of climate change on particular marine ecosystems (e.g. coral reefs (Hughes et al. 2017)), we believe priorities for wilderness protection could be informed by research assessing where such areas have been, or are likely to be significantly impacted by climate change, and where they can act as climate refugia.

Due to large-scale erosion of marine wilderness, those remaining areas are, almost by definition, irreplaceable – representing some of the last marine areas affected by no, or very low human pressure. Protecting wilderness areas will help preserve large, biologically connected ecosystems (Jones et al. 2007; Grober-Dunsmore et al. 2009; Wilhelm et al. 2014); species with large home ranges (e.g. tuna; (Pala 2009)); and hotspots of functional traits and endemic species (Graham & McClanahan 2013; Pinsky & Palumbi 2014; Friedlander et al. 2016; D'agata et al. 2016). It will also directly benefit humanity by preserving the carbon mitigation and adaptation values of intact marine ecosystems (Mcleod et al. 2011). However, it is crucial to prioritise wilderness conservation to those areas most at risk of being lost, and not repeat past mistakes by designating MPAs to minimise conflict with other activities (e.g. fishing and mining; (Devillers et al. 2015)). In highly impacted regions and coastal ecosystems, retaining intact ecosystems will likely require supplementing MPAs with other interventions to prevent impacts, such as land-based regulations to minimise sediment runoff (Klein et al. 2010). Given such little global marine wilderness remains in coastal areas, our realm-specific wilderness map (Figure 3.3) is useful to help direct such actions. It is also important to recognise that as with all global analyses, our wilderness maps rely on imperfect data, and we anticipate that refinements will occur as new data becomes available (e.g. Global Fishing Watch; (Kroodsma et al. 2018)), ensuring wilderness is mapped with increasing precision

As technological advances drive human impacts farther from land and deeper into the sea, it is also essential to consider the three-dimensional nature of the ocean. For example, fishing gear improvements have increased the mean depth of industrial fishing by 350m since 1950 (Watson & Morato 2013), and there are now almost 2000 oil and gas wells operating deeper than 400m (Sandrea & Sandrea 2007). Targeting conservation actions towards specific threats at specific depths will provide better protection of biodiversity across the entire water column. Wilderness conservation will also require an increased focus on high seas management. While legally challenging, prioritising conservation actions in at-risk areas beyond national jurisdiction is crucial for dealing with expanding human threats (Game et al. 2009). There is growing momentum behind the designation of large oceanic MPAs (e.g. Big Ocean; (Wilhelm et al. 2014)), and there are now extensive data to facilitate defensible selection and design of these large pelagic MPAs to protect high seas wilderness (Game et al. 2009). Current difficulties with ensuring enforcement and compliance in these remote areas are beginning to be overcome, with recent advances in satellite and remote vessel monitoring technology, such as Global Fishing Watch (Kroodsma et al. 2018). The need for improved high-seas management is also now being recognised by the international community, with the UN currently negotiating the “Paris Agreement for the Ocean” – a legally-binding high seas conservation treaty to be established under the existing Law of the Sea Convention (United Nations General Assembly 2017).

Wilderness loss is a globally significant problem with largely irreversible outcomes: once lost, the many environmental values of wilderness are very unlikely to be restored. We show that there is very little global marine wilderness remaining, highlighting the need for immediate action to protect what is left, and prevent an ocean-based recurrence of the catastrophic wilderness declines seen on land (Watson et al. 2016b). Proactively prioritizing and protecting the world’s most at-risk marine wilderness areas, while also securing highly threatened species and ecosystems, is now essential for conserving biodiversity and ensuring that large scale ecological and evolutionary processes continue.

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Supplementary Material

Table S3.1. Stressors to the marine environment, developed by Halpern et al. (2015), used to map marine wilderness. Two marine wilderness scenarios were analysed, one which included all 19 stressor layers (see Figure S3.1), and one that excluded climate change based stressors, leaving 15 stressor layers (see Figure 3.1).

Threat Category	***Stressor***
Fishing	Demersal Destructive Fishing Demersal Non-Destructive, High Bycatch Fishing Demersal Non-Destructive, Low Bycatch Fishing Pelagic, High Bycatch Fishing Pelagic, Low Bycatch Fishing Artisanal Fishing
Ocean-Based	Benthic Structures Commercial Shipping Invasive Species Ocean-Based Pollution
Land-Based	Nutrient Pollution Organic Pollution Inorganic Pollution Direct Impact
Climate Change	Sea Surface Temperate Anomalies UV Radiation Ocean Acidification Sea Level Rise

Table S3.2. Number of marine species whose distribution overlaps with marine wilderness areas. Data are shown for all species (bottom) and species in the six largest phyla, where the largest phyla (chordata) is split into its four largest classes (Actinopterygii, Elasmobranchii, Mammalia, Reptilia).

Phyla	*n species*	*n species in wilderness*	*% of species in wilderness*	*Average distribution range in wilderness (%)*
Actinopterygii	11156	10348	92.76	2.66
Arthropoda	3556	3276	92.13	6.11
Cnidaria	1041	1017	97.69	3.68
Chondrichthyes	808	716	88.61	1.91
Echinodermata	536	470	87.69	3.00
Mammalia	117	114	97.44	8.38
Mollusca	3659	3489	95.35	2.42
Porifera	377	368	97.61	3.41
Reptilia	32	31	96.88	2.62
Other	1603	1493	93.14	6.13
All species	22885	21322	93.17	3.73

Table S3.3 Average species richness, range rarity and proportional range rarity values for wilderness and non-wilderness areas across the marine ecoregions of the world.

	Species Richness		**Range Rarity**		**Proportional Range Rarity**	
Ecoregion	*Wilderness*	*Non-wilderness*	*Wilderness*	*Non-wilderness*	*Wilderness*	*Non-wilderness*
Aleutian Islands	511.00	198.97	33.16	8.23	0.07	0.02
Amazonia	36.25	615.53	4.74	20.51	0.15	0.06
Amsterdam-St Paul	397.16	402.78	4.11	2.75	0.01	0.00
Amundsen/Bellingshausen Sea	95.43	91.18	4.47	3.69	0.03	0.03
Antarctic Peninsula	147.84	242.14	7.68	16.25	0.03	0.05
Arabian (Persian) Gulf	57.00	197.96	9.78	15.03	0.17	0.08
Arafura Sea	2473.50	2192.11	48.28	34.61	0.02	0.01
Arnhem Coast to Gulf of Carpenteria	3489.43	3002.90	63.59	50.70	0.02	0.02
Auckland Island	472.24	569.89	6.92	13.49	0.01	0.02
Baffin Bay - Davis Strait	46.11	42.45	0.95	0.98	0.02	0.02
Banda Sea	1077.00	3176.21	9.18	57.16	0.01	0.01
Bassian	285.17	462.08	0.89	16.31	0.00	0.02
Beaufort Sea - continental coast and shelf	17.92	36.64	0.48	1.51	0.01	0.04
Beaufort-Amundsen-Viscount Melville-Queen Maud	27.25	53.01	0.67	1.26	0.03	0.02
Bight of Sofala/Swamp Coast	2371.50	1276.67	71.42	24.99	0.03	0.01
Black Sea	76.20	42.43	10.19	4.71	0.13	0.06
Bonaparte Coast	2933.78	2486.36	54.95	42.13	0.02	0.02
Bounty and Antipodes Islands	442.49	328.62	5.30	3.85	0.01	0.01
Bouvet Island	113.30	100.10	1.82	0.64	0.01	0.01
Campbell Island	387.87	479.38	5.84	9.98	0.01	0.02
Cargados Carajos/Tromelin Island	3255.00	751.78	73.97	8.72	0.02	0.01
Central New Zealand	589.26	795.45	9.79	28.21	0.01	0.03

Central Peru	495.13	581.74	1.30	16.81	0.00	0.02
Central Somali Coast	3153.00	834.78	85.14	12.99	0.03	0.01
Chagos	3830.50	747.31	80.00	7.80	0.02	0.00
Channels and Fjords of Southern Chile	127.78	281.85	2.07	10.83	0.01	0.02
Chatham Island	559.31	551.58	12.76	9.58	0.02	0.01
Chukchi Sea	33.64	51.64	0.89	1.35	0.02	0.02
Cocos Islands	427.30	433.58	3.02	2.85	0.00	0.00
Coral Sea	5886.00	1702.57	129.80	29.31	0.02	0.01
Crozet Islands	197.02	190.50	7.00	3.62	0.02	0.01
East Antarctic Dronning Maud Land	98.10	57.23	5.65	2.54	0.03	0.02
East Antarctic Enderby Land	129.92	51.80	8.36	2.80	0.04	0.02
East Antarctic Wilkes Land	144.82	103.12	8.29	4.92	0.04	0.02
East Caroline Islands	1205.17	731.17	16.80	8.51	0.00	0.00
East Greenland Shelf	63.18	134.17	1.91	3.10	0.02	0.02
East Siberian Sea	4.06	8.44	0.08	0.19	0.02	0.02
Eastern Bering Sea	96.53	198.02	3.47	8.54	0.04	0.04
Eastern Galapagos Islands	483.50	779.64	1.91	20.56	0.00	0.01
Exmouth to Broome	4547.00	1943.85	90.84	36.16	0.02	0.02
Fiji Islands	6026.00	1776.37	134.92	31.26	0.02	0.01
Gilbert/Ellis Islands	684.20	692.31	5.43	7.58	0.00	0.00
Greater Antilles	3054.20	1018.93	228.32	35.85	0.07	0.02
Guayaquil	350.60	626.15	1.17	21.97	0.00	0.02
Guianan	723.00	867.94	43.16	30.36	0.09	0.03
Gulf of Alaska	571.00	324.87	38.46	20.22	0.07	0.04
Gulf of Papua	4396.25	4582.40	80.78	85.11	0.02	0.02
Hawaii	266.75	500.54	0.70	9.17	0.00	0.01
Heard and Macdonald Islands	492.63	279.51	31.37	14.09	0.05	0.03
High Arctic Archipelago	3.21	15.98	0.07	0.34	0.01	0.02
Hudson Complex	60.13	61.60	1.48	1.35	0.02	0.02

Humboldtian	553.75	594.23	2.62	11.22	0.00	0.01
Juan Fernandez and Desventuradas	521.77	446.49	12.85	3.71	0.01	0.00
Kamchatka Shelf and Coast	215.00	157.54	12.05	5.07	0.04	0.02
Kara Sea	18.26	40.74	0.42	0.87	0.02	0.02
Kerguelen Islands	466.22	364.82	34.51	21.43	0.07	0.05
Lancaster Sound	29.78	41.52	0.69	0.95	0.02	0.02
Laptev Sea	11.97	12.58	0.30	0.28	0.02	0.02
Leeuwin	300.00	590.73	0.53	23.87	0.00	0.02
Line Islands	471.41	575.43	2.90	5.05	0.00	0.00
Macquarie Island	161.04	114.65	3.06	0.35	0.01	0.00
Malvinas/Falklands	468.13	368.74	31.84	17.76	0.07	0.04
Marquesas	477.95	570.62	5.90	10.38	0.00	0.00
Marshall Islands	906.46	566.52	10.13	7.19	0.00	0.00
Nicoya	351.00	594.40	1.76	27.88	0.01	0.02
North and East Barents Sea	22.59	89.88	0.54	2.08	0.02	0.02
North Greenland	9.12	37.51	0.16	0.75	0.01	0.02
North Patagonian Gulfs	401.60	456.46	29.10	30.75	0.07	0.06
Northeastern New Zealand	500.50	886.56	1.79	25.04	0.00	0.02
Northern and Central Red Sea	378.50	166.60	42.54	20.46	0.11	0.14
Northern Galapagos Islands	442.44	635.25	1.27	11.51	0.00	0.01
Northern Labrador	106.56	116.32	4.59	4.39	0.04	0.03
Panama Bight	523.00	587.43	23.55	22.47	0.03	0.02
Patagonian Shelf	317.14	353.78	19.09	19.40	0.06	0.05
Peter the First Island	54.30	53.19	1.08	0.69	0.01	0.01
Phoenix/Tokelau/Northern Cook Islands	483.69	371.43	2.67	2.56	0.00	0.00
Prince Edward Islands	249.19	215.52	2.82	3.28	0.01	0.01
Rapa-Pitcairn	30.69	57.19	0.71	0.63	0.00	0.00
Revillagigedos	415.00	480.34	0.65	2.98	0.00	0.00

Rio Grande	56.00	518.79	1.63	11.24	0.03	0.03
Ross Sea	44.64	17.00	2.04	0.70	0.01	0.01
Sea of Okhotsk	113.00	143.67	2.85	5.85	0.03	0.03
Seychelles	3894.00	868.03	90.89	11.15	0.02	0.00
Snares Island	539.85	671.90	9.28	20.32	0.02	0.03
Solomon Sea	6673.33	2286.54	136.22	40.34	0.02	0.01
South Georgia	332.50	172.14	27.67	9.99	0.05	0.03
South New Zealand	588.44	591.88	13.00	16.86	0.02	0.02
South Orkney Islands	159.31	183.10	8.88	10.80	0.03	0.03
South Sandwich Islands	147.43	87.56	7.25	2.55	0.02	0.02
South Shetland Islands	145.33	202.41	10.75	18.08	0.03	0.05
Southern Caribbean	156.00	1265.37	9.47	57.95	0.06	0.03
Southern Gulf of Mexico	1992.00	1078.85	122.63	43.08	0.06	0.02
Southern Java	953.50	967.34	15.96	11.41	0.02	0.01
Southern Red Sea	651.80	631.39	44.73	35.85	0.07	0.06
Southwestern Caribbean	2919.00	1171.60	198.81	52.13	0.07	0.03
St. Helena and Ascension Islands	234.00	441.93	0.30	1.22	0.00	0.00
Sunda Shelf/Java Sea	389.00	1928.39	7.75	31.14	0.02	0.02
Torres Strait Northern Great Barrier Reef	5065.50	3974.02	98.86	78.47	0.02	0.01
Trindade and Martin Vaz Islands	8.00	37.65	0.08	0.16	0.02	0.01
Tristan Gough	501.67	374.98	7.91	1.88	0.01	0.00
Tuamotus	318.17	350.42	2.31	8.34	0.00	0.01
Tunisian Plateau/Gulf of Sidra	293.00	240.36	19.13	11.97	0.07	0.03
Uruguay-Buenos Aires Shelf	527.50	459.81	33.45	24.43	0.05	0.07
Weddell Sea	60.93	42.16	3.03	2.02	0.03	0.02
West Greenland Shelf	56.42	136.50	2.99	5.05	0.03	0.03
Western and Northern Madagascar	4575.00	1057.34	118.43	17.30	0.03	0.01

Western Sumatra	322.69	1212.86	0.71	16.94	0.00	0.01
White Sea	95.29	89.22	3.19	2.96	0.03	0.03
Average	908.45	633.55	25.03	15.17	0.03	0.02

Table S3.4. Wilderness distribution across marine ecosystems. Total ecosystem extent, wilderness extent within EEZ and outside EEZ, and wilderness protection across coastal and offshore ecosystems. Values in parentheses are percentages, all other values are in square kilometres.

	Ecosystem	*Total Area (km^2)*	*Global Wilderness Area (%)*	*Global wilderness in EEZ (%)*	*Global wilderness outside EEZ (%)*	*Global wilderness inside MPA (%)*
Coastal Ecosystems	Coral	273414	842 (0.3)	216 (0.1)	626 (0.2)	219 (26)
	Seagrass	324038	1372 (0.4)	1348 (0.4)	24 (0)	357 (26)
	Rocky Reef	1484686	12039 (0.8)	10863 (0.7)	1176 (0.1)	7963 (66.1)
	Kelp	2162943	56255 (2.6)	52180 (2.4)	4075 (0.2)	7718 (13.7)
	Shallow soft bottom	15516319	5510229 (35.5)	4818595 (31.1)	691634 (4.5)	230317 (4.2)
Offshore Ecosystems	Seamounts	70137	6367 (9.1)	2600 (3.7)	3767 (5.4)	529 (8.3)
	Coastal shelf hard bottom	807467	24903 (3.1)	24890 (3.1)	13 (0)	19257 (77.3)
	Slope hard bottom	3838000	217220 (5.7)	188858 (4.9)	28362 (0.7)	110666 (50.9)
	Coastal shelf soft bottom	13223736	1489210 (11.3)	1435150 (10.9)	54060 (0.4)	119793 (8)
	Deep benthic hard bottom	26218704	3372462 (12.9)	1005901 (3.8)	2366561 (9)	416105 (12.3)
	Slope soft bottom	32573143	5991894 (18.4)	4917791 (15.1)	1074103 (3.3)	416422 (6.9)
	Deep benthic soft bottom	321986244	38679561 (12)	8353776 (2.6)	30325785 (9.4)	1327912 (3.4)

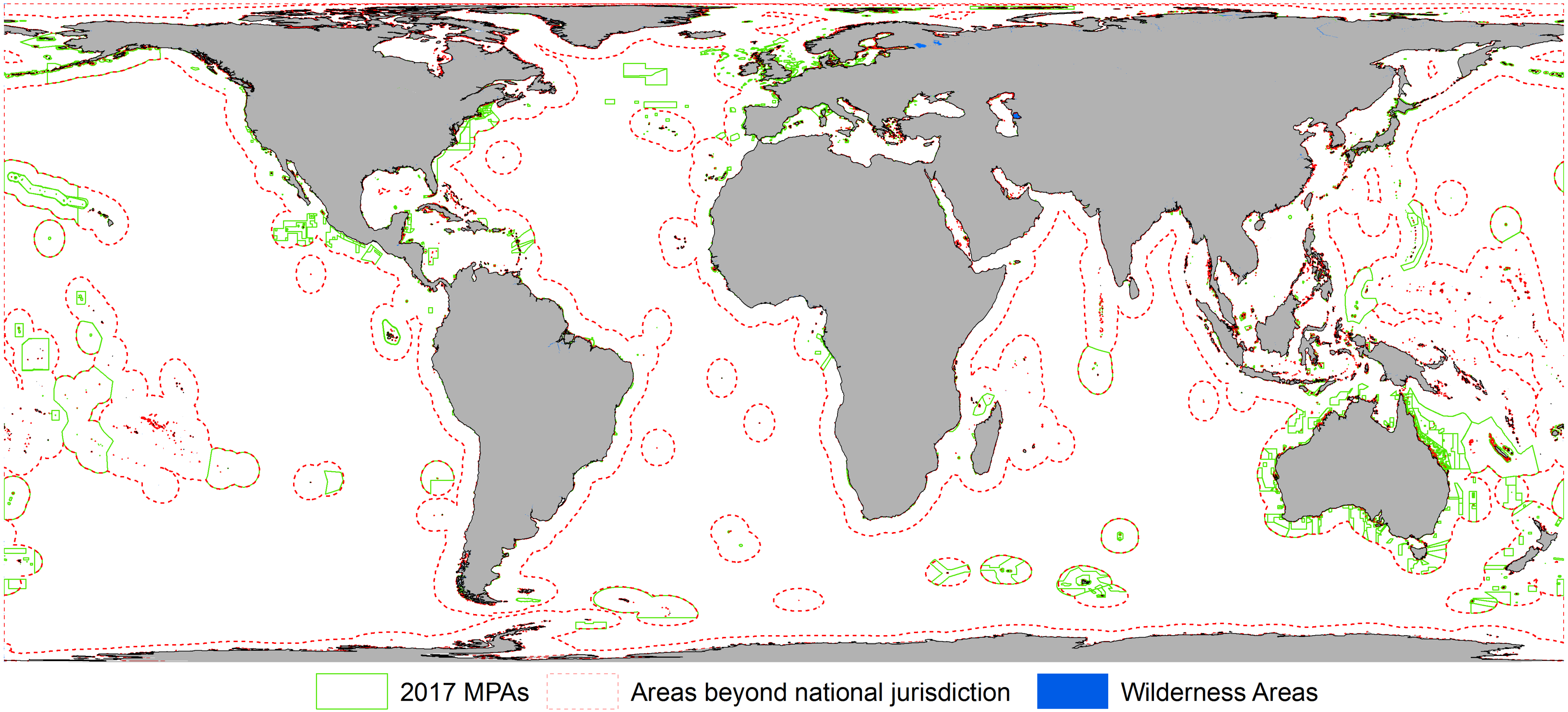

Figure S3.1. Global marine wilderness with climate change. Marine wilderness is defined as any area within the lowest 10% of impact for each of 19 global datasets measuring human impact on the marine environment (including 4 climate change variables), and also within the lowest 10% of cumulative marine impact (Halpern et al. 2015). Areas outside national jurisdiction (i.e. not within the Exclusive Economic Zone of any nation) are dotted red, while 2017 MPAs are outlined in green. Waters 200 nautical miles from the Antarctic coastline, while marked here as Exclusive Economic Zones, are in fact not under jurisdiction of any single nation.

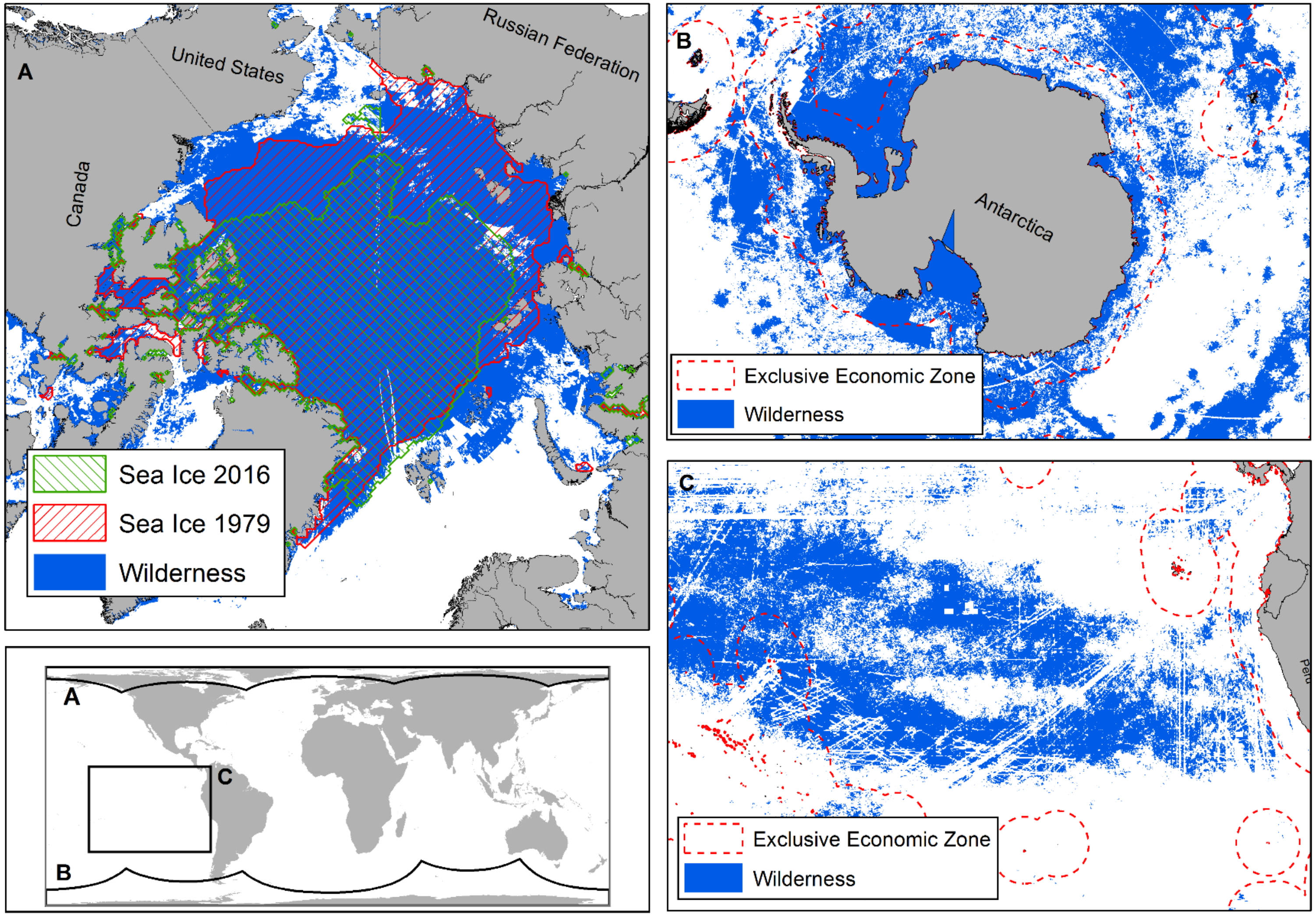

Figure S3.2. Regional contexts for global marine wilderness distribution. (A) Global marine wilderness in the Arctic (blue), and mean summer sea ice extent for 1979 (hashed red) and 2016 (hashed green). (B) Global marine wilderness in Antarctica (blue), and areas within exclusive economic zones (dotted red). (C) Global marine wilderness in the Eastern Pacific Ocean (blue), with linear shipping routes (e.g. to and from island nations) dividing wilderness areas. Waters 200 nautical miles from the Antarctic coastline, while marked here as Exclusive Economic Zones, are in fact not under jurisdiction of any single nation.

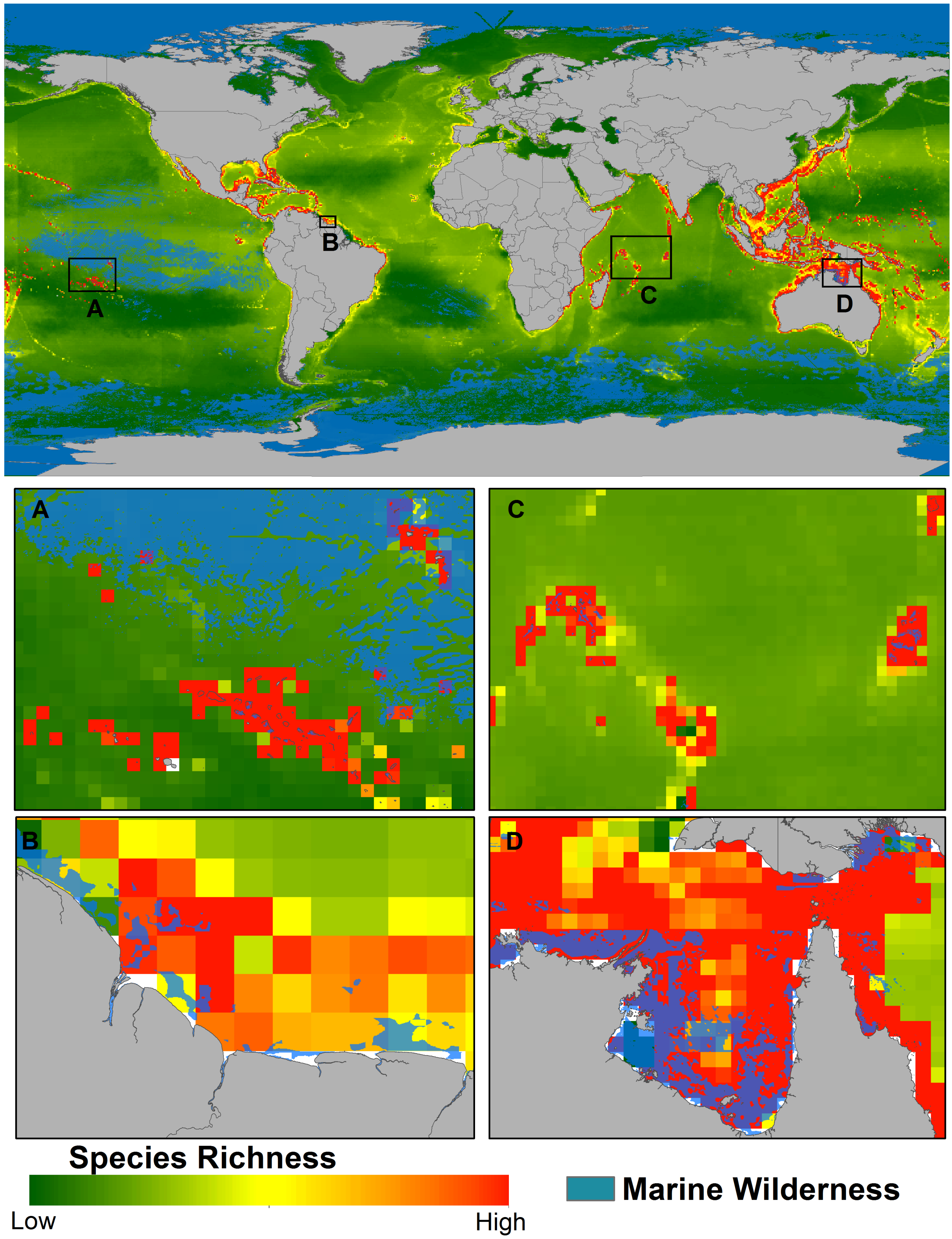

Figure S3.3. Global distribution of marine wilderness and species richness. Species richness is based on the distributions of 22,885 marine species in 0.5 degree square cells, as taken from the Aquamaps database (http://www.aquamaps.org/).

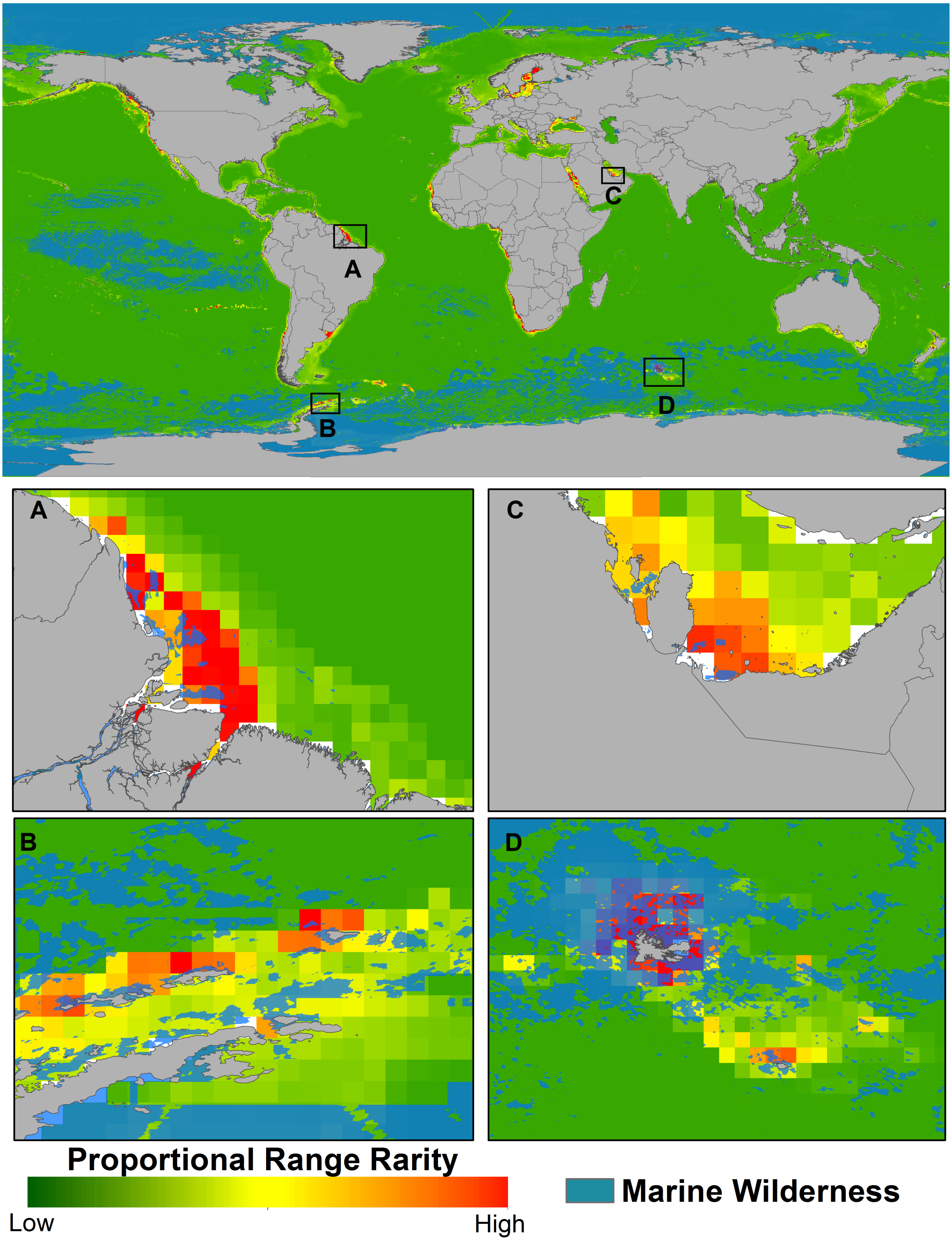

Figure S3.4. Global distribution of marine wilderness and proportional species range rarity. Proportional species range rarity identifies places that have species with restricted ranges, independent of the number of species present, and is based on the distributions of 22,885 marine species in 0.5 degree square cells, as taken from the Aquamaps database (http://www.aquamaps.org/).

Chapter 4

Jones KR, Klein CJ, Grantham, H, Possingham, HP, Watson, JEM. Global priorities for conserving Earth's marine species. *Nature Ecology and Evolution.* In prep.

Contributor	Statement of contribution
Jones, KR (Candidate)	Conception and design (65%) Analysis and interpretation (65%) Drafting and production (65%)
Klein, CJ	Conception and design (5%) Analysis and interpretation (5%) Drafting and production (5%)
Grantham, H	Conception and design (5%) Analysis and interpretation (5%) Drafting and production (5%)
Possingham, HP	Conception and design (5%) Analysis and interpretation (5%) Drafting and production (5%)
Watson, JEM	Conception and design (20%) Analysis and interpretation (20%) Drafting and production (20%)

Chapter 4 – Global priorities for conserving Earth's marine species.

Kendall R. Jones, Carissa J. Klein, Hedley Grantham, Hugh P. Possingham, James E.M. Watson

Summary

Despite numerous global policy commitments to preserve Earth's marine biodiversity, many species are poorly protected and in decline. Here, we identify priority areas for marine conservation action to represent 22,885 marine species that complement existing conservation management and priority areas. We find that adequately representing the distribution of all mapped marine species will require an additional 8.5 million km^2, which when combined with existing conservation areas covers 26% of the ocean. To guide conservation action, we determine if the threats to these priority areas are ocean-based (e.g. fishing) or land-based (e.g. nutrient run-off). Securing these areas through marine (e.g. marine protected areas) and terrestrial management (e.g. runoff reduction) will help protect marine biodiversity and provide a solid foundation for post-2020 conservation goals. These goals must be bold and multi-faceted, aimed not only at representing species and stopping extinctions, but also at securing intact ecosystems and retaining nature outside formally protected areas.

Main

Alongside human-forced climate change, biodiversity loss is the biggest environmental issue of our time (Newbold et al. 2016). Human activities associated with urbanisation, agriculture, mining, and fishing have led to large-scale habitat destruction and degradation, causing not only species declines and extinctions (McCauley et al. 2015; Newbold et al. 2015; Maxwell et al. 2016) but also the rapid erosion of intact ecosystems on land and in the sea (Allan et al., 2017; Halpern et al., 2015; Watson et al., 2016). The disparity between increasing conservation efforts, including a doubling of the protected area estate in just two decades (UNEP-WCMC & IUCN 2018a), and persistent biodiversity decline has led to a number of calls for more ambitious plans to halt biodiversity loss (Wilson 2016; Dinerstein et al. 2017; Watson & Venter 2017; Maron et al. 2018).

While there is a clear scientific basis for substantially increasing area-based conservation efforts (Larsen et al., 2015; Noss et al., 2012; O'Leary et al., 2016), some of the more public calls (such as "Half-earth" and "Nature needs Half" (Wilson 2016) have been criticized as both infeasible and lacking ecological relevance (Büscher et al., 2017). Discussions around the generation of new, "post-2020" international targets for biodiversity are now underway, and it is accepted that any increases in conservation targets must have solid foundations in ecological science to ensure that the full range of biodiversity is protected in the short and long-term (Watson & Venter 2017). This will likely involve not only targets for formal protection of biodiversity, but also for the retention of biodiversity outside protected areas (Maron et al. 2018). As these targets are developed, it is crucial to identify where and how conservation action is needed to safeguard biodiversity now, and assess the threats that may compromise ecological integrity in these areas in the future. This is especially true in the ocean, as existing conservation efforts poorly represent most marine species (Klein et al. 2015).

Here we provide a global assessment of priorities for the expansion of site-based conservation action to secure marine species. We first evaluate how well ~23,000 marine species are represented within current marine protected areas (MPAs), key biodiversity areas (KBAs; IUCN 2016), and the ocean's remaining wilderness areas (Jones et al. 2018). Marine protected areas can be critically important in stabilizing or increasing species populations (Babcock et al. 2010) and maintaining coral cover (Selig & Bruno 2010), and generally have higher biomass than unprotected areas (Edgar et al., 2014; but see Gill et al. 2017). Similarly, marine KBAs are sites contributing to the global persistence of biodiversity (IUCN 2016). They are often safeguarded by MPAs, or are priorities for MPA expansion, but can also inform non-PA based conservation measures and intergovernmental conventions (e.g. Convention on Biological Diversity, Ramsar, Convention on Migratory species; Dudley et al., 2014), or be managed as tourism or fisheries sites (Edgar et al. 2008). Marine wilderness areas, by definition, have very low human impact, and so alongside well managed MPAs are mostly free of threats to biodiversity, at least for now (Jones et al. 2018a). We hereafter refer to these areas (MPAs, KBAs and marine wilderness) as "existing conservation management and priority areas," as all offer potential conservation benefits through direct protection (i.e. MPAs) or because of their identified conservation priority (e.g. KBAs, marine wilderness areas).

Our analysis identifies species with none of their range contained within existing conservation areas, as well as those that do not meet a minimum representation target (10% of range represented; (Convention on Biological Diversity (CBD) 2014). We then use integer linear programming (Beyer et al. 2016) to identify additional conservation priorities to achieve 10% representation of each species while minimising the total area required. To assess the actions needed to protect species within these conservation priorities, we then map the intensity of 15 damaging human activities across them, using the most comprehensive database of human stressors to the ocean (Halpern et al. 2015). We distinguish between ocean-based stressors (e.g., fishing), which can be managed with MPAs or fisheries regulations, and land-based stressors (e.g., nutrient runoff), which require terrestrial management. By doing this, we present an action-oriented site-based plan to ameliorate threats to species. We do not address impacts from climate change because the sources of these impacts, and the potential solutions, are global in nature.

Results and Discussion

Current species protection

Using data on the global distribution of MPAs, we find that two-thirds of species (n = 15149) currently meet global protection targets of >10% (CBD, 2014; Figure 4.1A). Protection levels vary considerably across marine taxa. In coastally restricted species such as reptiles, over 90% are adequately represented and all species have >2% of their range within MPAs (Figure 4.1A). In contrast, three percent of arthropod species have none of their range protected, and only 30% of mammal species are adequately represented

(Figure 4.1A). In total, 7736 species (33%) have less than 10% of their range protected by current MPAs. Around half of these species have under five percent of their range protected, and 216 species (~1%) have no part of their range within MPAs (Figure 4.1A).

We repeated this analysis to include all existing conservation management and priority areas, finding that species representation improved, with 82% of all species (n = 18804) having >10% of their range protected (inside MPAs, KBAs or marine wilderness; Figure 5.1B). While only 33 (<0.1%) species have no part of their range protected, there are still 4081 (18%) species with <10% protection, and 500 species with <2% protection (Figure 4.1B). Low coverage species (<2% protected) are mostly found in the Atlantic Ocean, especially between Africa and South America, and also in the Pacific near China and Japan (Figure S4.1). Elasmobranchs (sharks and rays), and Porifera (sponges), are the least protected phyla overall, with one-third of species having <10% protection (Figure 4.1B).

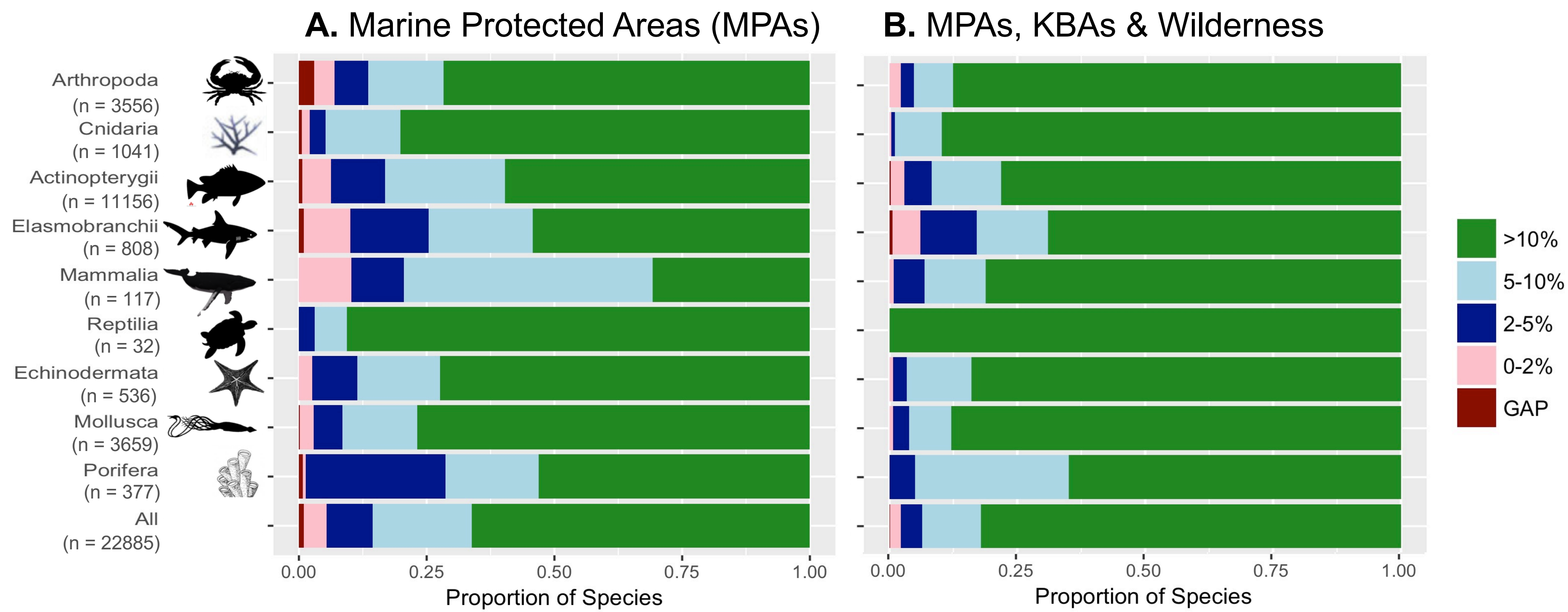

Figure 4.1. Percentage of marine species with 0% (dark red), 0–2% (pink), 2–5% (dark blue), 5–10% (light blue), and >10% (green) of their range overlapping with A. marine protected areas (MPAs), B. MPAs, key biodiversity areas (KBAs), and marine wilderness areas identified by Jones et al. (2018). Data are shown for all species (bottom) and species in the 6 largest phyla where the largest phyla (Chordata) is split into its 4 largest classes (Actinopterygii, Chondrichthyes, Mammalia, Reptilia).

Global conservation priorities

We mapped global marine conservation priorities using integer linear programming (Beyer et al. 2016), by locking in existing MPAs, KBAs and marine wilderness areas as existing conservation management and priority areas, and identifying additional priorities to capture at least 10% of each species range while minimising the total area of conservation zones (the size of conservation zone is treated as its “cost” in the integer linear programming problem, with no clustering function). We identified 8.5 million km^2 of new conservation priority areas in total, just over half of which (55.4%, 4.7 million km^2) are located within exclusive economic zones (excluding Antarctica; Figure 4.2; Figure S5.2). Combined with existing MPAs (25.2 million km^2), KBAs (6.6 million km^2), and marine wilderness (54 million km^2), conservation priority areas cover 94.3 million km^2 (26%) of the ocean (Figure 4.2).

Conservation priorities are primarily located in places where there are few existing conservation areas and high concentrations of poorly represented species. Key regions for these priority areas include the Northern Pacific Ocean near China and Japan and the Atlantic Ocean between West Africa and the Americas (Figure S4.1). Just over half (56%) of all coastal nations contain priority areas, although the amount within each country varies considerably (Figure 4.3). Of the conservation priorities within waters under national jurisdiction, over half are found in Asian and North American EEZ’s (Figure 4.3), while Europe and Oceania contain <10% each (Figure 4.3). Japan has the largest area of unprotected conservation priorities (835,000 km^2), almost double that of the next highest nation Brazil (452,000 km^2; Figure 4.3). Some nations with large MPA estates still contain a substantial amount of conservation priority areas. For example, the United States has the largest MPA estate in the world (UNEP-WCMC & IUCN 2018b), but its waters contain 364,000 km^2 of new conservation priority areas (Figure 4.3), in part because it has the largest EEZ in the world, spanning three oceans.

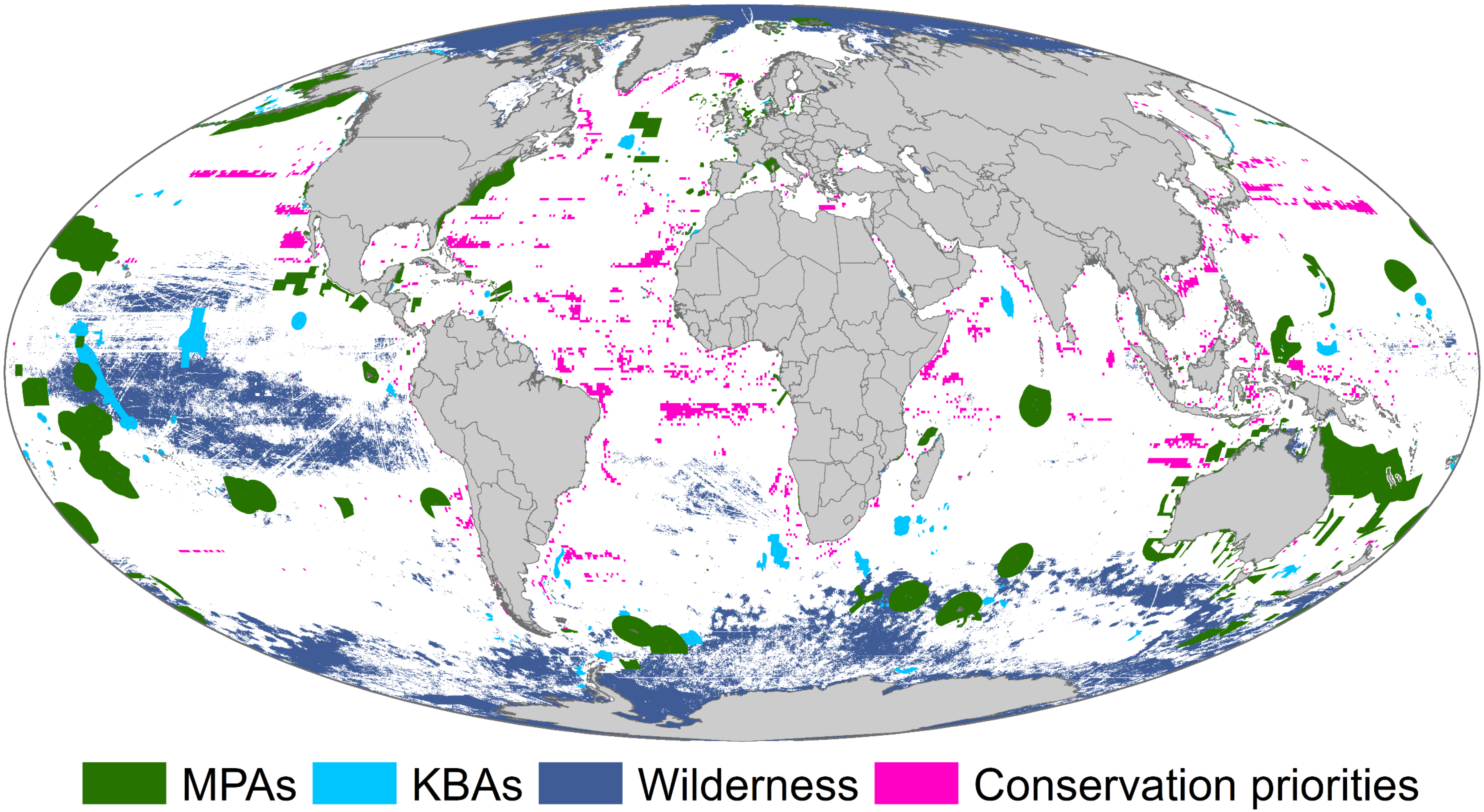

Figure 4.2. Minimum area required for conservation action to reach 10% coverage for approximately 23,000 marine species with known distributions, while accounting for existing marine protected areas (MPAs), key biodiversity areas (KBAs), and marine wilderness areas.

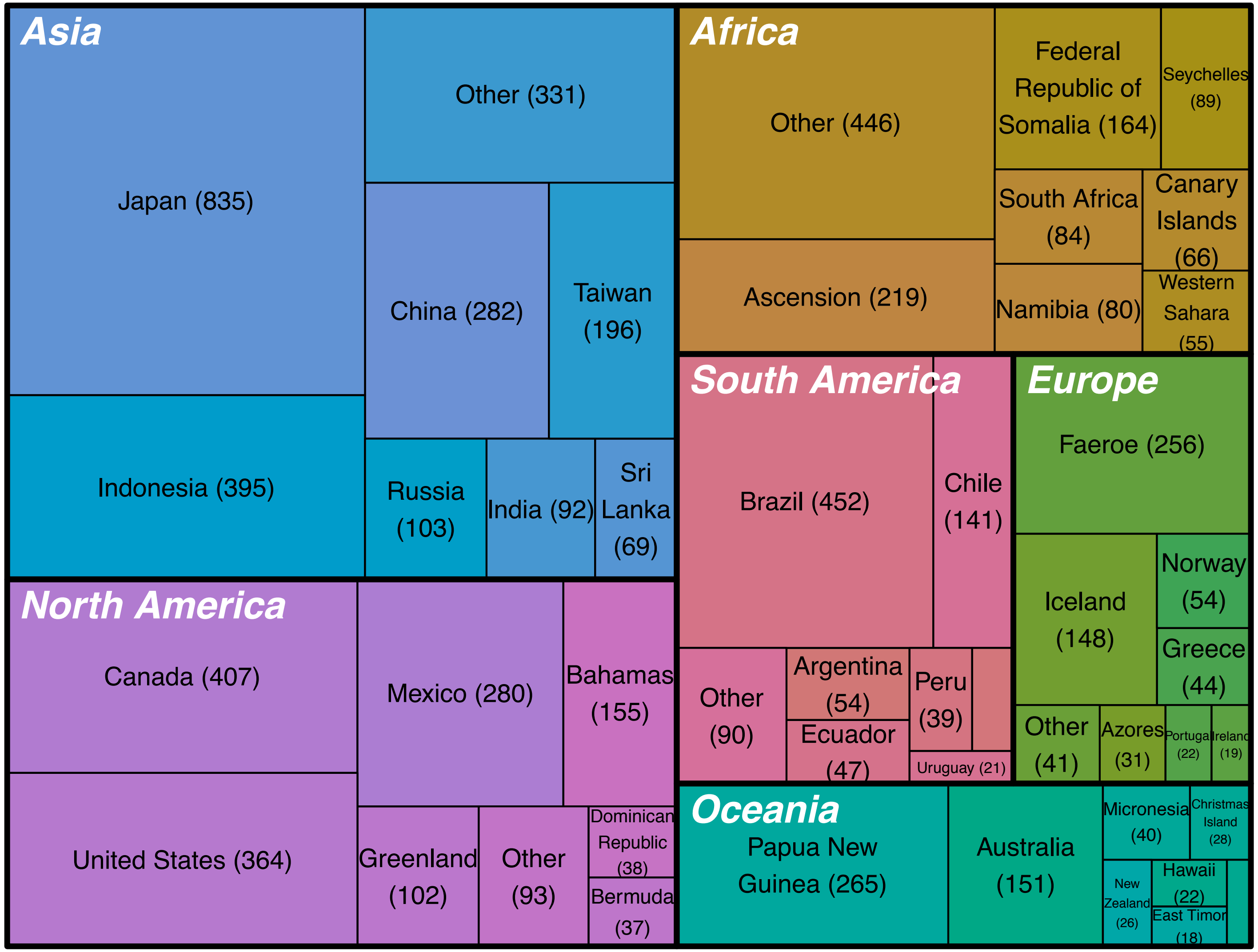

Figure 4.3. Area (thousands km²) of conservation priorities within Exclusive Economic Zones, separated by continent and country. The size of each section is proportional to the area of conservation priorities within each continent and country. Antarctica is excluded as it is the territory of multiple nations.

Ocean and land-based threats

To assess threats to species across conservation priority areas, we used the most comprehensive, globally consistent database on 19 human stressors to the marine environment (Halpern et al. 2015; Detailed summary in Table S4.1). We excluded four climate stressors as, due to their global nature, they are unable to be halted with local conservation action. We classified the 15 remaining stressors based on whether they are ocean-based (e.g. fishing, commercial shipping) and can thus be managed with MPAs or other spatial regulations, or are land-based (e.g. nutrient runoff) and will require terrestrial actions such as land-use management to reduce runoff. We then summed the values for each individual stressor layer within the ocean-based and land-based stressor groups, to give final ocean-based and land-based human impact values across all conservation priority areas.

Most conservation priority areas are impacted primarily by ocean-based threats, in large part because the footprint of land-based pressures is constrained to near-coastal areas. Key areas of ocean-based threats to priority areas are along the West coast of the USA or the East coast of Japan (Figure 4.4 – blue colours). The highest levels of ocean-based threats occur in the East-China Sea and in the North Sea off the Norwegian coast, which are both areas of intense industrial fishing activity (Kroodsma et al. 2018). Some priority areas, such as the South-China sea, are also threatened by militarisation – where base and outpost building is directly destroying some reefs and smothering others with large sediment plumes driven by dredging (Asner et al. 2017). Ocean-based threats are generally lower in high-seas areas than near-coastal priority areas, especially in the South Atlantic Ocean (Figure 4.4). While some coastal priority areas show very low ocean-based threats, in some cases this may be in part due to a lack of data on fishing activity. For example, in Somalia it is estimated that illegal, unregulated and unreported fishing catch is around 3-times higher than official estimates (Glaser et al. 2015). Other studies using automated positioning systems on commercial fishing ships have found that poor satellite coverage and intentional deactivation of transponders leads to similar data gaps, meaning that fishing effort is underestimated in many places where it is very likely to be high (e.g. SE Asia, Gulf of Mexico) (Kroodsma et al. 2018).

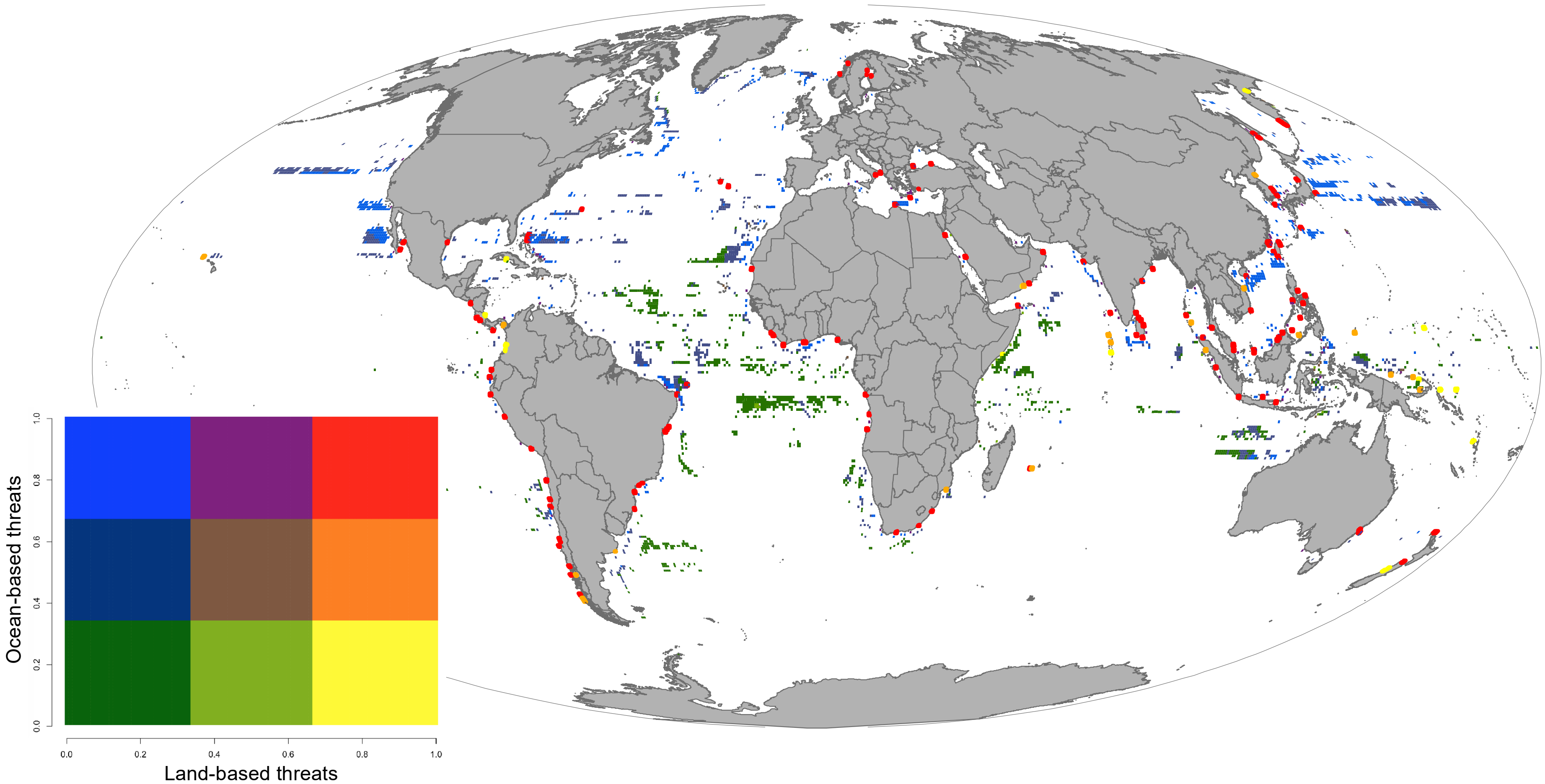

Figure 4.4. Threats to priority areas for conservation. Spatial relationship between ocean-based threats (e.g. fishing, shipping; blue areas), and land-based threats (e.g. sedimentation, nutrient runoff; yellow areas) across global priority areas for conservation. Areas with high levels of ocean and land-based threats are shown in red, and those with low levels of ocean and land-based threat are shown in green. Boundaries of areas within the top tercile of land-based threat level (orange/red/yellow colors) have been enlarged to increase visibility.

A small number of conservation priorities sites are impacted by high levels of both ocean and land-based threats (Figure 4.4 – red colours). These impacts are highest in areas where high fishing activity coincides with high levels of agriculture and livestock grazing in very large nearby drainage basins, such as the Gulf of Mexico and the South China Sea. Many of these areas, such as the Indus river in Pakistan, have been previously identified as threat hotspots where coordinated management of land and ocean-based impacts is vital (Halpern et al., 2009). There are few priority areas that are affected by high levels of land-based threats only (Figure 4.4 – yellow colours).

A substantial proportion of conservation priorities are currently facing relatively low overall threat. Urgent conservation action is less important in these places, such as priorities in the South Atlantic and Indian oceans (Figure 4.4 – green colours). However, given these areas contain low-threat habitat for many species, it is crucial to prevent threats from expanding into them. Monitoring such areas can be difficult, as they are often remote and located beyond national jurisdiction, but these difficulties are beginning to be overcome with advances in remote vessel monitoring technology, such as Global Fishing Watch (Merten et al. 2016).

Implications for future marine conservation

Future global strategies to address biodiversity loss will require rapid action to secure imperiled species and ecosystems, combined with proactive long-term approaches to maintain ecological and evolutionary processes (Brooks et al. 2006; Watson & Venter 2017). We show that effective conservation management of an additional 8.5 million km^2 – an expansion of the current global MPA estate by one-third (UNEP-WCMC & IUCN 2017) – could achieve a representation target of 10% for all marine species. Securing these areas, along with MPAs, KBAs and marine wilderness, would require just 26% of the ocean to be managed for conservation.

For effective conservation it is important to target management actions to the threats facing species in conservation priorities. Areas affected primarily by ocean-based threats are priorities for MPA designation or other area-based conservation measures, such as strictly enforced fisheries regulations (Graham et al. 2007; Kraak et al. 2012). However, many of these areas also support highly productive fisheries, meaning regulations can fail in the face of intense opposition from fishers (McClanahan et al. 2005; Grafton & Kompas

2005; Kamat 2014). Overcoming these difficulties will require identifying which species and ecosystems are most vulnerable to ocean-based impacts, and thus require strict protection to prevent extinctions, and also identifying where conservation outcomes can be achieved while allowing sustainable resource extraction. It may also be useful to target conservation actions towards specific threats at specific depths, for example by regulating bottom-trawling to protect benthic species, while still allowing for pelagic fishing (Venegas-Li et al. 2017). Targeting actions towards threats will also involve recognising when and where MPAs are unlikely to be an effective conservation tool on their own. In areas where land-based stressors play a dominant role in determining ecosystem condition, marine conservation efforts will have little benefit unless the adjacent land is also managed for conservation (Halpern et al. 2013b; Klein et al. 2014).

While addressing land and ocean-based threats is important in the immediate term, conservation strategies must also look forward to assess the future risk posed by climate change. Local conservation actions are unable to stop or reverse the impacts of climate change, but there are many actions that can increase the ability of biodiversity to adapt to a changing climate. For example, marine protected areas have been shown to enhance recovery and resilience of degraded coral reefs (Mumby & Harborne 2010; Mellin et al. 2016), and reducing land-based stressors can increase reef resilience to climate change (Carilli et al. 2009b). Maintaining and increasing connectivity, both within and between MPAs and wilderness areas, will facilitate the large-scale ecological and evolutionary processes essential for climate change adaptation (Saura et al. 2018) The conservation priorities identified here can help direct the use of fine-scale, connectivity-focused conservation planning methods (Beger et al. 2015; Álvarez-Romero et al. 2017). It is also important to recognize and plan for the impacts of human responses to climate change, which include shifting fishing effort to track fish stocks (Pinsky & Fogarty 2012; Engelhard et al. 2014), building seawalls to prevent sea-level rise (Grantham et al. 2011), or expanding agriculture into previously unsuitable areas (Bradley et al. 2012). By recognizing and planning for human responses to climate change, many can be turned from bane to boon for biodiversity. For example, mangrove or coral-reef protection and restoration instead of seawall construction can reduce the impacts of sea-level rise on people while also providing numerous biodiversity benefits (Alongi 2008; Maxwell et al. 2015b; Beck et al. 2018). Alternatively, creation and restoration of flooded habitats like tidal wetland may deliver substantial coastal protection benefits, while also providing habitat for biodiversity and food production in the form of fish and shellfish (Temmerman et al. 2013).

Because over 46% of priority areas are located in the high seas, developing and implementing conservation actions in these areas will be crucial for future conservation agreements. Conservation action in these areas is legally challenging and has so far been limited, with only 1.18% of the high seas currently protected (UNEP-WCMC & IUCN 2018b). Given the difficulties in establishing MPAs in the high seas, one option is to use existing international and regional agreements achieve conservation goals. For example, Regional Fisheries Management Organisations (RFMOs) — international organizations formed by countries to manage shared fishing interests in a certain area — are already used to set catch and fishing effort limits (Game et al. 2009). In some areas, RFMOs have even been used to close large areas of the high seas to damaging bottom-trawl fishing (Gjerde et al. 2008), so an extension of their powers to create high seas conservation areas is certainly feasible. Alternatively, given that 54% of high seas fishing would be unprofitable without government subsidies, subsidy reform could also act as a useful management tool for high seas fisheries (Sala et al. 2018). The need for high-seas management is also now being recognised by the international community, with the UN currently negotiating a legally binding high- seas conservation treaty to be established under the existing Law of the Sea Convention (United Nations General Assembly 2017).

Developing quantifiable metrics for conservation targets beyond areal PA coverage, such as connectivity or habitat quality, is also critical for informing future conservation agreements. Recent research has developed methods that quantitatively measure global terrestrial connectivity, but focus only on land within protected areas (Saura et al. 2018). Given the need for future conservation strategies to move beyond PA extent, this metric could be improved by considering unprotected but good-quality habitat or extending it to the marine realm where connectivity is more difficult to measure. Advances in remote sensing methods could also allow nations to easily report on the state of their protected areas and the success of conservation efforts. For example, remotely sensed human pressure data can be useful for assessing the condition of protected areas (Ban et al. 2010; Jones et al. 2018b), and vessel tracking technology has recently been used to remotely assess the effectiveness of large MPAs for reef-shark protection (White et al. 2017). These and similar methods could be expanded to provide a low-cost global mechanism for monitoring MPA effectiveness, which will be especially important to make future high-seas conservation treaties meaningful and enforceable (United Nations General Assembly 2017).

While our analysis uses the best available data on the global distribution of species and threats, it is subject to several caveats worthy of discussion. We assumed that protection of all areas within a species' range contribute equally towards its protection, and did not consider areas important for different life-history stages (e.g., breeding grounds, feeding areas). Further, while we use the largest database of marine species distributions currently available (Kaschner et al. 2016), this is still a tiny fraction of the estimated 2.2 million marine eukaryotic species (Mora et al. 2011b) As such, it is also important to consider biogeographical surrogates for biodiversity, such as ecoregions and provinces (The Nature Conservancy 2012) which are currently used to measure representativeness of the MPA network. Our approach could be applied within single ecoregions or EEZs to identify finer-scale priorities for achieving representation. We also assume that MPAs and KBAs are effective in stopping threats to biodiversity within their boundaries. This likely overestimates the true conservation impact of existing MPAs/KBAs, given that many allow extractive activities and/or lack the capacity for effective management (Gill et al. 2017). While our analysis can help identify priorities for establishing new MPAs, recent research shows that this should be combined with upgrading established PAs to ensure they are well-managed and societally supported (Pringle 2017). We are also unable to account for synergistic interactions between threats, for example fishing pressure and nutrient-runoff, which can lead to greater than predicted impacts on biodiversity (Harley et al. 2006; Brook et al. 2008). However, we do identify areas where ocean and land-based threats occur together, and thus where synergies may be more likely.

With the 2020 deadline for achieving global conservation targets fast approaching, we highlight priorities for conservation action to fulfill current goals and secure marine biodiversity now. Safeguarding priority areas will require a one-third expansion of the current MPA estate – the same level of growth required to meet 2020 protection targets under the CBD. Moving beyond these priorities to also secure other crucial areas, such as KBAs (IUCN 2016) and intact wilderness areas (Jones et al. 2018) would only require protecting 26% of Earth's oceans. This is a realistic, ecologically relevant coverage target for the conservation community to strive towards, and if combined with targets to retain nature outside formally protected areas (Maron et al. 2018), represents a bold but achievable plan for the future of marine conservation.

Methods

All spatial data described below were processed using ESRI ArcGIS v10.5 in Mollweide equal-area projection. All prioritisation analyses were conducted using R statistical software 3.3.

Gap analysis

Data on the global distribution of protected areas (PAs) were obtained from the 2017 World Database on Protected Areas (UNEP-WCMC & IUCN 2017). Following similar global PA studies (Butchart et al. 2012), we extracted PAs from the WDPA database by selecting those areas that had a status of “designated”, “inscribed”, or “established”, and were not designated as UNESCO Man and Biosphere Reserves. We included only PAs with detailed geographic information in the database, excluding those represented as a point only. We then used a layer of terrestrial country boundaries to identify marine PAs (MPAs) by clipping PA polygons to only include those which have some overlap with marine area (http://datadryad.org/resource/doi:10.5061/dryad.6gb90.2).

Data on Key Biodiversity Areas (KBAs) were obtained from the World Database of Key Biodiversity Areas (http://www.keybiodiversityareas.org/). We used a layer of terrestrial country boundaries to clip KBA polygons to only include those which overlap with marine area (http://datadryad.org/resource/doi:10.5061/dryad.6gb90.2). Data on marine wilderness was obtained from Jones et al. (2018a). This data identifies areas that have little to no impact across 15 human stressors to the marine environment (excluding 4 climate stressors), and also a low combined impact from 19 human stressors (including climate stressors (Halpern et al. 2015). To avoid double counting areas that are covered by MPAs, KBAs, and marine wilderness, we merged these three layers and dissolved areas where they overlapped.

Data on marine biodiversity was obtained from Aquamaps (Kaschner et al. 2016), a species distribution modelling tool that produces standardised global range maps for 22,885 aquatic species. This is the most comprehensive and highest resolution data available on the distribution of marine biodiversity globally, and includes Animalia (fishes, marine mammals, and invertebrates), Plantae (fleshy algae, seagrass), Chromista (calcifying algae) and Protozoa. The species distribution maps predict relative probabilities of species occurrence (ranging from 0.00–1.00) at a resolution of 0.5-degree cells. It is assumed that the preferred range is where probability is 1, outside the range limits is where probability is 0, and between these two thresholds the relative environmental suitability decreases linearly. As there is no recommended threshold to use, we follow previous studies and report on results using probability threshold of 0.5 or greater (Klein et al. 2015).

To assess coverage of marine species distributions in MPAs, KBAs and wilderness areas, we determined the proportion of protected area (MPA, KBA and wilderness) in each 0.5-degree cell. As we do not know the exact distribution of species within each cell, we assumed that the area of a species' range represented in protected areas was equal to the protected area coverage for grid cells that species was present in. To test the sensitivity of our results to the probability threshold used to determine species distributions within each 0.5-degree cell, we repeated the previous analyses using probability thresholds ranging from 0.25 – 1. The number of species within each coverage group (e.g. no coverage, 0-2% coverage etc.) varied by less than 1% across all probability thresholds tested (Table S4.2), and thus our results are relatively insensitive to species distribution modelling uncertainties. Furthermore, previous studies using Aquamaps data found that varying probability thresholds makes very little difference to global scale analyses (Selig et al. 2014; Klein et al. 2015).

Spatial prioritisation analysis

We used integer linear programming to identify spatial priorities that meet a 10% coverage target for each of the 22,885 Aquamaps species, while accounting for the level of protection in existing MPAs, KBAs and wilderness, and minimizing the total cost of selected cells, with area as the cost, following (Beyer et al. 2016). This is frequently referred to as the minimum-set problem in spatial conservation planning (Moilanen et al. 2009a). We used the software package Gurobi (version 5.6.2) to find solutions to this minimum-set problem and set Gurobi to achieve a solution within 0.05% of the optimum.

We used 0.5-degree cells as our planning units (areas which can be selected or not selected for conservation), as this is the same scale as our species distribution data. We extracted all planning units containing species distribution records from Aquamaps (n = 178,234) and assigned each planning unit a cost value equal to the area of the cell that is not covered by an MPA, KBA or marine wilderness area. Thus, the cost value reflects the additional area per cell which requires management if selected for conservation.

Assessing threats facing priority areas

We considered the impact of human threats to marine ecosystems using normalized cumulative human impact data from Halpern et al. (2008, 2015). This threat database includes 19 individual human stressors, but we excluded four climate change stressors. We then categorized threats as ocean-based or land-based, depending on their origin (see Table S4.2 for full list and justification). Ocean-based threats have clear marine origins, such as fishing and shipping, can therefore potentially be managed through effective MPAs of other ocean-use regulations, whereas land-based threats (e.g. nutrient runoff, coastal armouring) originate on land and will require land-management to address. All measures of fishing pressure, shipping (shipping lanes and ship-based pollution) and ocean structures (e.g. oil rigs) were considered as ‘ocean-based’ in our analysis, while all other threats were considered land-based. Using this information, we used the zonal statistics tool in ArcMap 10.5 to calculate the mean level of ocean and land-based threat within each planning unit selected as a priority area in our spatial prioritisation analysis.

Supplementary Material

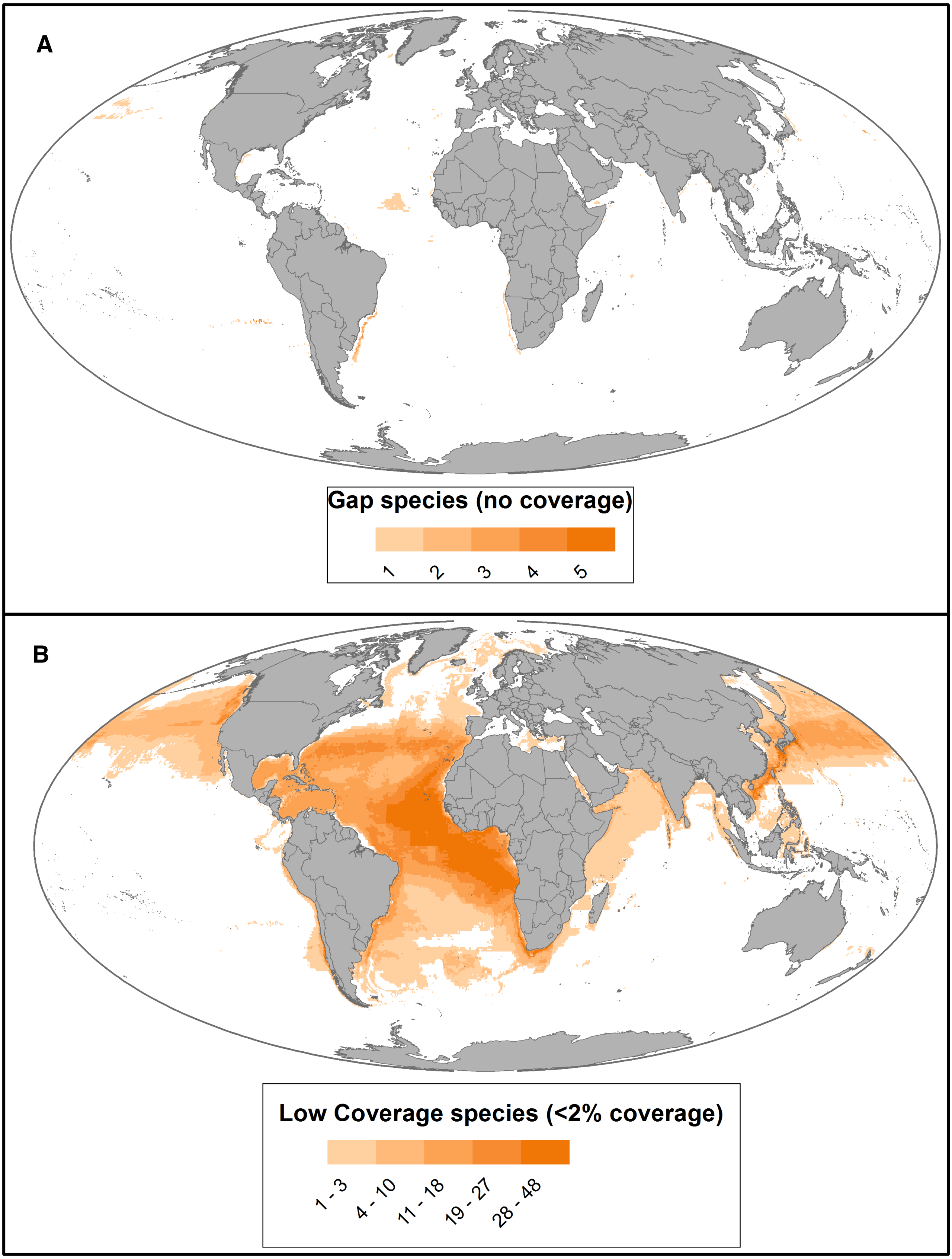

Figure S4.1. A) Density map of gap species (no range represented in MPAs, KBAs or marine wilderness) and; B) very low coverage species (<2% of range represented in MPAs, KBAs or marine wilderness).

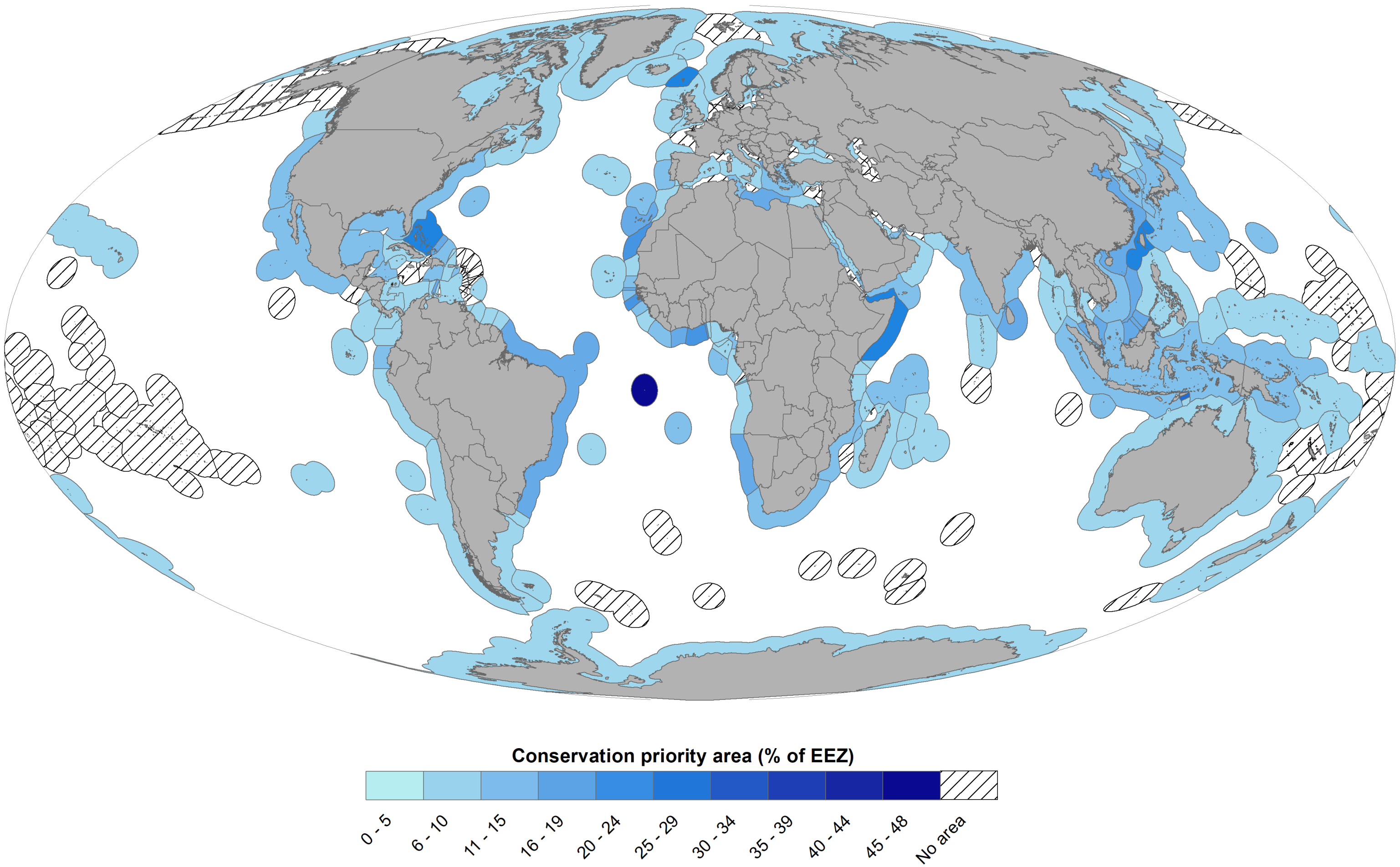

Figure S4.2. Area (% of EEZ) of conservation priorities within Exclusive Economic Zones. Hatched areas contain no conservation priorities.

Table S4.1. Proportion of marine species with 0% (gap), 0–2%, 2–5%, 5–10%, and >10% of their range overlapping with marine protected areas (IUCN I-VI), key biodiversity areas, and marine wilderness areas, for species probability thresholds ranging from 0.25–1.

Aquamaps probability threshold	*Gap (no coverage)*	*Covered 0-2%*	*Covered 2-5%*	*Covered 5-10%*	*Covered >10%*
0.25	0.1%	1.8%	4.0%	11.3%	82.8%
0.5	0.1%	2.0%	4.2%	11.4%	82.2%
0.75	0.2%	2.5%	4.5%	11.7%	81.1%
1	0.1%	1.8%	4.0%	11.3%	82.8%

Table S4.2. Classification of threats based on whether they are ocean-based or land-based (additional information on data layers used can be found in Halpern et al. (2008; 2015).

Threat Category	*Threat*	*Data*
Ocean-based	Fishing & Shipping	Demersal destructive fishing
		Demersal non-destructive fishing (high by-catch)
		Demersal non-destructive fishing (low by-catch)
		Pelagic fishing (high by-catch)
		Pelagic fishing (low by-catch)
		Artisanal Fishing
		Shipping
		Ocean pollution (ship-based)
	Structures	Benthic structures (e.g. oil rigs)
Land-based	Pollution	Organic (pesticide) pollution
		Nutrient (fertilizer) pollution
		Inorganic pollution
		Light Pollution
	Coastal development	Direct human impacts (population density).

Chapter 5

Jones, KR, Maina, JM, Kark, S, McClanahan, TM, Klein, CJ, Beger M. Incorporating feasibility and collaboration into regional management planning for recovery of coral reef fisheries. *Marine Ecology Progress Series*. In review (round 2).

Contributor	Statement of contribution
Jones, KR (Candidate)	Conception and design (70%) Analysis and interpretation (70%) Drafting and production (70%)
Maina, JM	Conception and design (5%) Analysis and interpretation (10%) Drafting and production (5%)
Kark, S	Conception and design (5%) Analysis and interpretation (5%) Drafting and production (5%)
McClanahan, TM	Conception and design (10%) Analysis and interpretation (5%) Drafting and production (5%)
Klein, CJ	Conception and design (5%) Analysis and interpretation (5%) Drafting and production (5%)
Beger, M	Conception and design (5%) Analysis and interpretation (5%) Drafting and production (10%)

Chapter 5 – Incorporating feasibility and collaboration into large-scale planning for regional recovery of coral reef fisheries

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Abstract

Broad-scale overharvesting of fish is one of the major drivers of marine biodiversity loss and poverty, particularly in countries with high dependence on coral reefs. Given the heterogeneity of fishing effort and management success, and the scarcity of management resources, it is necessary to identify broad-scale locations for promoting successful fisheries management and conservation. Here we assessed how fisheries management and conservation priorities in the Western Indian Ocean would change if the objectives were to a) minimize lost fishing opportunity, b) minimize the time for fish biomass to recover, c) avoid locations of low management feasibility based on historical management outcomes, and (d) incorporate international collaboration to optimize the rate for achieving goals. When prioritizing for rapid recovery of fish biomass rather than minimizing lost fishing opportunity, we found priority management zones changed by over 60% in some countries. While this could provide faster recovery of fisheries, it is crucial to consider the impacts of lost fishing opportunity on people in areas where alternative livelihoods are limited, and assess how this may affect compliance with conservation areas and fisheries restrictions. When locations of low management feasibility were avoided, the recovery time of fish biomass across the region increased four-fold. International collaborations prioritized management zones in remote, high biomass, and low fishing pressure reefs and reduced the recovery time of fish five-fold compared to non-collaboration scenarios. Thus, many of these conservation objectives favored wealthy and sparsely populated over poorer and natural resource dependent countries. Consequently, this study shows how prioritization policies, incentives, decisions, and conflicts will produce highly variable outcomes and challenges for sustainability.

Introduction

Coral reef fisheries are harvested beyond sustainable levels in many regions, which is often linked to loss of biodiversity and ecosystem functions (Dulvy et al. 2004; Mora et al. 2011a; McClanahan et al. 2011; Bellwood et al. 2011). Local fishery management, along with reduction of regional and global drivers of degradation, is imperative for recovery of reefs and sustainable fisheries (Hughes et al. 2010; Graham et al. 2013). Prioritizing locations for restrictions on fisheries or marine protected areas (MPAs) that utilizes marine spatial planning methods is expected to improve fisheries and the services provided by marine ecosystems (Fernandes et al. 2005; Gaines et al. 2010). However, planning less frequently considers the outcomes of different priorities, assumptions, incentives, decisions, and consequences of large-scale collaboration histories, instead aiming to minimize the adverse impacts of conservation plans on fisheries (Ban & Klein 2009; Kristian et al. 2015).

While fisheries policies and management actions propose to achieve sustainable fisheries, a lack of clear and scaled metrics of success has led to poor planning in many cases (Worm et al. 2009). One useful metric is reef fish biomass, because it is easily measured and associated with predictable declines in ecological states, processes, and ecosystem services (McClanahan et al. 2011; Pereira et al. 2013; Karr et al. 2015; MacNeil et al. 2015). Therefore, reef biomass is an integrative metric that can be used for setting management objectives with clear ecological thresholds (McClanahan 2018a). For example, in the Western Indian Ocean (WIO), maximum sustainable fisheries yield and ecological health occurs when total reef biomass is between 300-600 kg/ha (McClanahan et al. 2011). Conservation areas, where all ecological processes are maintained, should have biomass ~1150 kg/ha in the WIO (McClanahan et al. 2015). Consequently, biomass thresholds and recovery rates can inform spatial prioritisation objectives (McClanahan et al. 2016).

Increasing agreement and compliance with management plans should be a primary objective when developing sustainable fisheries policies (MacNeil et al. 2015; McClanahan et al. 2016). Therefore, there is a need to consider how socioeconomic and political characteristics influence the likelihood of achieving strong compliance (hereafter referred to as “management feasibility”) (Mascia 2003; McClanahan et al. 2016). The factors influencing management feasibility are diverse, including strength of governance (Ostrom

2007), perceptions of management legitimacy (McClanahan & Abunge 2016), and willingness of management entities to collaborate (Knight et al. 2010). While some maps of feasibility have been developed across a variety of spatial scales (O'Connor et al. 2003; Knight et al. 2010; Mills et al. 2013), it is rarely considered in spatial prioritization (Polasky 2008; Mills et al. 2013). By making feasibility a constraint in spatial prioritization, the risk of inappropriate placement and compliance failures are minimized.

International collaboration is also important in socio-politically complex regions where conflicts occur on borders and management resources are scarce, such as the western Indian Ocean (WIO) (Cordner 2010; Bueger 2013; Kark et al. 2015). Collaboration, when successful, has been shown to substantially reduce the cost and area required for managing terrestrial and marine environments (Kark et al. 2009; Mazor et al. 2013). Management costs and effectiveness vary across the WIO and collaboration has the potential to reduce shared costs to achieve desired outcomes, such as maintaining fish populations. Transboundary conservation has, for example, been identified as a regional priority between Kenya, Tanzania, and Mozambique to reap potential benefits of collaboration (Nairobi Convention 2015).

By explicitly incorporating management feasibility and international collaboration into management objectives, we built on previous spatial prioritizations using fish biomass recovery information (McClanahan et al., 2016). First, we assessed how using fish biomass recovery changed the spatial distribution of fishery management priority zones, compared to the common zoning method of minimizing lost fishing opportunity. Second, we tested the influence of management feasibility on regional management priorities with a feasibility index using measures of fish biomass uncertainty, effectiveness of existing management, and estimates of collaboration potential between WIO countries. Finally, we explored potential socio-politically relevant scenarios of international collaboration to consider how collaboration can improve fish biomass recovery goals.

Methods

The study area covers the mapped coral reefs in the large region of Kenya to South Africa, and east to the Maldives and Chagos. A previous study developed a 2.5 km^2 grid of fish biomass model based on a publicly available map of (Reefs at Risk - http://www.wri.org/our-work/project/reefs-risk) and seven predictor variables and their interactions (McClanahan et al. 2016). Variables were those known to influence the large-scale distributions of fish and included strictness of management, compliance with management, the presence of fishing, distance to markets and market population, and three measures of sea surface temperature (Cinner et al. 2016). Smaller-scale local influences, such as benthic cover and larval connectivity, were not included. Many benthic cover variables have been shown to have a minor influence, only appropriate for fished and small-scale studies, and therefore lacking influence on the 2.5 km^2 scale used and available for mapping at this large scale (McClanahan & Jadot 2017; McClanahan 2018b). Larval connectivity may be important but given that little information is known for this region and our study pools hundreds of species with different reproductive life histories into a single biomass metric, it was also not evaluated. Time-to-recovery maps were developed using fish biomass recovery rates (kg/year) to thresholds for sustainable fishing (450 kg/ha) conservation areas (1150 kg/ha). McClanahan et al. (2011) based these thresholds on the fact that maximum sustained fishing yield in the WIO occurs between 300-600 kg/ha and selected the sustainable fishing threshold as the mid-range estimate for sustainable fishing production (450 kg/ha). They also used a conservation threshold as 1150 kg/ha because below this level is where the first measured changes in ecological processes (e.g. carnivory and herbivory) begin to appear. For full methodological details on fish biomass modeling and biomass thresholds see McClanahan et al. (2016).

Spatial prioritization for reef fishery management

We used the conservation planning software Marxan with Zones (Watts et al. 2009) to identify priority areas for fisheries management. Marxan with Zones uses a simulated annealing algorithm to determine sets of sites that fulfill pre-determined quantitative targets for biodiversity features while minimizing cost, and also allows for the selection of different management zones (Watts et al., 2009), such as conservation zones or sustainable fishing areas. The cost values used in Marxan can reflect actual monetary costs (e.g. land purchase price), or any other value which it is desirable to minimise (e.g. lost fishing opportunity). We used 2.5 km^2 grids as planning units, and used the area of WCMC coral reef distribution (UNEP-WCMC et al. 2010) in each planning unit as a biodiversity feature to be conserved. We explore questions using different planning objectives, but for all objectives we set targets (i.e. proportion of reef in a zone) to include 50% of reef area in sustainable fishing zones and 20% in conservation zones, while accounting for existing high compliance fishery closures (McClanahan et al., 2016). We conducted ten Marxan runs of 100 repetitions for each objective, producing ten 'best solution' outputs for each objective. The 'best solution' output is the reserve system that performs best at reaching its conservation target with minimal cost. To map Marxan results we considered a planning unit to be selected as a conservation or sustainable fishing zone if it was selected in eight of the ten 'best solution' outputs. Using these base methods, we analyzed the following three spatial prioritization objectives, which differ only in the values we use to be minimized by Marxan with zones (see Table S5.1 for a summary of objectives):

Fishing opportunity baseline objective

Our baseline spatial prioritization objective used estimates of artisanal fishing landings as the value to be minimized in Marxan. Minimizing lost fishing opportunity is a common approach in spatial prioritization analyses (Klein et al. 2010; Mazor et al. 2013; Grantham et al. 2013), and we hereafter refer to this objective as the fishing opportunity baseline objective. Fish landing estimates were taken from Halpern et al. (Halpern et al. 2008) which modeled fish landings from national FAO small scale fisheries statistics and is freely available (doi:10.5063/F19Z92TW). These data give approximate annual artisanal fishing catch at a 1-km^2 resolution. As our planning units were 2.5 km^2, we used the average artisanal fishing catch within each planning unit as value to be minimized in Marxan. Because the artisanal fishing data does not cover remote islands and atolls, we assigned planning units without artisanal fishing data the lowest quartile value of artisanal fishing estimates for the region. Therefore, the Marxan with Zones algorithm ensures that conservation and sustainable fisheries zones contain at least 20% and 50% of coral reef in the WIO, respectively, while minimizing the amount of lost opportunity for artisanal fishing due to the placement of management zones.

Time to recovery objective

Our second spatial prioritization objective followed McClanahan et al. (2016), using Marxan to minimize fish biomass recovery time (hereafter the time to recovery objective). Compared to the fishing opportunity baseline objective, this substitutes fish biomass recovery time for artisanal fishing catch as the value to be minimized. Thus, our time to recovery value for the sustainable fishing zone reflects how long it would take for fish biomass to recover to 450 kg/ha. Similarly, the time to recovery value for the conservation zone reflects how long it would take for biomass to recover to 1150 kg/ha.

Management feasibility objective

To examine the impacts of incorporating management feasibility, we used the following equation to create a feasibility score (*F*) that represented the raw time to recovery values used in the fish biomass recovery objective, weighted by a measure of management feasibility (hereafter the management feasibility objective). *F* was used as the value to be minimized in Marxan with Zones and calculated using the following equation (see Figure S5.1 & S5.2 for maps of F values):

$$F_{i\ (i=1 \ldots n)} = T_i(E_i + C_1 + R_i)$$

T_i represents the time to recovery of coral reef in planning unit *i* in years, and *n* is the total number of planning units. *E* represents the percentage of successfully managed MPA's in a country and was taken from Rocliffe et al. (2014) for all countries except Bassas Da India, British Indian Ocean Territory, Glorioso, Ile Europa, Ile Tromelin, and the Maldives, which were assigned *E* from Reefs at Risk Revisited (Burke et al. 2011). These values were then normalized between 0-100 using a fuzzy logic linearly decreasing membership function. *E* was included because new management activities are likely to be more feasible in areas where current management practices are successful.

C represents the potential for collaboration between countries, and was calculated by normalizing country-level collaboration scores from Levin et al. (2018) between 0-100 using a fuzzy logic linearly decreasing membership function and spatially assigning these country scores to planning units. These collaboration scores were derived using linkages between nations based on biodiversity (number of shared species), trade (import/export value between countries), governance (number of shared environmental agreements), and spatial location (geographic relationship) (Levin et al. 2018). We used Theissen polygons (Thiessen 1911) to determine the nearest Exclusive Economic Zone (EEZ) boundary for each planning unit, and assigned planning units the collaboration score for the 2 countries that share boundaries (Figure S3). For example, a planning unit where the closest EEZ boundary is between Kenya and Tanzania would receive the *C* value for Kenya-Tanzania collaboration. Areas of high collaborative potential may be more feasible for management when considering cross-boundary collaboration, especially for reefs located between two countries or territories (Levin et al. 2018).

R_i represents a measure of model over-estimation of fish biomass recovery time for planning unit *i* and is computed from the residuals of the biomass prediction model. To calculate *R*, we used the predicted biomass at upper and lower 95% confidence intervals (CI) from McClanahan et al (2016) to calculate time to recovery. This allowed us to produce optimistic estimates of time to recovery (i.e. from using upper CI) and conservative estimates of time to recovery (i.e. from using lower CI). We then computed *R* as the ratio of conservative time to recovery estimates (lower CI) and optimistic time to recovery estimates (upper CI), from the mean predictions of biomass recovery time (taken from McClanahan et al. 2016). These values were then normalized between 0-100 using a fuzzy logic linearly decreasing membership function. Our feasibility metric penalizes areas where optimistic biomass predictions (upper CI) are further from mean predictions than conservative biomass predictions (lower CI), because modelled fish biomass in these areas is more likely to be overestimated than underestimated. We included variable *R* to penalize areas where biomass overestimation is more likely than underestimation, because if biomass is overestimated the actual time to recovery for that area will be longer than anticipated. In the reverse situation, time to recovery will be under-estimated and management activities will be required for a shorter time than anticipated.

Cross-boundary collaboration scenarios

To investigate the role of cross-boundary collaboration in spatial management prioritization, we allocated planning units to countries or regions using Exclusive Economic Zones (e.g. Kenya, Glorioso Islands). We compared three international collaboration scenarios, *sensu* Kark et al. (2009) and Mazor et al. (2013). These were 1) full collaboration scenario with all countries collaborating; 2) partial collaboration scenario, where countries that are currently part of conservation/environmental management agreements collaborate; and 3) no collaboration scenario where each country acts in isolation. For the partial collaboration scenario we used two groups of collaborating countries: Kenya and Tanzania, who have identified transnational collaboration as a regional priority as per the recent convention of parties (COP8) of the Nairobi convention (Nairobi Convention, 2015), and members of the Indian Ocean Commission (Comoros, Madagascar, Mauritius, Seychelles and La Reunion; Comission de L'ocean Indien 2011).

Comparing prioritization objectives and collaboration scenarios

To compare management priorities under the a) fishing opportunity baseline; b) time to recovery; and c) management feasibility objectives, we calculated the area of sustainable fishing and conservation zones under each objective within each country. We also compared the spatial arrangement of selected areas under each objective. Finally, we calculated the Fleiss' Kappa statistic (Fleiss 1971) to summarize the difference in selection frequency across all planning units, where 1 indicates that the combination of planning units selected is identical under each objective, and 0 indicates that all scenarios are distinct. To examine the role of international collaboration scenarios, we compared the area and spatial arrangement of priority areas in each country with respect to the three levels of collaboration, under both the time to recovery and feasibility objectives.

Results

Comparison of objectives

Management priorities set under the time to recovery and management feasibility objectives differed markedly from the fishing opportunity baseline objective that aimed to minimize lost fishing opportunity within management zones. Conservation zones were 50% larger in the fishing opportunity baseline objective compared to the time to recovery objective, whereas the area of sustainable fishing zones was similar across all objectives (Table 5.1). The time required for fish biomass recovery in conservation zones was 13 times lower under the time to recovery objective than fishing opportunity baseline, with similar reductions seen for sustainable fishing zones (Table 5.1). Average time to recovery increased six-fold for conservation zones under the management feasibility objective compared to the time to recovery objective but sustainable fishing zones had similar biomass recovery times (Table 5.1).

Table 5.1. Average time-to-recovery (T_r) and number of planning units (PU's) selected in conservation and sustainable fishing zones identified under three different prioritization objectives.

	Conservation zones		Sustainable fishing zones	
	T_r (years)	# of PU's selected	T_r (years)	# of PU's selected
Time to recovery objective	0.7	1702	0.5	4574
Management feasibility objective	4.2	3371	0.7	3816
Fishing opportunity baseline	9.4	3436	2.0	4904

When comparing the time to recovery and management feasibility objectives to the lost fishing opportunity baseline objective, the area of management zones within individual countries differed by up to 51% for conservation zones (Figure 5.1a) and 62% for sustainable fishing zones (Figure 5.1b). For example, the Seychelles had 42% more area included in conservation zones under the time to recovery objective compared to the fishing opportunity baseline objective. Conversely, Mozambique had 15% less area included in sustainable fishing zones under the time to recovery objective compared to the fishing opportunity baseline objective (Figure 5.1b). These results reflect the fact that Seychelles has high fish biomass levels and is thus a high priority under the time to recovery objective, whereas fish biomass in Mozambique is much lower due to high levels of fishing. Incorporating management feasibility also resulted in considerable differences with the time to recovery objective. For example, Madagascar had 15% more reef area included in sustainable fishing zones under the management feasibility objective compared to the time to recovery objective, while Tanzania had 18% less (Figure 5.1b). A number of countries showed very small differences between all objectives, such as Kenya and Mauritius (Figure 5.1a & 5.1b).

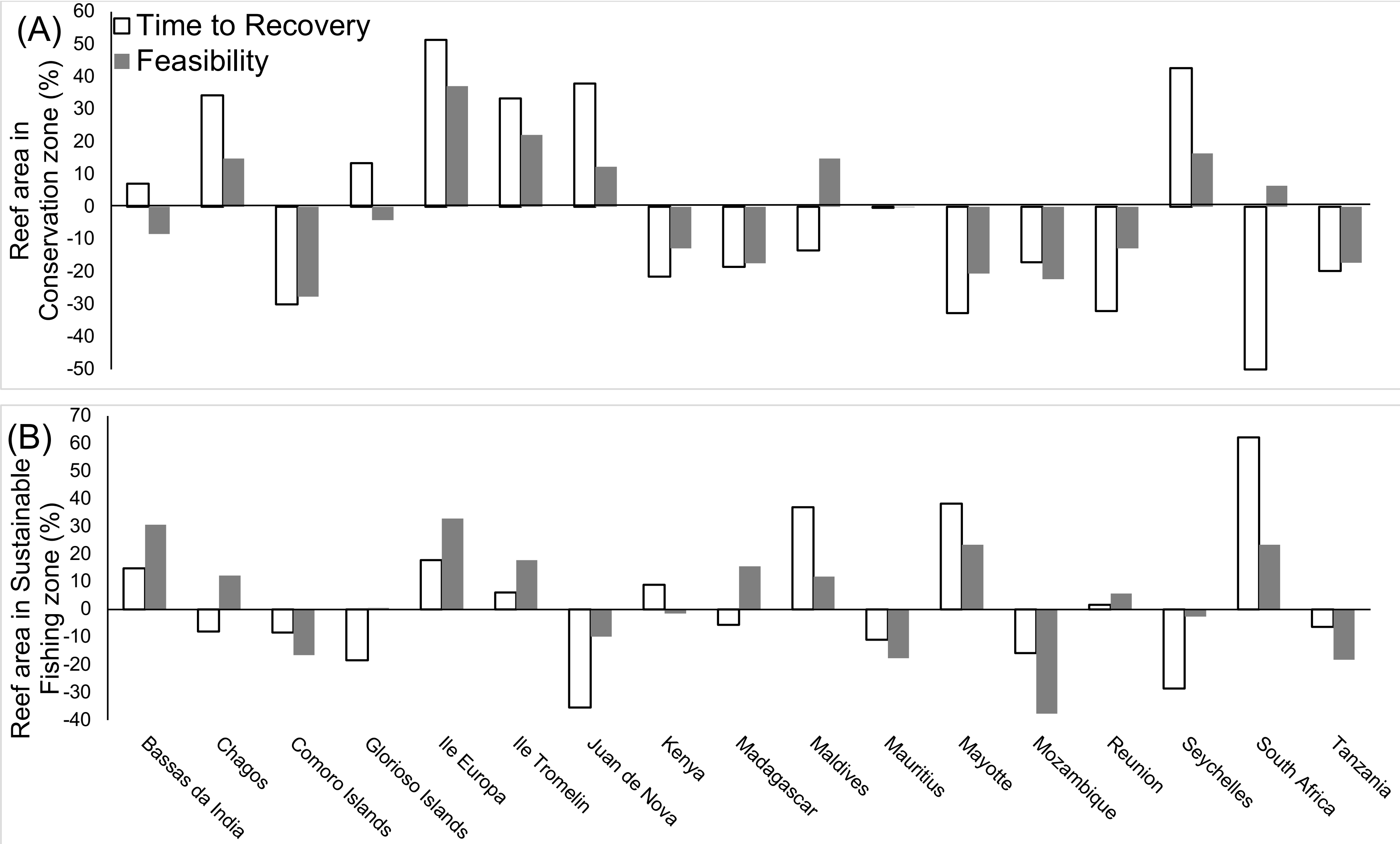

Figure 5.1. Average difference from fishing opportunity baseline objective, expressed as reef area included in conservation and sustainable fishing zones, for priorities identified under the time to recovery objective (white) and the management feasibility objective (grey): (A) Difference from fishing opportunity baseline objective for conservation zones, (B) Difference from fishing opportunity baseline objective for sustainable fishing zones. Conservation zones and sustainable fishing zones contain 20% and 50% of total WIO reef area, respectively. Values are the average of ten “best solution” outputs from Marxan with Zones

Broad priority areas for management zones remained similar under both the time to recovery and management feasibility objectives, with conservation priorities concentrated in the Seychelles, Maldives and Chagos (Figure 5.2). However, there were differences within countries for both the spatial arrangement and total area of management zones (Figure 5.3). For example, reefs in the central Maldives were assigned a much higher priority under the time to recovery objective, whereas reefs in the north and south were high priorities under the management feasibility objective. Some areas of Northern Madagascar became more important under the time to recovery objective (Figure 5.3), despite Madagascar overall having 21% less reef area in sustainable fishing zones under this objective. Similar spatial differences were seen between the time to recovery objective and the fishing opportunity baseline, and between the management feasibility objective and the fishing opportunity baseline (Figure S5.4, S5.5). When comparing across all objectives, the Fleiss' Kappa statistic was 0.25 and 0.47 for sustainable fishing and conservation zones respectively, indicating a low level of similarity between objectives (Table S5.2).

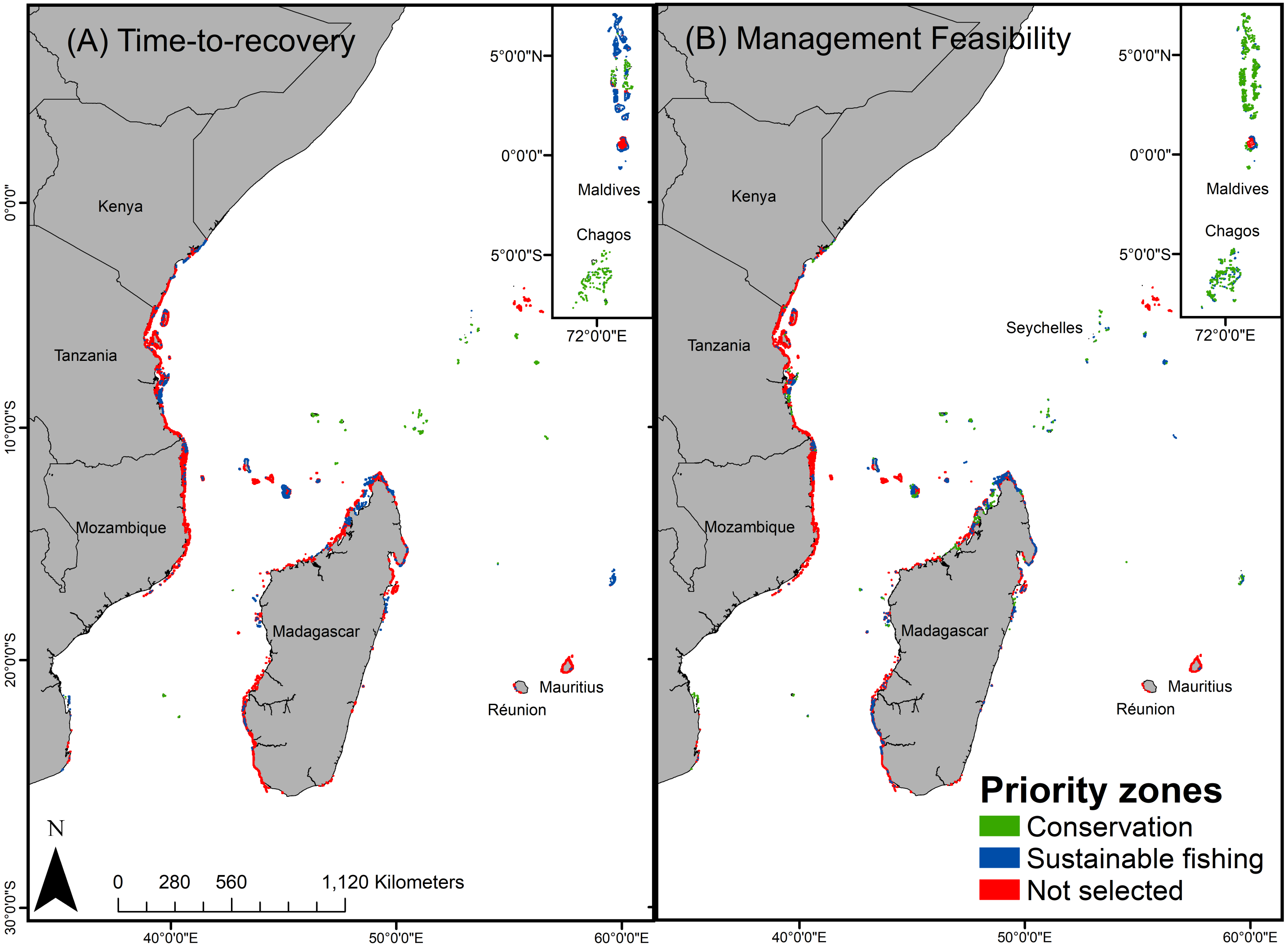

Figure 5.2. Priority areas (selected in >80% of Marxan with Zones runs) for conservation and sustainable fishing zones, from 10 "best solution" Marxan with Zones outputs: (A) Priorities identified to minimize the time required for fish biomass recovery to sustainable fishing (450 kg/ha) and conservation (1150 kg/ha) thresholds (time to recovery objective). (B) Priorities identified to minimize time to recovery and avoid areas of low management feasibility (management feasibility objective). Each scenario contains 20% of total reef area as conservation zones, and 50% as sustainable fishing zones.

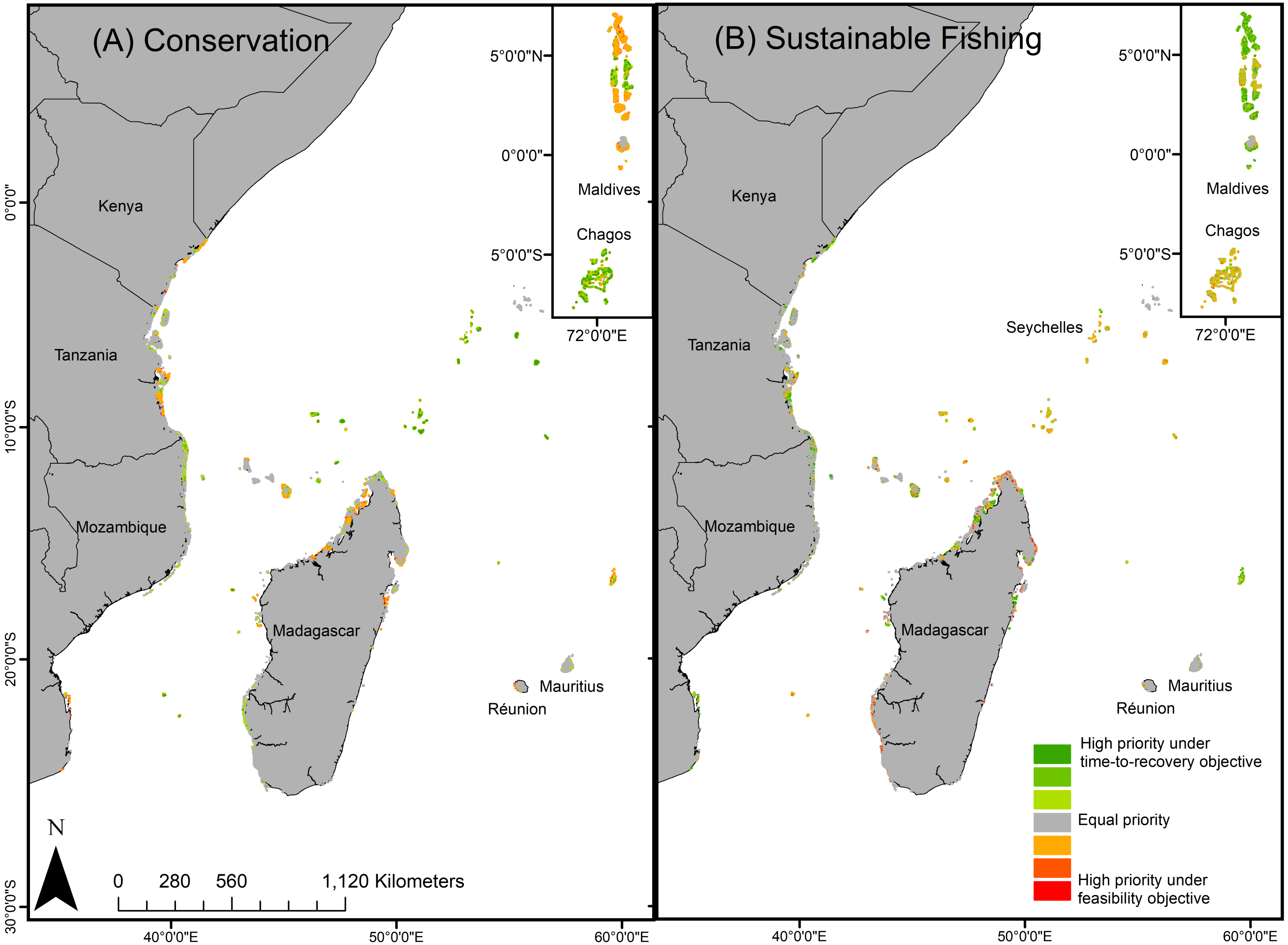

Figure 5.3. Difference in planning unit selection frequency for A) Conservation zones, and B) Sustainable fishing zones under time to recovery and management feasibility objectives. Planning units are grey if they had equal selection frequencies under both objectives.

Cross-boundary collaboration priorities

Cross-boundary collaboration reduced overall time to recovery and the area of management zones, by redistributing management priorities toward island nations with high fish biomass, such as the Seychelles and Chagos. Results were very similar under both time to recovery and management feasibility objectives, so here we report on the results of the time to recovery objective. Under a no collaboration scenario the time required for fish biomass recovery was increased 5.4 times in conservation zones, and 3.4 times in sustainable fishing zones, compared to the full collaboration scenario (Table 5.2). The partial collaboration scenario reduced recovery time by 37% in conservation zones, and over 150% for sustainable fishing zones (Table 5.2). A full collaboration scenario also required around 21% less area for conservation zones, and 38% less for sustainable fishing zones, compared to a scenario without collaboration (Table 5.2).

Table 5.2. Average time-to-recovery (T_r) and number of planning units (PU's) selected in conservation and sustainable fishing zones identified under three different scenarios of international collaboration.

	Conservation zones		Sustainable fishing zones	
	T_r (years)	# of PU's selected	T_r (years)	# of PU's selected
Full Collaboration	0.7	1702	0.5	4574
Partial Collaboration	2.4	1632	0.7	4468
No Collaboration	3.8	2128	1.7	7267

Collaboration substantially changed the location of management priorities, concentrating priorities in remote locations with high fish biomass (Figure 5.4). For example, Chagos had 62% of its reef contained in conservation zones under a full collaboration scenario, but only 24% under a partial collaboration scenario (Figure 5.4b). Conversely, Reunion island had only 13% of its reef contained in sustainable fishing zones under full collaboration, but this rose to 51% under the no collaboration scenarios (Figure 5.4a). In some nations, the effect of collaboration had contrasting effects for conservation zones and sustainable fishing zones. The Seychelles contained around 30% more reef in conservation zones under both collaboration scenarios, but around 20% less reef within sustainable fishing zones (Figure 5.4).

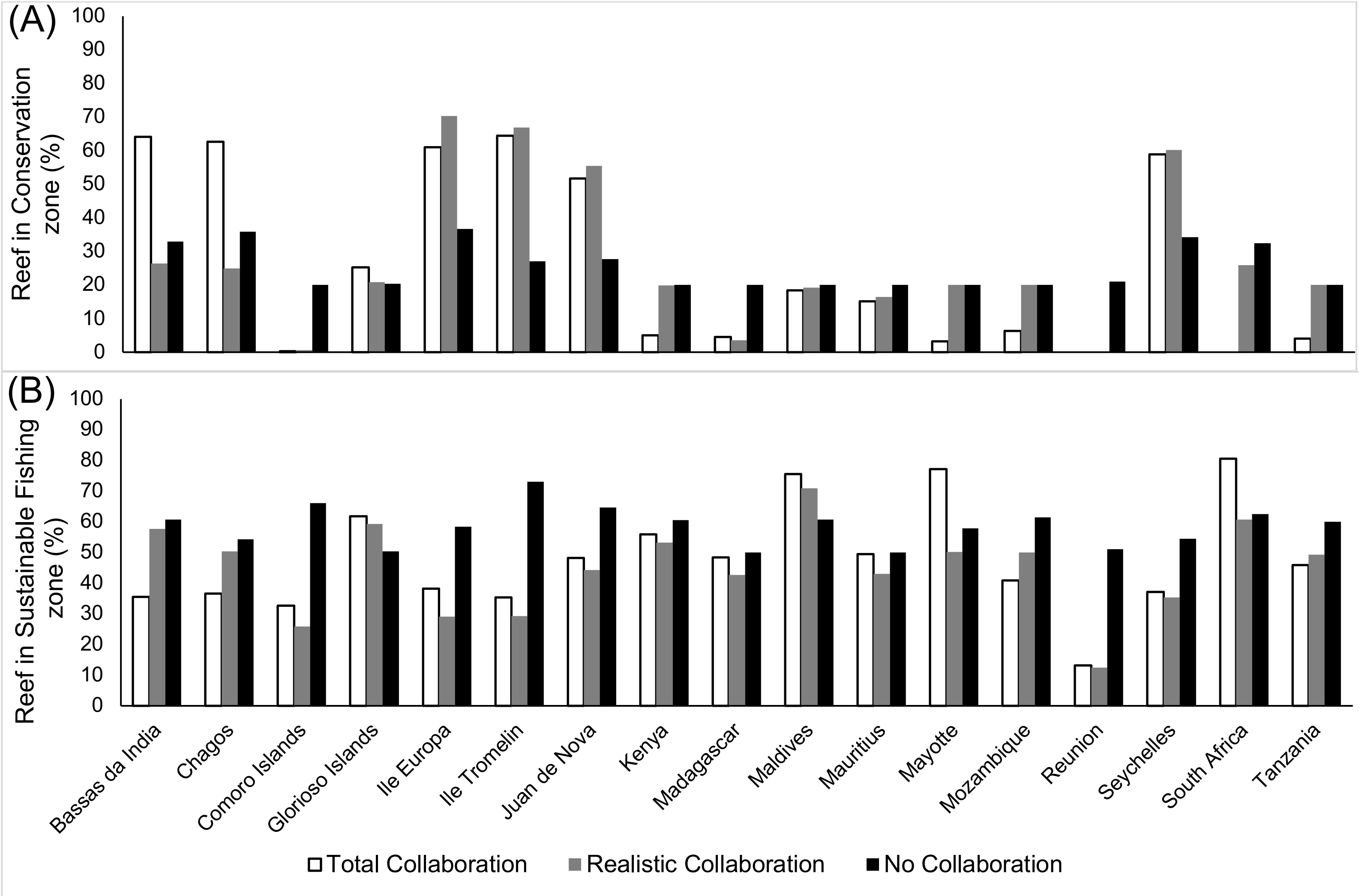

Figure 5.4. Percentage of reef of each country contained in priority areas identified under 3 international collaboration scenarios, under time to recovery objective. (A) Percentage of reef in each country contained in conservation zones: (B) Percentage of reef in each country contained in sustinable fishing zones. Values are the average of ten “best solution” outputs from Marxan.

Discussion

Incorporating management feasibility and fish biomass recovery into spatial prioritization considerably changed the spatial arrangement of priority locations compared to the baseline where lost fishing opportunity was the main consideration. Furthermore, the time required for fish biomass to recover increased substantially when avoiding zoning locations of low management feasibility. These increases were attributable to management zones being shifted from infeasible high biomass reefs to lower biomass areas with greater feasibility. Consequently, incorporating management feasibility into spatial prioritizations can help avoid spending resources where effective management seems unlikely (Mills et al. 2013). Clearly, managing fisheries for socio-economic goals such as food and income is important, but conservation may be challenged and expensive if feasibility is not addressed first (Hicks 2011; McClanahan & Abunge 2016).

Fishery closures or MPA's often face considerable opposition from fishers, and the imposition of MPA's or other fishery management policies, such as gear restrictions, catch quotas, is unlikely to succeed without broad consensus and community support (Jameson et al. 2002; Beger et al. 2004; McClanahan et al. 2005; FAO 2006; Kamat 2014). Providing information on the length of time required for management to meet demonstrable ecological targets and incorporating fish biomass recovery into management planning should increase knowledge and gain support from stakeholders. Where many people are highly dependent on coral reefs for food and income, such as the WIO (Donner & Potere 2007), stakeholder perceptions and participation are critical to avoiding compliance failures. (Graham et al. 2007; McClanahan 2010; Levy 2010).

International collaborations decrease costs of conservation and fishery management efforts but result in management zones being asymmetrically distributed (Table 5.2, Figure 5.4). Fully collaborative conservation plans lead to some countries being exempt from conservation zones (e.g. South Africa, Reunion), while others face additional management responsibilities (e.g. Seychelles). As such, the efficiencies gained by collaboration must be balanced with social equity considerations (Kark et al. 2009, 2015; Halpern et al. 2013a). Other spatial prioritization analyses come to similar conclusions for the WIO (Maina et al. 2015; McClanahan et al. 2016) and other marine regions (Kark et al. 2009; Mazor et al. 2013; Beger et al. 2015). Consequently, any gains achieved through regional collaboration will also need to balance considerations of sharing costs and responsibilities equitably.

Among the many considerations of collaborative natural resource management are the broader suite of economic, political and social barriers that influence implementation decisions (Sandwith et al. 2001).

The prioritization approach used here favors protecting high-biomass areas, which essentially triages low biomass sites. Protecting high biomass is one of a number of goals of management and therefore alternative and possibly a portfolio of goals and zoning approaches should be considered. For example, McClanahan et al. (2016) proposed prioritizing the recovery of severely degraded and the surrounding reefs. Another approach not considered here is to consider larval dispersal in spatial prioritizations to promote population recovery and persistence (Beger et al. 2010, 2015; Álvarez-Romero et al. 2017; Krueck et al. 2017; Magris et al. 2018). Depending on spatial scales, future work should consider using larval dispersal models (Treml et al. 2008; Kool et al. 2011) or genetic measures (Selkoe & Toonen 2011; Beger et al. 2014) to represent the larval connectivity within MPA networks. Given the empirical needs and computation complexity of larval dispersal information, some simpler approaches are needed to inform MPA placement (e.g. minimize distance between MPAs and fishing grounds, Krueck et a. 2017). Including the costs of various management options, such as fisheries closures versus gear restrictions, has also been shown to substantially alter management priorities (Ban et al. 2011; McGowan et al. 2018). Furthermore, while total fish biomass is a useful holistic metric of reef function, it does not consider the different recovery rates of fish that are important for recovery of reef function (MacNeil et al. 2015; Martin et al. 2017). Consequently, future research priorities should be to 1) combine spatial prioritization approaches to identify areas that overlap under multiple objectives (Allnutt et al. 2012), and 2) consider differential recovery rates and ecological functions of fish (McClanahan et al. 2015).

The data and estimates of management feasibility used here have a number of limitations. Firstly, we use only one conservation feature – the area of coral reef per planning unit. While unlikely to change our main conclusions, incorporating better data on species distributions or biogeographical habitats, along with other conservation objectives (e.g. achieving representation) would likely alter the location of management priorities (Allnutt et al. 2012). Secondly, while our analyses were conducted at a broad spatial scale, the size of fisheries closures in the WIO is relatively small and compliance in these closures is mainly a local scale issue. Local scale studies which build upon our analysis could add important nuance to fisheries management plans. Thirdly, the management feasibility metric used here is dependent on national-level data and could be improved by incorporating more local scale assessments. Management feasibility is influenced by several factors not captured in our metric, including human values and perceptions, as well as economic, ecological and technical issues (Salomon et al. 2011; Pascoe et al. 2014; McClanahan & Abunge 2016). Future studies should also consider the ability of local authorities to effectively enforce fishery closures, and the existence and competency of interacting governance networks (Nagendra & Ostrom 2012; Morrison 2017). Finally, perceptions of fishing restrictions and potential willingness to comply with regulations is known to vary considerably within and between WIO countries (Daw et al. 2012; McClanahan & Abunge 2016). Data on the perception of fishing restrictions by local communities could be used to assess the likelihood of compliance with fisheries closures/restrictions, thereby improving future management feasibility metrics.

There are also a number of limitations with the artisanal fishing data used in the fishing opportunity baseline objective, although they are the only high-resolution artisanal fishing data available across the entire WIO. These data use coastal population and distance-to-land to spatially model the small-scale distribution of national scale catches (Halpern et al. 2008) This likely overestimates fishing catch on reefs near populated coastal ports, especially when fish landings at these ports reflect fishing effort from a large surrounding area. While artisanal fishing is notoriously difficult to estimate (Zeller et al. 2006; Halpern et al. 2008), incorporating local-scale data on landings at specific ports would help to avoid overestimation around densely populated areas. Furthermore, the artisanal fishing data does not discern between fisheries (e.g. reef fisheries, pelagic/offshore fisheries), and so reef fishing pressure is likely overestimated in places where fishers often target pelagic species such as the Maldives (Hemmings et al. 2014). This will unduly reduce their selection by the Marxan with Zones objective function aiming to minimize cost. Consequently, incorporating data on catches of specific fish taxa (e.g. Watson 2017) could refine estimates of artisanal fishing to ensure they capture reef fishing effort specifically.

This study demonstrates how incorporating fish biomass recovery, management feasibility and international collaboration affects fishery management priorities in the WIO - favoring remote and lightly fished regions. We also show that incorporating management feasibility redistributes priorities to wealthier nations or those with histories of more effective management. Both outcomes result in an uneven distribution of management priorities and may further burden people in poorer countries where effective fishery management is badly needed to promote food security. It is clear that for spatial prioritization analyses to be useful and incorporated into decision making, many possible values, incentives, scenarios, and metrics must be considered (Allnut et al. 2012; McClanahan et al. 2016).

Acknowledgements

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Supplementary Material

Table S5.1. Targets for sustainable fishing and conservation zones, and cost values used in spatial prioritization analysis objectives.

Objective Name	*Sustainable Fishing Target*	*Conservation Target*	*Values to be minimized in Marxan with Zones*	*Data sources*
a) Lost fishing opportunity baseline objective	50% of reef area	20% of reef area	Artisanal fish landings	Halpern et al. (2015)
b) Time to recovery objective	50% of reef area	20% of reef area	Fish biomass recovery time	McClanahan et al. (2016)
c) Feasibility objective	50% of reef area	20% of reef area	Fish biomass recovery values, modified using management feasibility equation	McClanahan et al. (2016); Levin et al. (2018); Rocliffe et al. (2014); Burke et al. (2011)

Table S5.2. Fleiss' kappa (*K*) values comparing selection frequency of planning units across the fishing opportunity baseline, time to recovery and management feasibility objectives, for each management zone. A value of 1 indicates that the combination of planning units selected is identical under each objective, and 0 indicates that all scenarios are distinct.

Management Zone	***K***
Sustainable Fishing	0.253
Conservation	0.476
Not Selected	0.402

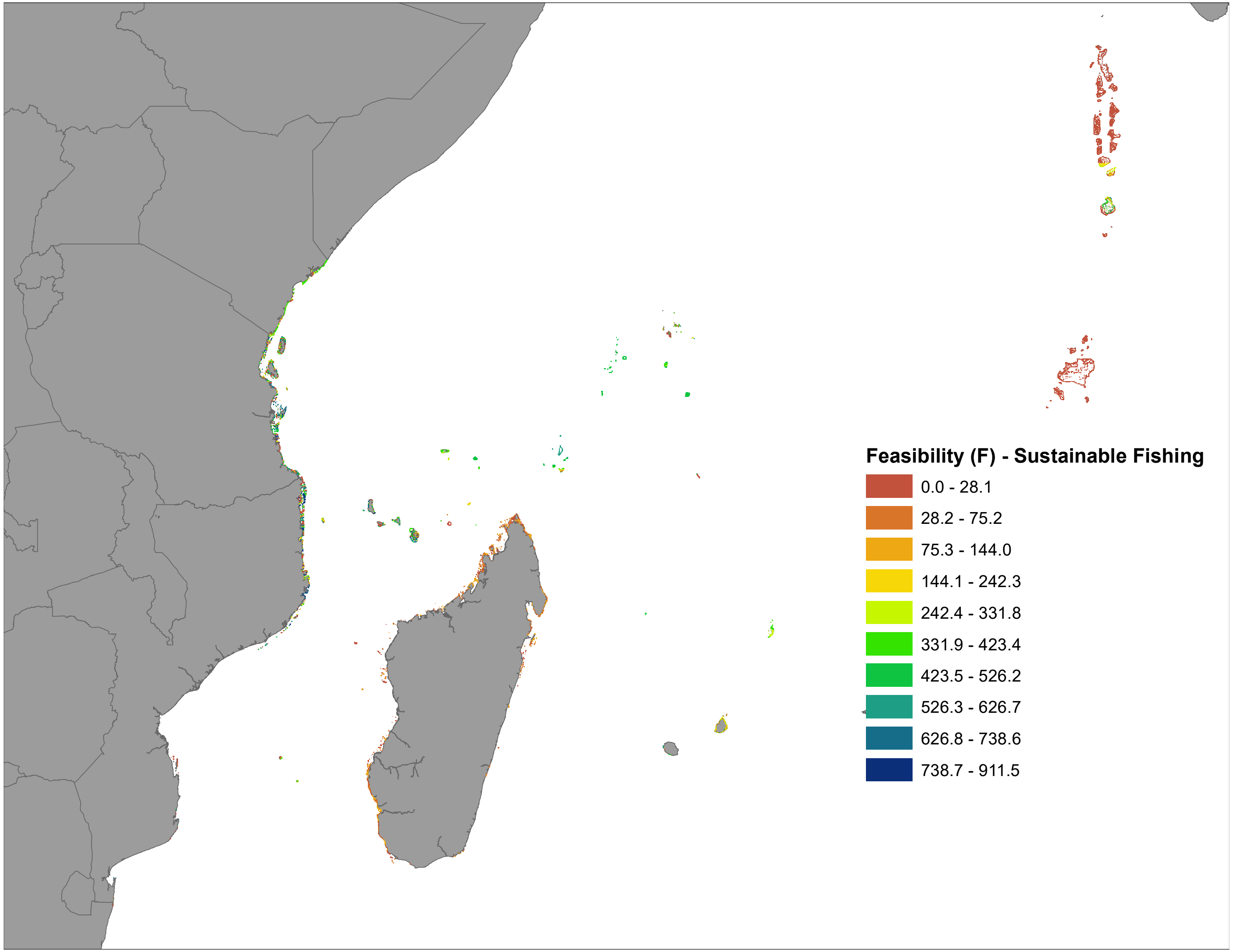

Figure S5.1. Management feasibility (F) values per planning unit for sustainable fishing zones. These values were minimized in Marxan with Zones analysis.

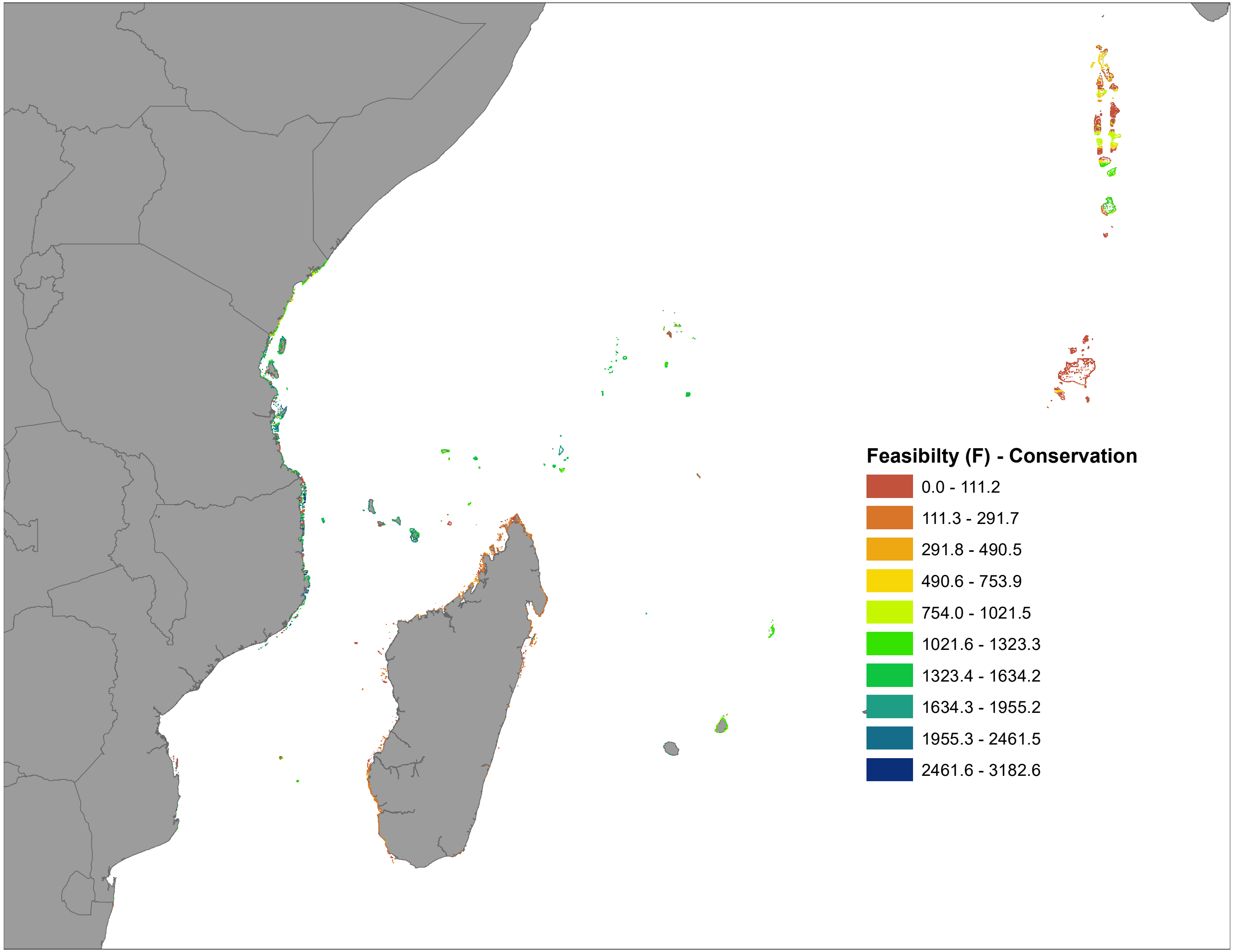

Figure S5.2. Management feasibility (F) values per planning unit for conservation zones. These values were minimized in Marxan with Zones analysis.

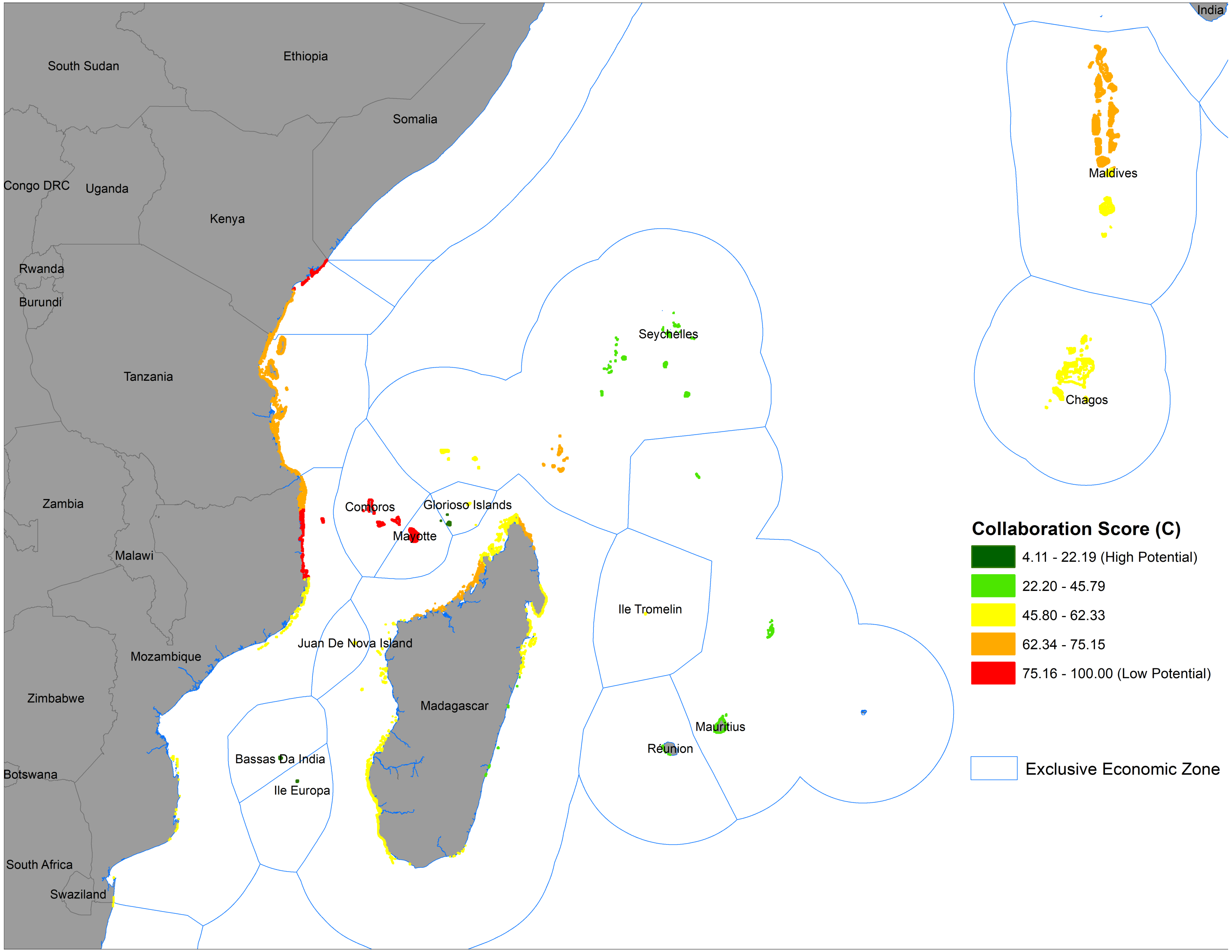

Figure S5.3. Collaboration Score (C) values per planning unit, as used in management feasibility calculations. Raw values were taken from Levin et al (2018) and rescaled between 0-100 using a fuzzy logic linearly decreasing membership function. Low values represent greater collaboration potential.

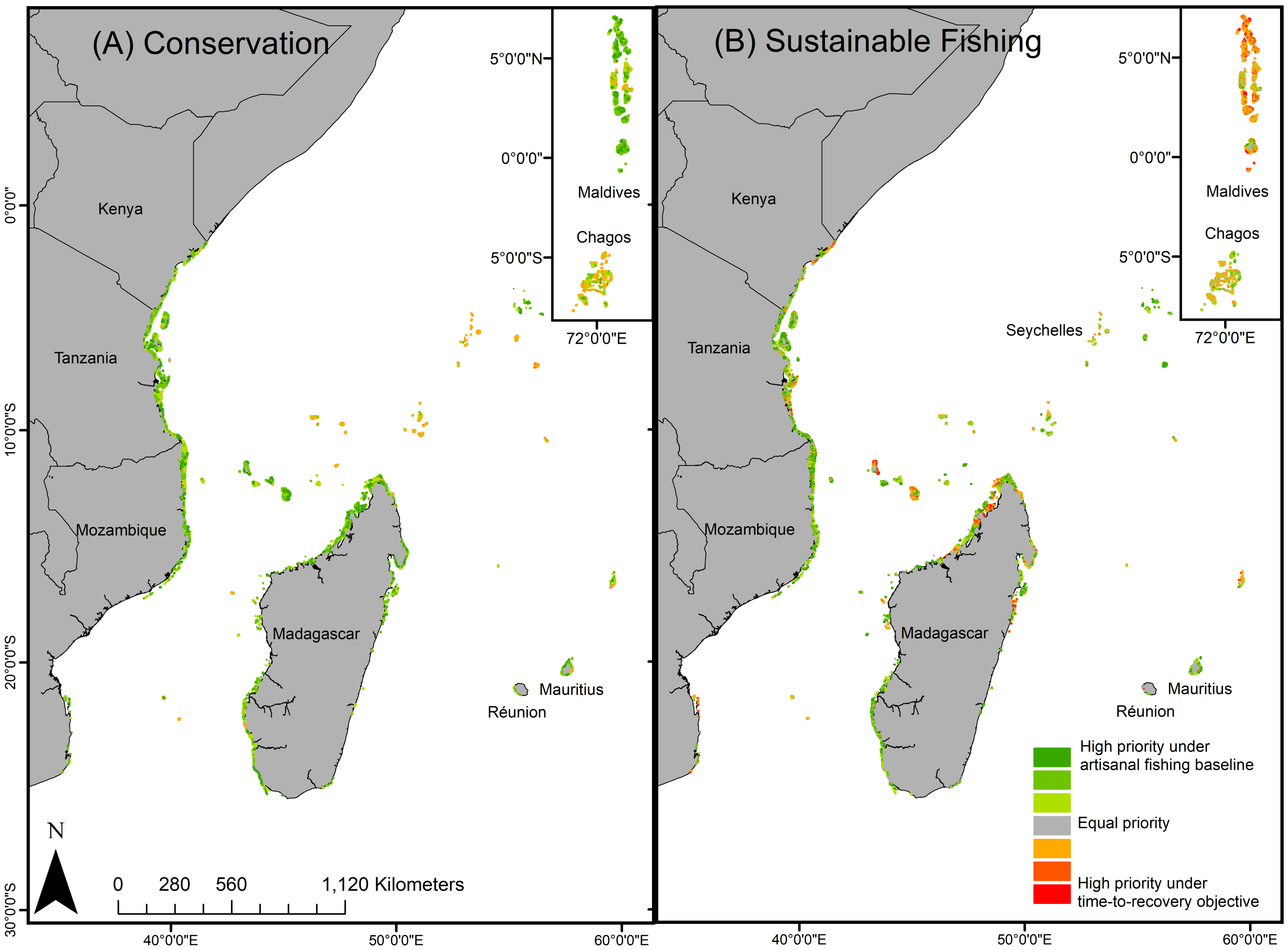

Figure S5.4. Difference in planning unit selection frequency for A) Conservation zones, and B) Sustainable fishing zones under the fishing opportunity baseline and time to recovery objectives, from 10 'best solution' Marxan with Zones outputs. Planning units are grey if they had equal selection frequencies under both objectives.

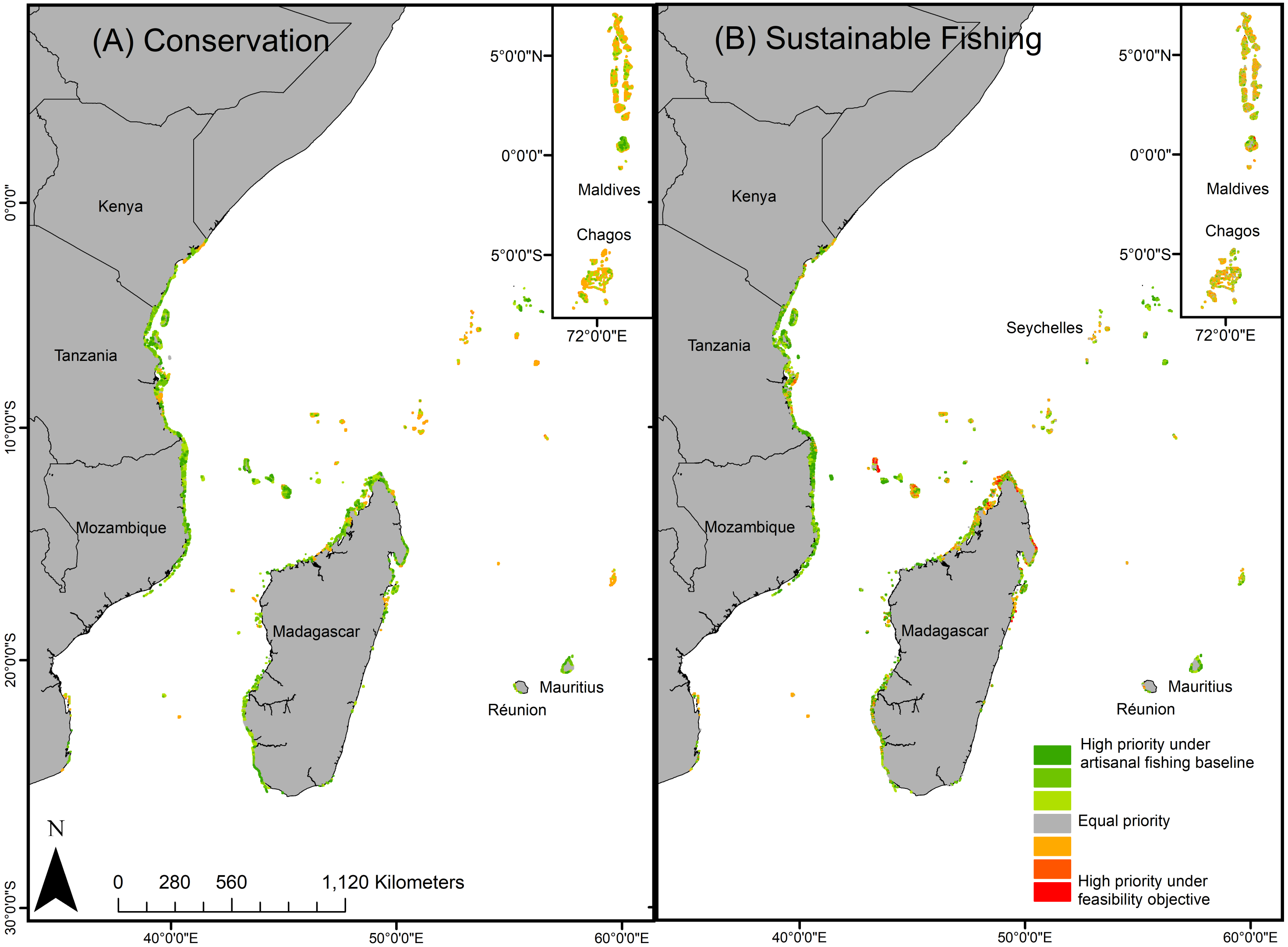

Figure S5.5. Difference in planning unit selection frequency for A) Conservation zones, and B) Sustainable fishing zones under the fishing opportunity baseline and feasibility objectives, from 10 'best solution' Marxan with Zones outputs. Planning units are grey if they had equal selection frequencies under both objectives.

Chapter 6 – Conclusions

This thesis tackles a broad array of conservation issues in the marine realm but can summarised by one major question: how can we best conserve marine biodiversity in the face of various threatening human activities including ocean-based threats (e.g. overharvesting, shipping), land-based threats (e.g. nutrient runoff), and anthropogenic climate change? I have developed new tools and techniques that make significant progress towards answering this question, and summarise them here. Further, I discuss some of the key limitations to my research and identify future research directions which could substantially improve marine conservation practice and policy.

Marine conservation and climate change

The impacts that anthropogenic climate change will have, and is already having, on biodiversity are becoming increasingly well known (Walther et al. 2002; Parmesan & Yohe 2003; Brander 2007; Brierley & Kingsford 2009; Hughes et al. 2017). In response, the conservation science community has developed an increasing number of methodologies for spatially prioritising conservation action to help preserve biodiversity in the face of climate change.

In **Chapter 2**, I presented the first systematic review of published spatial conservation prioritisation approaches that incorporate climate change. I discovered that the vast majority (89%) of approaches utilise forecasts of species distributions under various climate change scenarios to either identify future species habitat (52%), or to identify refugia which shelter species from climate change (37%). I found very few approaches which attempt to incorporate human responses to climate change, or discrete (one-off) impacts, such as coral bleaching or extreme weather events.

Chapter 2 showed that the main limitation with incorporating climate change into spatial conservation prioritisation had to do with uncertainty, which comes in two basic forms – (i) predicting how the climate will change; and, (ii) uncertainty in predicting how all species (including humans) will respond to this change. It is thought that uncertainty in climate predictions can be reduced by combining a variety of climate models and future emissions scenarios (an ‘ensemble’ approach), but **chapter 2** showed that less than half of all spatial prioritisation studies made any attempt to deal with uncertainties in climate modelling. Uncertainty in predicting how species will respond to climate change is even harder to deal with, as most species distribution models rely on uncertain assumptions about species biology, ignoring key ecological processes and interactions which determine species distributions (Kearney & Porter 2009). Predicting how humans will respond to climate change is even more difficult again, and very few tools exist to do so, despite the fact that this is likely to be the biggest climate change impact that species will have to deal with (Appendix 1 - Maxwell et al. 2015b). Given the severe uncertainty plaguing predictive approaches to conservation planning when we consider climate change that I found in this review, **chapters 3 & 5** of this thesis tackled the issue of climate change using a more pragmatic approach, one which does not rely on uncertain climate predictions. These chapters focus on strategies that will always strengthen current conservation actions, and will therefore have positive benefits to biodiversity in the face of future climate change, regardless of how it emerges.

By mapping global and realm-specific marine wilderness areas, all of which have a very high relative resilience to climate change due to their high genetic diversity and intact nature, **chapter 3** identifies opportunities for wilderness conservation which can help biodiversity persist in the face of climate change. However, it is important to consider the limitations of this approach**.** Most importantly, including climate change impacts to date in the individual stressor analysis of **chapter 3** resulted in almost no wilderness areas remaining. This is an important caveat as it is clear that climate change is already significantly impacting marine biodiversity, causing species range shifts (Parmesan & Yohe 2003; Pinsky & Fogarty 2012), catastrophic coral bleaching events (Hoegh-Guldberg 1999), and even preventing calcifying organisms from producing shells (Fabry et al. 2008). As such, the results of **chapter 3** must be interpreted with the caveat that wilderness areas are already being impacted by climate change, and indeed some wilderness areas may have already undergone catastrophic climate-driven events such as coral bleaching. Future studies should assess the exposure and vulnerability of wilderness to climate change and species’ response to this, so as to identify those areas which are likely to be climate refugia and also those areas which will be highly impacted.

To preserve the full range of biodiversity in the face of climate change, it is also crucial that wilderness conservation is combined with approaches that protect highly threatened species (see **chapter 4**), and approaches which attempt to plan for species responses to climate change. While wilderness areas may be resilient to climate change, and their identification does not rely on uncertain climate and species distribution models, they are not guaranteed to retain historical assemblages of biodiversity (Stein et al. 2014), and may not be useful for rare or range-restricted species which do not occur in wilderness. As such, **chapter 3** does not aim to identify priorities for wilderness conservation, but instead suggests that the importance of wilderness be recognised in global and national strategies for biodiversity conservation, and that targets for wilderness conservation be added to global conservation agreements.

Facilitating ecosystem recovery

Given the widespread nature of human impacts to the ocean, and the massive losses of marine wilderness (especially in coastal ecosystems) documented by **chapter 3**, it is clear that preserving marine biodiversity will also require recovery and restoration of degraded ecosystems. In **chapter 5** I presented a regional case study which identified conservation priorities to facilitate rapid recovery of degraded coral reef ecosystems in the Western Indian Ocean. This study found that using fish biomass recovery rates in spatial prioritisation can substantially reduce the time needed for reef fish stocks to recover to fish biomass thresholds where ecological processes and species diversity are maintained. Further, we showed that incorporating data on the feasibility of management actions (MPAs in this case) into the spatial prioritisation process can reduce the likelihood of conservation actions occurring in places where they are likely to fail.

In an era of widespread biodiversity declines and shifting baselines, especially in heavily exploited ecosystems such as coral reefs, facilitating ecosystem recovery will be a crucial goal. This can be done through active restoration efforts, such as planting seagrass or seeding coral reef "seeding", or through passive restoration efforts, where stressors inhibiting natural ecosystem recovery are removed (Bayraktarov et al. 2016). Recent studies have shown that over 80% of currently fished reefs are missing at least half of the fish biomass that would be expected without fishing, leading to severe consequences for key ecosystem functions such as predation (MacNeil et al. 2015). This means that, at least for many coral reef ecosystems, fisheries restrictions and MPAs can lead to recovery and maintenance of key ecosystem functions without the need for expensive active restoration efforts. It is also vital to consider the spillover of fish from an MPA to the surrounding waters which may be heavily fished. With no spillover the surrounding fishery will receive no benefit as fish are not leaving the MPA, and with full spillover there is effectively no MPA as all fish leave the MPA and can then be harvested. Previous studies have shown that MPAs are most beneficial in terms of spillover when the fisheries surrounding them are poorly managed (Buxton et al. 2014), which is the case in much of the world, especially in developing regions where dependence on natural resources is high. However, it is also important to note that intense human impacts in the seascape surrounding MPAs diminishes their effectiveness at sustaining reef fish biomass and the presence of top predators, even where compliance is high (Cinner et al. 2018). Therefore, while facilitating ecosystem recovery is crucial in highly impacted areas, it is also vitally important to maintain areas of low human impact (e.g. the wilderness areas mapped in **chapter 3**).

Facilitating ecosystem recovery will not only lead to recovery and maintenance of key ecosystem functions, it is likely to also increase the resilience of ecosystems to climate change. Degradation due to local stressors such as overfishing has been shown to reduce coral reef resilience to acute stressors (e.g. thermal stress; Hughes et al. 2007; Carilli et al. 2009b; Mumby & Harborne 2010). As such, facilitating recovery of coral reef habitat may increase the likelihood that these ecosystems survive the impacts of climate change, and will also deliver biodiversity conservation benefits regardless. However, by aiming to minimise fish biomass recovery time, this approach essentially triages the most degraded reefs, as they have low fish biomass and thus long recovery times. In places like the Western Indian Ocean, where there is high dependence on reefs for food and income, this is unlikely to be practical. Future research should assess spatial variation in fish biomass recovery rates under fishery regulations other than strict MPAs, such as gear restrictions or catch quotas, as these kinds of regulations may be more socio-politically feasible (McClanahan & Abunge 2016). While fish biomass recovery rates under various fishery management regulations are fairly well understood (McClanahan et al. 2007; Abesamis et al. 2014; MacNeil et al. 2015), there is little research examining the spatial variation in fish recovery (e.g. McClanahan et al. 2016).

A limitation in **chapter 5** is its use of fish biomass as a proxy for reef condition. By doing so, it does not account for the considerable diversity of demographic and life-history strategies that make up reef fish communities. A more nuanced approach could consider separate fish functional groups (herbivores, top predators etc.), as they likely have different recovery rates and biomass thresholds at which the ecological processes they provide are affected. Fisheries regulations could then be tailored to prevent decline of certain functional groups or endangered species, while still allowing for harvest of others. Furthermore, the data I used to represent fishing effort across the region is very coarse and misses important local details. For example, the Maldives has high population densities and low travel times to markets, which would normally suggest significant fishing pressure on reefs. However, most fish catch in the Maldives comes from pole and line fishing targeting offshore tuna resources, thereby reducing fishing pressure on reefs (Hemmings et al. 2014). Using more detailed data on fishing activity at the national or sub-national scale would allow for more nuanced predictions of fish biomass recovery, and would likely increase the socio-political feasibility of the resulting conservation priorities. This may be possible in moor data-rich regions such as the main Hawaiian islands. It will also be extremely useful to assess how selecting multiple small areas as fisheries reserves compares to fewer large reserves in terms of management feasibility.

Implications for international marine conservation policy

Despite the development of numerous international conservation agreements, such as the Convention on Biological Diversity (Convention on Biological Diversity (CBD) 2014), and massive recent expansion of the global protected area estate (UNEP-WCMC & IUCN 2017), biodiversity remains in crisis, with endangered species and intact habitat being lost at rapid rates (McCauley et al. 2015; Watson et al. 2016b). Even if fully achieved by 2020, current commitments potentially leave 90% of the ocean and 83% of land not effectively conserved. As such, there is a strong scientific basis for substantially increasing the scope of global conservation agreements to avoid widespread biodiversity declines and maintain ecosystem services (Noss et al. 2012; Larsen et al. 2015; Wilson 2016; O'Leary et al. 2016; Dinerstein et al. 2017; Watson & Venter 2017; Maron et al. 2018). These agreements must be multi-faceted, focusing not only on securing imperiled biodiversity, but also on facilitating recovery of degraded ecosystems and preserving large intact land/seascapes. Looking across the chapters of this thesis highlights some important conclusions that can help inform the development of the post 2020 conservation agenda.

High seas conservation

One of the most important conclusions emerging from this thesis as a whole, and a clear gap in current global conservation agreements, is the need to develop, prioritise and implement conservation actions in areas of the ocean that are beyond national jurisdiction (hereafter "high seas"). **Chapter 3** showed that most remaining marine wilderness areas are located in the high seas, and **chapter 4** found that 43% of conservation priority areas for representing marine biodiversity are found in the high seas. Conservation action in these areas is legally challenging given the obvious jurisdictional issues, and has so far been limited, with only 1.18% of the high seas protected (UNEP-WCMC & IUCN 2018b). Increasing the level of protection across the high seas must now become a key part of any future conservation agenda that is focussed on the retention of biodiversity across the high seas, especially as technological advances drive human actions further and deeper into the ocean (Ramirez-Llodra et al. 2011; Mengerink et al. 2014). The need for improved high-seas management is now being recognised by the international community, with the UN currently negotiating the "Paris Agreement for the Ocean" – a legally-binding high seas conservation treaty to be established under the existing Law of the Sea Convention (United Nations General Assembly 2017), so the time for big thinking and big action is ripe.

While the increased designation of high seas MPAs will be essential to preserve imperilled biodiversity found beyond national waters, the vast majority of the ocean is likely to remain outside formal protected areas. It is thus crucial to have a broad strategy for retaining high seas biodiversity, which includes MPAs but does not exclusively rely on them (Maron et al. 2018). **Chapter 4** found that although there are extensive conservation priority areas in the high seas, many are under low threat from activities that MPAs have the potential to stop (e.g. fishing, shipping). In many areas MPAs are unlikely to be the best tool for conservation, and other effective area-based conservation measures (OECMs) should be used. For example, species-targeted gear restrictions might be preferable to MPAs for pelagic megafauna with wide distributions, or for species that are only threatened by a single fishery (Game et al. 2009). Another option is to harness existing international and regional agreements to regulate conservation action in these areas. RFMOs have already been used to restrict bottom-trawl fishing (Gjerde et al. 2008), so an extension of their powers to create high seas OECMs is certainly feasible. Expansion or creation of international conservation treaties may also be an effective way to manage the high seas. For example, the Antarctic Treaty System is acknowledged as a successful model for cooperative regulation of one of the world's largest commons (Chown et al. 2012), so similar agreements could be useful for managing Earth's largest common – the high seas.

Other OECMs may come in the form of privately managed conservation areas, or sites managed for non-conservation purposes but which deliver high conservation benefits ((e.g. shipwrecks, war graves; Laffoley et al. 2017). Alternatively, given that 54% of high seas fishing would be unprofitable without government subsidies, subsidy reform could also act as a useful management tool for high seas fisheries (Sala et al. 2018).

Effective conservation requires halting threats to biodiversity, and in the case of wilderness conservation, preventing threats from expanding in the first place. Even low-levels of human activities can erode the vital values of wilderness (D'agata et al. 2016; Watson et al. 2016b), so reacting to stop threats after they are already occurring will likely result in wilderness loss. Instead, wilderness conservation may require identifying and pre-emptively acting in places where wilderness is most likely to be eroded in the future, including in the high seas. Many of these places will be those where humans are responding to climate change, so conserving wilderness will require predicting and planning for human responses to ensure they do not impact wilderness areas. Predicting exactly how individuals will respond is riddled with uncertainty, so focusing on heavily impacted regions or industries may be a more robust option. For example, with the summer sea-ice minimum reducing each year due to anthropogenic climate change, it is almost certain that now un-tapped oil, gas and fisheries resources in arctic regions will begin to be exploited (Harris et al. 2017). Alternatively, as marine species distributions shift under climate change (Poloczanska et al. 2013), species-specific fishing activity is likely to shift in response (Engelhard et al. 2014). New technology which allows for remote monitoring of human activities, such as Global Fishing Watch, could also be used to identify places where human activities are expanding in almost real-time (Merten et al. 2016; Kroodsma et al. 2018).

International collaboration for conservation

Beyond the actions needed to conserve marine biodiversity identified in **chapters 3-5**, there is a need for an increased focus on international collaboration to achieve positive marine biodiversity conservation. **Chapter 5** assesses the benefits of international collaboration directly, echoing previous studies which show that it can provide substantial efficiency gains in terms of area and cost required to meet conservation targets (Kark et al. 2009, 2015). **Chapters 3 & 4** clearly show that wilderness and current conservation priorities are asymmetrically distributed between countries, suggesting collaboration will be crucial for their conservation. International collaboration is the necessary ingredient for effective conservation across the high seas and could be achieved through multi-country MPAs, RFMOs or OECMs. Collaboration should also to help ease the burden on countries which contain significant marine wilderness (**chapter 3**) or globally significant conservation priority areas (**chapter 4**).

There are a number of potential mechanisms which could be used to facilitate collaborative conservation. Many conservation priority areas occur in developing nations which lack the resources required to manage large sections of their EEZs. Further, many are home to large populations which depend on marine resources for food and income (FAO 2016), so MPAs often face intense opposition (Grafton & Kompas 2005).Therefore, platforms for cross-country compensations or subsidies, along with alternative livelihoods and food sources, are likely to be required for effective conservation in these regions. Such platforms are likely to be more feasible in places with existing collaborations for conservation, or where collaborative legislation and initiatives already exist, such as the European Union (Kark et al. 2009). In terms of global conservation targets, there is also potential for a mechanism which allows countries to trade conservation commitments in a similar manner to existing emissions trading schemes. This would allow nations to fund conservation actions in other countries and have them contribute to global conservation targets. Alternatively, debt-for-nature swaps, where conservation programmes are financed through exchange or cancellation of foreign debt, could provide substantial resources for conservation if debtor and creditor nations are willing to collaborate (Potier 1991).

In the specific case of globally important marine wilderness areas, a small number of countries in the Arctic and Pacific, such as Canada, Russia, and French Polynesia, hold almost all remaining wilderness within EEZs. If international policies recognise the vital values of wilderness and set targets for its conservation, as has been suggested by numerous studies (Graham & McClanahan 2013; Watson et al. 2016b; Lovejoy 2016; Allan et al. 2017a), these nations will also bear the most responsibility for wilderness conservation. To support these countries, international funding sources such as the World Bank or the Global Environment Facility could serve as platforms which redistribute funding from nations with little wilderness to nations with large amounts. These types of programs are already being used in the Amazon, where the Amazon Region Protected Areas program supports PA establishment and sustainable resource management using funding from the World Bank, Global Environment Facility, and the German Development Bank (World Wildlife Fund 2018). Because very few countries contain substantial amounts of marine wilderness, there is also potential for an intergovernmental treaty to address wilderness conservation issues, similar to the Antarctic treaty or Arctic Council that govern environmental decisions in polar regions (Chown et al. 2012).

Future research directions

This thesis highlights the importance of high seas conservation and international collaboration for future marine conservation, along with the need to better incorporate the full range of climate change impacts into marine spatial prioritisation. However, as with most science, the knowledge gained by answering the main questions of this thesis has led to more unanswered questions. Within the discussion sections of each chapter I have highlighted research directions relevant to the specific study. Here I discuss overall directions for future research in marine conservation planning, many of which have been raised consistently throughout this thesis.

Predicting and incorporating human responses to climate change

The human response to climate change is a neglected but important topic, both in this thesis and in the conservation planning literature as a whole (see **chapter 2; appendix 1**). Given that human responses to climate change are likely to be as severe, or even worse for biodiveristy than the direct impacts of climate change (Watson & Segan 10; Wetzel et al. 2012; Watson 2014; Segan et al. 2015), predicting and countering these responses is crucial. Some studies have shown changes in human behaviours due to climate change, such as fishing efforts shifting with fish distributions (Pinsky and Fogarty, 2012) or increased conflict in protected areas under drought (Bradley et al., 2012). Others have predicted how human behaviour will change in response to future climate change, by projecting how the distributions of commercially important fish species will change by 2055 (Cheung et al. 2010). However, these approaches are often hamstrung by very high uncertainty, both in predictions of climate change and how humans will respond.

One way to reduce uncertainty in predictions of the human response to climate change is to focus on agricultural suitability changes, which have massive implications for the marine coastal zone (Fabricius 2005). The spatial distribution of human activity across the globe is strongly linked with agricultural suitability, with over 92% of variation in terrestrial human impact values explained by the agricultural suitability of land alone (Venter et al. 2016). Therefore, by using climate-change based predictions of future agricultural suitability (Ramankutty et al. 2002; Beck 2013), future terrestrial human impacts could be forecasted with reasonable confidence. These predictions will be useful to inform terrestrial conservation planning, but also to explore how land-based impacts to marine ecosystems are likely to shift under climate change. By using broad-scale models of fertilizer and pesticide runoff, such as those developed by Halpern et al. (2008), future hotspots for land-based runoff management could be identified, along with areas where land-based management may become less important. Predictions of future agricultural suitability could also be used to predict where reliance on fisheries (and thus fishing effort) is likely to increase or decrease as climate change alters agricultural output and forces people into different livelihoods (Lobell & Field 2007; Allison et al. 2009).

While predicting how fishing effort will shift with climate change is hampered by uncertainty when considering single target species, using an ensemble of multiple species distributions, or focusing on broader ecosystem mapping may help reduce this uncertainty. For example, the Aquamaps dataset used in **chapter 4** contains species distribution models for almost ~23,000 marine species, many of which are commercially targeted. These species distribution models can be forecasted using climate change metrics, such as climate velocity (García Molinos et al. 2016), to identify places where the distributions of numerous commercially valuable species will occur in the future. Fishing effort has already been shown to track shifting species distributions under climate change (Pinsky & Fogarty 2012; Engelhard et al. 2014), so it is a relatively safe assumption that this will continue into the future. Alternatively, predictions could focus on broad ecosystems, such as coral reefs or kelp forest, which are migrating poleward to track suitable climate (Poloczanska et al. 2013). These predictions could then be used to pre-emptively protect wilderness areas or conservation priority areas from future fishing activity.

Determining the effect of model uncertainty in ridge-to-reef conservation

A crucial role of marine conservation planning is to consider and mitigate land-based threats that can have significant impacts on marine biodiversity (Halpern et al. 2009). Incorporation of such threats involves identifying which are critical for marine conservation, knowing their sources and the area they will influence, the effects and magnitude of their impacts on both biodiversity and humans, predicting how they will shift with a changing climate, and understanding how different management decisions will affect these impacts (Allison et al. 1998; Wilson et al. 2005).

The impact of land-based threats to marine ecosystems is clear (McLaughlin et al. 2003; Islam & Tanaka 2004; Álvarez-Romero et al. 2011), and emerging research has shown that analyses which connect marine benefits to land-use scenarios have potential for planning effective land-sea conservation interventions (Klein et al., 2014, 2012). However, because the full ridge-to-reef chain is a complex series of processes, and many models require detailed data, it is time and data intensive to gain information on each part of the chain (Brown et al. 2017). These challenges are especially pronounced in data-poor, developing regions, which are also where many ecosystems (e.g. coral reefs) are in desperate need of conservation action. Therefore, it is crucial that conservation practitioners have an understanding of which parts of the ridge-to-reef chain are important for decision making so they can focus time and resources on improving their knowledge of these components.

The emerging field of value-of-information (VOI) analysis could be a useful tool to quantify the costs and benefits of reducing uncertainty in ridge-to-reef models (Maxwell et al., 2015; Raiffa and Schlaifer, 1961). Because the ridge-to-reef chain is a series of complex processes, VOI analysis can be used to determine where in the process chain reducing uncertainty is most worthwhile as it will result in an altered management strategy. For example, will obtaining detailed land-use data significantly affect predictions of runoff, and therefore change management priorities? Or, are management decisions driven by data on fish habitat or other factors, in which case improving land-use data will be a waste of time and resources? Given that conservation is plagued by a lack of resources, answering these questions will provide managers working across the coastal boundary with guidance as to where in the land-sea process chain it is most important to reduce uncertainty.

Assessing human impacts on biodiversity within MPAs

Throughout this thesis, and indeed across many broad-scale conservation planning studies, MPAs are assumed to be effective at stopping threats to marine biodiversity (Maina et al. 2015; Davidson & Dulvy 2017). While there is no doubt that well-managed MPAs can protect biodiversity (Selig & Bruno 2010; Gill et al. 2017), it is also clear that many lack the management capacity to enforce regulations (Gill et al. 2017), allow numerous extractive activities such as fishing and mining (Lester & Halpern 2008), or are affected by land-based impacts they cannot prevent (Halpern et al. 2009; Kroon et al. 2012). As such, reporting solely on MPA area as a measure of progress towards global conservation targets likely vastly overestimates the true level of marine area protected. In **Appendix 2** I showed that one-third of the terrestrial PA estate is currently under intense human pressure, and that discounting these high-pressure areas substantially compromises progress towards global conservation targets. These results of **Appendix 2** make a clear case that nations reporting solely on the area of protected land may be over-estimating the true level of protection for biodiversity and highlight the need for international reporting on PAs to include robust, reproducible measures of human pressure and ecological condition. Similar analyses have never been conducted in the ocean, despite global human pressure data (Halpern et al. 2008, 2015) and remote sensed fishing activity data (Merten et al. 2016; Kroodsma et al. 2018) being freely available. Conducting an objective assessment of human threats within the global MPA estate would improve measures of progress towards global conservation targets, and similar methods could also be used to assess the effectiveness of OECMs for halting human impacts. Furthermore, it would be useful to assess how pressure inside MPAs depends on factors that have been previously shown to correlate with MPA effectiveness, such as available staff and financial resources, degree of fishing permitted, and local stakeholder perceptions (Edgar et al. 2014; McClanahan & Abunge 2016).

Concluding remarks

In various forms, marine conservation activities have been underway for millennia. From designated "tambu" areas for communal resource management in traditional Pacific Island societies, to the ~15,000 nationally designated MPAs that the United Nation's reports today, humanity seems to intrinsically recognise the importance of preserving the oceans' biological diversity and the services it provides. However, given the unparalleled scale and severity of human impacts to the ocean, it is clear that big changes in how we plan for nature conservation are now crucial (Maron et al. 2018). Just as the global community has united to halt climate change under the Paris Agreement, what is needed now is a similarly clear, agreed, science-based global strategy for biodiversity conservation. This thesis helps to advance the science needed to develop such a strategy for the ocean and ensure that marine biodiversity is preserved for future generations. Once again, the recklessness of ignoring such science may be best put into perspective by Carl Sagan:

There is perhaps no better demonstration of the folly of human conceits than this distant image of our tiny world. To me, it underscores our responsibility to deal more kindly with one another, and to preserve and cherish the pale blue dot, the only home we've ever known.

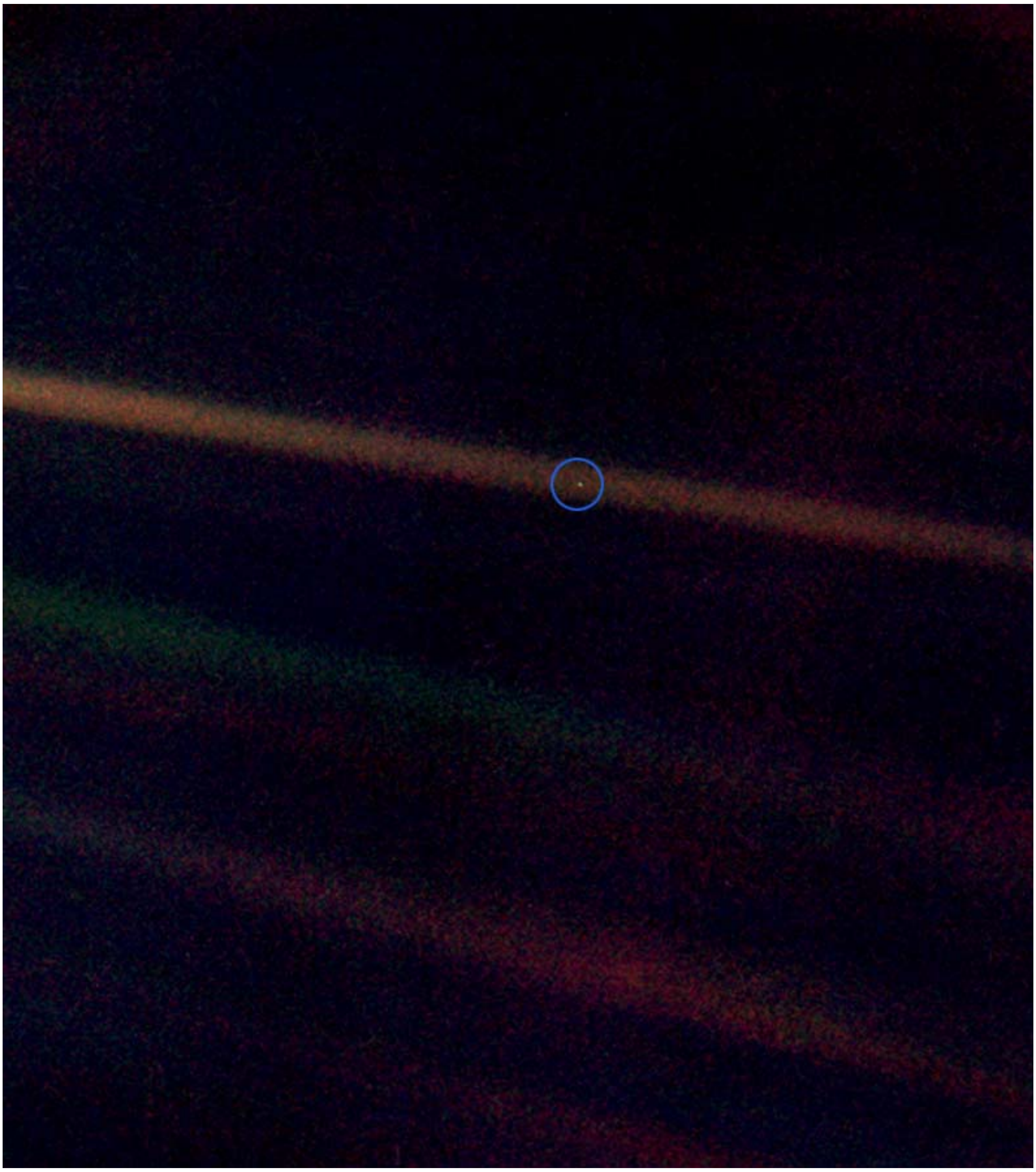

Figure 6.1. The “Pale Blue Dot” photograph of Earth taken by the Voyager I spacecraft on July 6, 1990. The Earth (circled in blue) is the relatively bright speck of light about halfway across the uppermost sunbeam.

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Appendix 1 - Integrating human responses to climate change into conservation vulnerability assessments and adaptation planning

Sean L. Maxwell, Oscar Venter, Kendall R. Jones, James E.M. Watson

Abstract

The impact of climate change on biodiversity is now evident, with the direct impacts of changing temperature and rainfall regimes, seasonality, and increases in magnitude and frequency of extreme events on species distributions, populations and overall ecosystem function being increasingly publicised. These changes in the climate system are also impacting human communities, and a range of human responses across terrestrial and marine realms are being witnessed, including changed agricultural activities, shifting fishing effort and human migration. Failing to account for the human responses to climate change is likely to compromise climate-smart conservation efforts. Here, using a well-established climate adaptation planning framework to show that it is possible to include the human response to climate change into both species and site based vulnerability assessments and overall adaptation plans. By explicitly taking into account human responses, conservation planners will have a better ability to evaluate the potential success of future conservation actions as well as better identify opportunities where win-wins can occur between human-oriented and biodiversity-based climate adaptation strategies.

Introduction

Rapid, human-forced climate change is well underway (Hansen et al. 2012, IPCC 2014b) and is an increasingly documented threat to species, ecosystems and ecological processes across the planet (Thomas et al. 2004, Foden et al. 2013, Urban 2015). The conservation community has responded to this challenge by attempting to make their strategies more robust to the impacts of climate change (Hansen et al. 2010, Groves et al. 2012, Akcakaya et al. 2014, Stein et al. 2014, Schmitz et al. 2015). 'Climate-smart' conservation has been described in differing ways in the published literature (Cross et al. 2012, Stein et al. 2014) but the fundamentals remain constant – first, identify the feature targeted for conservation and specify a management objective; second, assess the potential effects of plausible future climate scenarios on the chosen conservation feature and identify management actions to achieve the stated objective under each scenario; third, prioritize and implement management actions and; finally, monitor action effectiveness and adjust ineffective actions or revisit planning as needed (generalized framework shown in Fig. 1).

Climate smart adaptation is now widely adopted in the conservation realm, with active examples of implemented projects ranging from protected area corridor planning in Africa's Albertine Rift (Seimon et al. 2011), to planning for beaver (*Castor canadensis*) conservation in North America (Cross et al. 2012). It is also now increasingly becoming a pre-requisite to demonstrate phases of climate-smart conservation when accessing climate adaptation funding. For instance, the Doris Duke Charitable Foundation asks for all applicants to go through this process to access considerable climate change funding in North America (amounting to $257 million in grants between 1997 and 2013 for wildlife conservation in the United States; Doris Duke Foundation, 2013). The MacArthur Foundation, who paid out $16.7 million in 2013 alone to conservation and sustainable development (Macarthur Foundation, 2015), also require climate adaptation grantees to follow the climate-smart conservation principles.

The primary focus of climate-smart conservation to date has been to assess and plan for the 'direct' impacts of climate change (Lawler 2009, Seimon et al. 2011, Chapman et al. 2014, Tingley et al. 2014, Pacifici et al. 2015), where direct impacts on biodiversity refer to those that arise from changes in the climate, such as coral bleaching (Hughes et al. 2003), changes in phenology (Dalleau et al. 2012, Lane et al. 2012), or climate-driven habitat changes (Hamilton et al. 2014). Direct impacts also include impacts that arise from interactions between climate change and more traditional biodiversity threats, including habitat fragmentation (Mantyka-Pringle et al. 2012), or ecological processes such as fire (Keith et al. 2008) or invasive species (Bradley et al. 2009). One potential reason for this focus is that the vast majority of documented impacts from climate change in the conservation literature are direct impacts (Chapman et al. 2014), including declining body size (Gardner et al. 2011) and chick survival (Aubry et al. 2013) in birds, reduced population growth rates in mammals (Lane et al. 2012), changes in turtle nesting seasonality (Dalleau et al. 2012), and constriction of plant and animal-rich cloud forests (Ponce-Reyes et al. 2012).

Climate change is also impacting human societies around the world (IPCC 2012) and we are witnessing humans responding to the challenges and opportunities that climate change presents (Table 1; Box 1; Turner et al. 2010, Lesnikowski et al. 2015). For example, there are now many instances of local communities altering their agricultural systems to maintain otherwise declining yields in the face of changing seasons and rainfall patterns (Howden et al. 2007, Liu et al. 2008). Some communities that cannot maintain yields are now migrating away from their agricultural lands entirely (Feng et al. 2010).

Box 1. Examples of human adaptation responses to climate change that can have positive and negative impacts on biodiversity: **(A)** Drought driven Mulga harvesting in Queensland, Australia (Fensham et al. 2012); **(B)** Protective sea wall built using blasted coral to protect local communities against sea-level rise, Papua New Guinea (Grantham et al. 2011); **(C)** Agroforestry plantation encourage a microclimate that supports high yields whilst providing migration corridors for tropical species that are threatened by climate change (Bhagwat et al. 2008); **(D)** Native mangrove species restoration for coastal defense, Zambales, Philippines (Alongi 2008). (Photo credit: (A) Michelle Venter, (B) US Dept. of Agriculture, (C) James Watson, (D) Trees for the future, http://flic.kr/p/b8256t)

Table 1. Table 1. Published examples of different human responses to local climatic changes that have, or are likely to cause, indirect impacts to species and ecosystems of conservation concern.

Climate-related pressure	Human response	Potential indirect impacts on species and ecosystems
Increased rainfall variability	Build water storage infrastructure (dams, reservoirs, bores)	Changes in natural river flows (McCartney & Smakhtin 2010)
		Disruption of migratory processes (Preece & Jones 2002)
Distribution changes in economically important fish species	Associated shifts in fishing effort	Overfishing if not accounted for in management practices (Pinsky & Fogarty 2012)
Climate-induced changes in agricultural suitability	Shift or intensify agriculture in regions that become more climatically suitable	Progressive fragmentation and loss of wildlife habitat (Bradley et al. 2012, Morrison & Lindell 2011)
Reduced sea ice and permafrost in the Arctic	Shift or intensify transport, fishing and oil extraction activities	Increased risk of oil spills, marine mammal boat strikes, bycatch and entanglement impacts from these activities (Wetzel et al. 2012)
Inundation from sea level rise	Human displacement and relocation of agriculture	Mammalian habitat loss due to relocation of urban and agricultural areas (Grantham et al. 2011; Greste 2009)
Erosion from sea level rise	Construction of physical barriers for coastal armoring	Changes in trophic structure and reduced species diversity (Dugan et al. 2008)
		Coral reef destruction (Grantham et al. 2011)
Recurrent severe drought	Increased groundwater extraction	Exacerbated drought impacts on endemic cave dwelling species (Shu et al. 2013)
	Switching to alternative forms of income or food	Increased poaching of elephants or resource extraction within protected areas (Bradley et al. 2012, Ogutu et al. 2009)
	Pastoralists increase herd size to facilitate herd recovery	Competitive displacement or harassment of wildlife by livestock and herders (Boydston et al. 2003, Mukinya 1973, World Bank 2015)

Recent temperature and rainfall anomalies in sub-Saharan Africa, for example, have caused the net displacement of five million people between 1960 and 2000 (Marchiori et al. 2012) and are also leading some coastal fisher communities to shift their fishing grounds (Pinsky and Fogarty 2012). The rapidly changing climate in the higher latitudes of the northern hemisphere, which is reducing permafrost, snow and ice, is already altering transportation networks and infrastructure associated with mining, oil and gas developments (Prowse et al. 2009). The increasing frequency and magnitude of extreme weather and climate events witnessed around the world (IPCC 2012) has meant there are now many examples of coastal communities preparing for natural disaster relief by constructing physical barriers (Grantham et al. 2011) or by planting or protecting natural defense mechanisms against coastal inundation and erosion, such as mangroves and reefs (Rao et al. 2013).

There has also been a shift in the global policy realm, with regional-scale adaptation now playing an equally important part in international climate negotiations next to mitigation (Hsu et al. 2015). In the last few years, governments have increasingly recognised the importance of implementing policies to safeguard or promote ecosystem services in a changing climate to allow humans to better adapt to climate change, including protecting forests to reduce avalanches and landslides (UNFCCC 2011), restoring urban forests to prevent heat traps, improve air quality and regulate stormwater runoff (Edmonton City Council 2012), and implementing agroforestry programs to adapt to irregular rainfall patterns (Bhagwat et al. 2008, UNFCCC 2011).

A growing literature argues the majority of human responses to climate change are inextricably linked to environmental changes that interfere with the natural adaptive responses to climate change that species and ecosystems have relied upon in the past (Mackey et al. 2008, Brodie et al. 2012, Tingley et al. 2014). Impacts on species or ecosystems that result from humans responding to climate change are increasingly referred to as the 'indirect impacts' of climate change (Turner et al. 2010, Chapman et al. 2014, Watson 2014), and we follow this convention. Many applications of the climate-smart conservation framework do not accommodate the indirect impacts of climate change on biodiversity, which constrains our ability to assess and plan for them (Brodie et al. 2012, Watson 2014). Here we argue that indirect impacts can be accommodated without a radical departure from how climate-smart conservation is currently done.

Building on four existing steps of the well-established climate-smart conservation framework (Figure 1), this review will demonstrate different ways to integrate the indirect impacts from humans responding to climate change into vulnerability assessments and adaptation plans. We first show that it is possible for vulnerability assessments to capture the degree to which human responses alter species and ecosystems ability to adapt to climate change. After assessing the potential indirect impacts of climate change, we argue that actively revising conservation goals and objectives can reveal more pragmatic conservation goals and objectives that incorporate – or even take advantage of – likely human responses to climate change. Current climate adaptation actions that involve resisting indirect impacts, accommodating change in land and seascapes and promoting dual benefits for humans and biodiversity can address the indirect impacts of human responses to climate change. However, these actions have different levels of risk of achieving overall conservation goals and broader societal values and needs under climate change, as well as different overall feasibility of long-term success, both of which are important to consider when evaluating and selecting adaptation actions. This review clarifies the connections between climate-induced changes in human behaviour and the current thinking around climate-smart conservation, and in so doing, helps facilitate the integration of human responses into climate vulnerability assessments and adaptation plans.

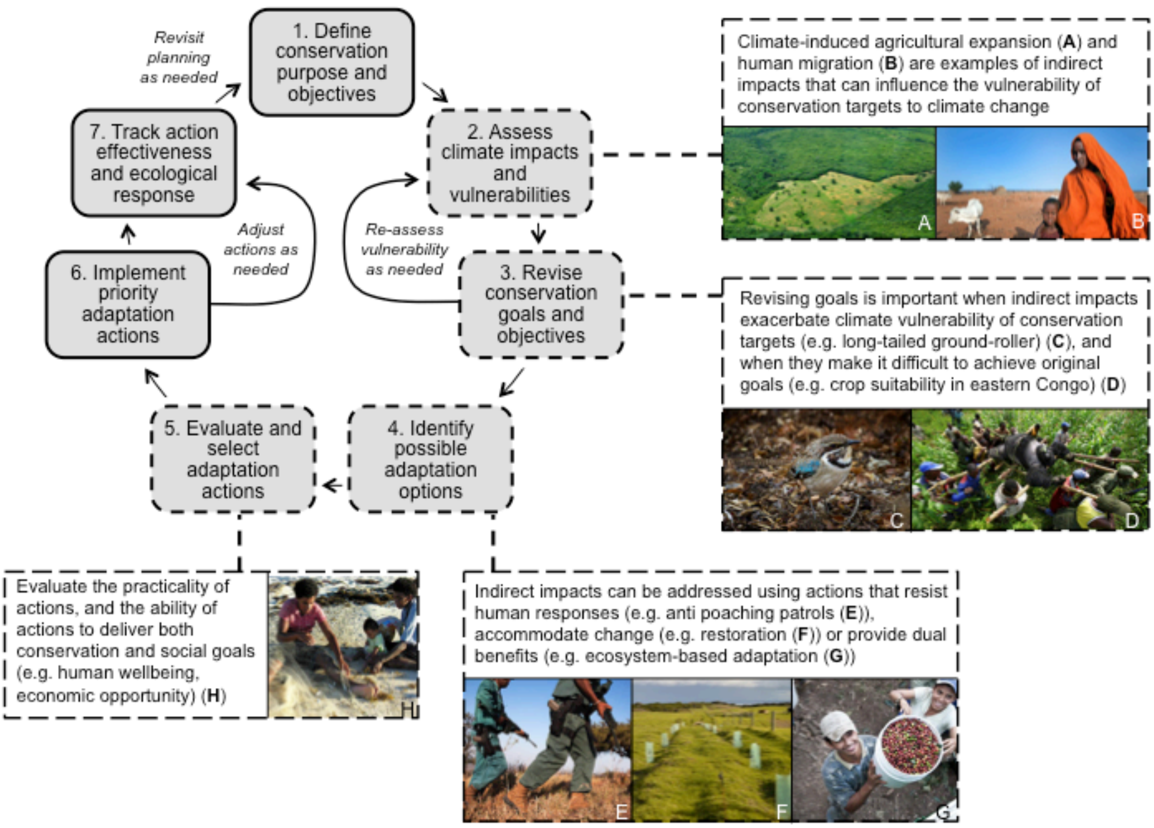


Figure 1. The climate-smart conservation cycle (Stein et al. 2014). The four phases of the cycle that are surrounded by a dashed line indicate where human responses to climate change should be integrated. The four boxes connecting to these four phases provide suggestions on how the integration may be achieved. (Photo credit: (A) Neil Palmer, (B)

Petterik Wiggers, (C) Francesco Veronesi, (D) Brent Stirton/Getty Images, (E & I) James Allan, (F) Sean Maxwell, (G) Conservation International, (H) Jo Munday)

Assessing climate impacts and vulnerabilities

Current methods for assessing vulnerability climate change

Vulnerability assessments are an important early phase of climate-smart conservation (Step 2 in Figure 1) because they can identify if, and for what reasons, climate change may pose a threat to the persistence of a species or ecosystems of conservation importance (herein 'conservation target'). 'Vulnerability' in this context refers to the extent to which a conservation target is predisposed to adverse effects from climate change (Stein et al. 2014). Climate change vulnerability assessments provide the critical foundation upon which conservation actions or policies are developed. Beyond planning, vulnerability assessments also play an important role in informing conservation inventories (e.g. the International Union for Nature Conservation (IUCN) Red List of Threatened species, www.iucnredlist.org; Akcakaya et al. 2014) which guide significant conservation investment as well as some national legislation (Walsh et al. 2013).

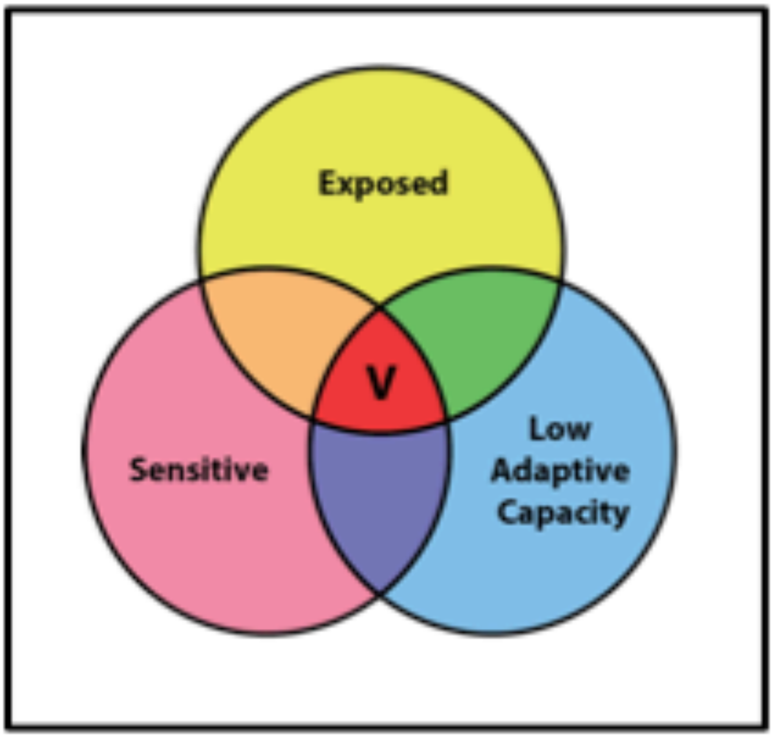


Figure 2. Conceptual framework for assessing species and ecosystem vulnerability to climate change. Yellow and pink circles represent exposure and sensitivity respectively, where exposure is a measure of change in climate and climate-induced environmental

impacts within the area occupied by a species or system, and sensitivity is a measure of how much a species or system will be affected by particular changes in climatic variables. The blue circle represents low adaptive capacity, which is the inability of a species or system to adjust to climate change, to take advantage of opportunities, or to cope with the consequences of climate change. Where the circles intersect, '**V**' represents a given species or ecosystems level of vulnerability to climate change. Exposed and sensitive species or ecosystems with low adaptive capacity are highly vulnerable to climate change. Schematic adapted from Foden and colleagues (Foden et al. 2013).

Amongst a wealth of ways to assess vulnerability to climate change (Williams et al. 2008, Watson et al. 2013, Pacifici et al. 2015) the International Panel on Climate Change (IPCC) have adopted a conceptual framework where vulnerability is considered to be a product of three measurable elements: exposure, sensitivity and adaptive capacity (IPCC 2007). Exposure is a measure of change in climate (e.g. temperature, wind, precipitation) and climate-induced environmental impacts (e.g. sea-level rise, ocean acidification) within the area occupied by a species or system (Dawson et al. 2011, Stein et al. 2014). Sensitivity is a measure of how much a species or system will be affected by particular changes in climatic variables (Foden et al. 2013, Pacifici et al. 2015). Put together, exposure and sensitivity determine the potential impact of climate change on a species or ecosystem. The third element of vulnerability, adaptive capacity, is 'the potential, capability, or ability of a species or ecosystem to adjust to climate change, to moderate potential damages, to take advantage of opportunities, or to cope with the consequences' (IPCC 2007). Species or ecosystems found to have high exposure and sensitivity, and low adaptive capacity are said to have high vulnerability to climate change (Figure 2; Foden et al. 2013).

It is generally accepted that the sensitivity of an individual, species or ecosystem is governed by intrinsic factors, such as physiological traits (e.g. temperature or pH tolerance), phenology cycles (e.g. timing of insect emergence; DeLucia et al. 2012), ecological linkages (e.g. predator-prey cycles; Hunsicker et al. 2013), and strict habitat dependencies (e.g. wading birds and mudflats; Iwamura et al. 2013). In contrast, adaptive capacity is thought to be a function of both intrinsic factors, including life history characteristics (e.g. dispersal and colonization ability; Berg et al. 2010), evolutionary potential (e.g. generation time, population size; Hoffmann and Sgro 2011) and phenotypic plasticity (e.g. acclimation; Matesanz et al. 2010), and extrinsic factors such as habitat quality and connectivity, pollution, and water availability (Glick et al. 2011).

Species persisted through past climate changes via a number of adaptive responses (Mackey et al. 2008). Microevolution, for instance, refers to genetic changes that occur over time within a population, and can occur rapidly to help species keep up with environmental changes (Thompson 2005). Confronted with altered temperatures in their wetlands, wood frog (*Rana sylvatica*) populations have undergone microevolution in thermal tolerance (Skelly and Freidenburg 2000), thermal preference (Freidenburg and Skelly 2004), and temperature-related development rate (Skelly 2004) in less than 40 years. Dispersing away from unfavorable changes in climate has also been an important adaptation response for species in the past (Gilmore et al. 2007, Younger et al. 2015), particularly for long-lived species with slow rates of microevolution (e.g. penguins; Forcada and Trathan 2009). Climate refugia are locations where species survive periods of regionally adverse climate, and are thought to be critical for species persistence through climate change (Lovejoy and Hannah 2005, Gavin et al. 2014). European beech (*Fagus sylvatica*) colonization across central and northern Europe since the last glacial maxima originated predominantly from climate refugia in the northern periphery of the Mediterranean (e.g. eastern and western Alps; Magri 2008, de Lafontaine et al. 2013).

Human influence on climate vulnerability

During past periods of climate change, human influence on the environment and ecosystem processes did not limit the adaptive responses of species. This is clearly no longer the case. Humanity's footprint is now appearing on at least 83% of the earth's surface, and almost 98% of the areas where rice, wheat, or maize can be grown is influenced by one or more of these crops (Sanderson et al. 2002). No area within the marine realm is free from human influence, and 41% of the marine environment is strongly affected by human activities (Halpern et al. 2008). Such modification of land and seascapes leaves many species and ecosystems with little chance to utilise their full range of adaptive responses to climate change (Kareiva et al. 2007, Eastwood et al. 2008, Lawler et al. 2013).

In addition to the anthropogenic forces that have already altered the function and state of many ecosystems, human responses to climate change will influence the ability of species to cope, adjust or disperse away from climate impacts (Figure 3). For example, when tropical forested ecosystems become more accessible during the wet season due to changes in the length and severity of the dry season, there is evidence of humans responding opportunistically by increasing logging and hunting efforts (Robinson et al. 1999). This change in behavior can restrict animal and plant dispersal across the landscape (Peres and Palacios 2007, Brodie et al. 2009, Corlett 2009) and exacerbate their vulnerability to the drying conditions. In contrast, agroforesty is an adaptive strategy being adopted by farmers in tropical regions to adapt to the impacts of a drying climate on banana, coffee and cocoa plantations (Bhagwat et al. 2008, Birdlife International 2010).

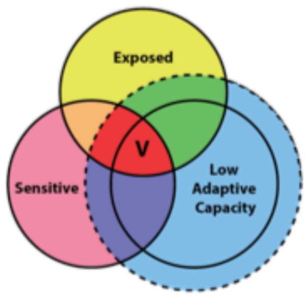
	Biodiversity-friendly response	**Non-biodiversity-friendly response**
Examples of human responses to climate change	• Abandon agricultural lands • Carbon trading mechanisms that involve forest conservation • Increase eco-tourism ventures • Mangrove restoration	• Increase logging and hunting • Increase ground water extraction • Dam construction • Sea wall construction
Potential indirect impacts to conservation targets		
	• Adaptive capacity is enhanced • Vulnerability to climate change decreases	• Adaptive capacity is constrained • Vulnerability to climate change increases

Figure 3. Conceptual demonstration of how human responses to climate change can have positive and negative influences on species and ecosystem vulnerability to climate change. Colours in vulnerability diagrams reflect those in Figure 2. Biodiversity friendly human responses will present opportunities to enhance the adaptive capacity of climate imperilled conservation targets, reducing their overall vulnerability to climate change. Non-biodiversity-friendly responses will exacerbate climate vulnerability of species and ecosystems by reducing their adaptive capacity.

By intentionally managing shade trees within food crops to encourage a microclimate that supports high yields, agroforestry can provide migration corridors for tropical species that are threatened by climate change (Bhagwat et al. 2008). The adoption of agroforestry by farmers is also linked with declines in unsustainable timber harvesting and illegal grazing of livestock in nearby natural areas (McNeely and Schroth 2006).

Increased frequency and magnitude of extreme weather and climate events are now triggering a series of human responses that have implications for species threatened with climate change. We are witnessing planned and unplanned resettlement of communities that reside in flood or drought prone areas (McGranahan et al. 2007, Arnall 2014), which precipitates a variety of environmental problems, including legal and illegal land colonization, deforestation, fires and overhunting (Laurance et al. 2001, Fearnside 2006, Laurance et al. 2006, Blake et al. 2007, Adeney et al. 2009, Laurance et al. 2009). These indirect impacts place additional stress on species coping with flood and drought impacts themselves, and are often exacerbated by poor governance (Fearnside 1986, Fearnside 2006, Turner et al. 2010).

Human resettlement is occasionally required to make way for dams, which serve to secure potable water or mitigate flood impacts for vulnerable communities (Hirji and Davis 2009, Watts et al. 2011). These constructions impose additional indirect climate impacts by increasing temperature-related stress in aquatic organisms (Preece and Jones 2002) and blocking animal migrations (Raymond 1979). Sea walls and other physical barriers humans construct to protect themselves from storm surge events, flooding and coastal erosion can similarly result in damage to coastal ecosystems without appropriate planning (Dugan et al. 2008). However, there are more biodiversity-friendly options for coastal defence that are being adopted by local communities and governments, such as restoring or conserving mangrove and coral ecosystems (Barbier et al. 2008), which could enhance species and system adaptive capacity to climate change by providing vital nursery habitat for marine organisms and connecting remnant mangrove communities (Barbier et al. 2011). The Chinese government recently restored several thousand square kilometres of floodplains to attenuate climate variability and flooding impacts. This process involved the removal of dikes and other hard structures, allowing for improved water quality and conservation of threatened species (Pittock and Xu 2013).

Indirect impacts are increasingly likely in drought-affected arable landscapes. Increased ground water extraction for agriculture or human consumption exacerbates drought impacts on endemic cave dwelling species (Shu et al. 2013). After ground forage has been exhausted during drought events, livestock owners in Queensland, Australia are left with little choice but to clear large areas of mulga (*Acacia aneura*) forest for livestock, which use the tree’s phyloids as fodder (Everist et al. 1958). While this practice has a relatively benign effect on plant diversity (Fensham et al. 2012), the indirect impacts on dependent bird, small mammal and invertebrate communities in times of drought is unknown. There is also potential for climate-imperiled species to benefit from some human response to drought. Agricultural land abandonment due to climate-driven crop failures (Feng et al. 2010) may enable species to inhabit or move through previously impermeable landscapes (Bowen et al. 2007, Smallbone et al. 2014).

Some well-intentioned human efforts to limit greenhouse gas emissions have lead to perverse biodiversity consequences. Palm oil plantations, many of which are grown to produce biofuel, now cover over 13 million hectares of the earth's surface (primarily in South-East Asia; Danielsen et al. 2009). As these plantations continue to replace tropical rainforest, they impose restrictions on the range of climate adaptation responses for forest dependent species. Recognising the biological and climate impacts of tropical forest clearance, climate change mitigation strategies have started to put a monetary value on intact tropical rainforest through programs such as Reduced Emissions from Deforestation and forest Degradation (REDD+; Brodie et al. 2012, Venter and Koh 2012). REDD+ is one human response that has large positive potential for increasing species adaptive capacity, as it may enhance conservation efforts in the world's most biodiverse ecosystem.

Integrating human responses to climate change into vulnerability assessments

Social-ecological system (SES) frameworks play a critical role in linking land and seascapes with human behavior, and are valuable tools when predicting how complex system dynamics will play out over long time-scales (Holdo et al. 2009, Ban et al. 2013). These frameworks enable explicit modeling of how human responses to climate change influence species or ecosystem vulnerability to climate change (and vice versa), which make it a very useful approach to integrating indirect impacts of climate change into conservation vulnerability assessments. SES frameworks have been increasingly used to great effect in the tropical marine conservation realm to expose the high degree of co-dependency between the social and ecological systems – where vulnerability to climate change is visibly and quantitatively influenced by each system (Cinner et al. 2013, Maina et al. 2015). These models are also usefully applied when evaluating and selecting between different conservation adaptation actions (McClanahan et al. 2008).

The challenge for the conservation science community is to capture within vulnerability assessments the indirect impacts of humans responding to climate change when social-ecological models are not available for the species or site of conservation interest. One obvious way for doing this is to utilize existing information from other, non-conservation and non-natural resource management sectors, on likely human actions under different scenarios of climate change. Where this information is spatially-explicit, it is possible to undertake conservation vulnerability assessments that integrate how landscapes or seascapes may be modified as humans respond to climate change, and how these modifications can influence dispersal pathways and climate refugia (see Pacifici et al. 2015 for a review on approaches used to model vulnerability to climate change).

The United Nations Framework Convention on Climate Change (UNFCCC) coordinate National Adaptation Programmes of Action (NAPA), which identify urgent and immediate actions needed in the least developed countries to prevent damaging impacts from climate change (UNFCCC 2009). The actions proposed in NAPAs involve land-use change (e.g. coastal reforestation in Bangladesh and Cambodia, dam construction in Burundi and Lao), future land acquisitions, and population displacement and resettlement (McDowell 2013). Such actions are highly relevant to conservation efforts and spatially-explicit information sourced from funded NAPA projects would provide valuable insight into human-climate adaptation that is likely to influence species and ecosystems vulnerability to climate change in surrounding regions. Wheeler and colleagues (Wheeler 2011) provide another freely available dataset that ranks 233 countries according to their vulnerability to weather-related disasters, sea-level-rise and loss of agricultural productivity. The dataset acts as a decision making tool for donors who wish to identify and fund the most cost-effective adaptation actions within countries, and thus may help identify where and how human adaptation efforts will be undertaken.

Government planning documents used in concert with predictions of agricultural suitability under climate change (Tubiello et al. 2007) can provide realistic scenarios of where future agricultural expansion is likely to occur. Laurance and colleagues (Laurance et al. 2014) mapped global regions where the expansion of transportation routes are likely to have large social and agricultural benefits under future climate change (for more information, see www.global-roadmap.org). Such information could be usefully applied when assessing climate vulnerability of species, particularly those reliant on dispersal ability to adapt to climate change.

There are now some examples, when spatially explicit data on likely human responses is available, of how likely human responses to climate change can be integrated into climate-smart vulnerability assessments. Segan and colleagues (Segan et al. 2015), for example, used the mean impact of climate change on human populations forecasted in 2050 (as assessed by Midgley et al. 2011) to inform the climate vulnerability on threatened bird species and Important Bird Areas (Evans and Fishpool 2001) across southern Africa. A key finding of this study was that one-fifth of species, and one-tenth of sites previously thought to be at relatively low vulnerability to climate change shifted to high vulnerability when the likely indirect impacts of climate change integrated into the assessment.(Segan et al. 2015). However, these types of assessments are still rare, and additional studies that utilise information on where human populations are likely to respond to climate change to inform species and ecosystem range changes (Rondinini et al. 2011, Barbet-Massin et al. 2012) and extinction risk (Keith et al. 2008) are needed to improve our understanding of how indirect impacts of climate change effect the vulnerability of conservation targets.

Revise conservation goals and objectives

In the context of climate-smart conservation, a 'goal' refers to an overarching vision as to *why* conservation effort is needed (e.g. to make harlequin frogs (*Atelopus sp.*) less vulnerable to climate change), but does not specify what will be done to achieve the vision. An 'objective' refers to a more specific statement about *what* can be done to meet the goal (e.g. secure cool and wet microhabitats). Put together, goals and objectives frame the design, implementation and measurement of conservation actions, and setting appropriate goals and objectives is critical to arrive at the desired conservation outcomes (Cross et al. 2012, Stein et al. 2014). There are at least two broad reasons why it is important to revise goals and objectives after integrating indirect impacts of climate change into vulnerability assessments (Step 3 in Figure. 1).

First, if human responses to climate change found to exacerbate species or ecosystem vulnerability to climate change, conservation goals must be revised to adequately focus on those species or sites perceived to be under threat by this response. Segan and colleagues (Segan et al. 2015) showed that climate change clearly poses a threat to the endangered long-tailed ground-roller (*Uratelornis chimaera*), but that threat was only apparent when likely human responses to climate change were incorporated into the vulnerability assessment (the species was not vulnerable to the direct impacts of climate change; Figure 1C). Similarly, in Manus Island (Papua New Guinea), a recent assessment showed that many of the coral reefs that were considered not very vulnerable to the direct impacts of climate change, became vulnerable when considering likely human responses of nearby fishing villages (Maina et al. 2015). In instances such as these, failing to revise goals and objectives to focus on the indirect impacts of climate change will lead to inefficient allocation of conservation resources, or the selection of conservation actions that do not address the most pressing threats to species persistence.

Second, there will be cases when human responses to climate change will make it very difficult or impossible to reach the goals and objectives that were originally agreed. In the Virunga National Park in eastern Democratic Republic of the Congo, for example, the economic and physical displacement of people in response to changing crop suitability with climate change (Seimon et al. 2011, Bradley et al. 2012) undermines efforts to conserve critically endangered Virunga mountain gorillas (*Gorilla beringei beringei*; Maekawa et al. 2013). In 2007, ten gorillas were massacred to send a message to the park staff not to interfere with other economic interests in the park (Figure 1D; Refisch and Hammill 2012). A more pragmatic conservation goal in this case may be engage with the human community to reduce their vulnerability to climate change via ecosystem-based adaptation strategies (UNFCCC 2011), and by doing so, mitigate indirect impacts of climate change on conservation targets. Other human-orientated conservation goals include sustaining or restoring key ecosystem services (e.g., pollination, water purification or carbon sequestration), maintaining sustainable levels of harvestable or extracted resources (e.g., fish, timber), or providing physical protection from extreme events (e.g. storm surges and flooding), and are likely to be important to consider in these circumstances (Skroch and Lopez-Hoffman 2010, UNFCCC 2011, Ingram et al. 2012, Stein et al. 2014).

Identify possible adaptation actions based on revised goals

Conservation actions lay out *how* objectives and goals are to be achieved. Here we discuss actions to avoid, mitigate, and offset the indirect impacts of climate change on conservation targets. The particular action, or suite of actions chosen to address indirect impacts will always be context dependent, but they generally fall into one of three broad strategies: resistance actions, actions that accommodate change, and actions that simultaneously address the vulnerability of people and biodiversity (Figure 4). These strategies are not mutually exclusive, and adaptation efforts may adopt multiple actions from more than one strategy, or a single action that itself spans more than one strategies.

Resistance actions

Indirect impacts can be mitigated by resisting human responses to climate change in regions of conservation importance. Resistance actions aim to increase the adaptive capacity of species and ecosystems relative to a scenario where humans could potentially respond to climate change without being restricted by these actions. For example, Bradley and colleagues (Bradley et al. 2012) found that areas set aside for biodiversity conservation in South Africa are likely to be increasingly exploited for food and fuel under future climate change. One option to combat this is to invest in stronger enforcement of extractive-use regulations within reserve boundaries (e.g. anti-poaching patrols (Figure 1E). Furthermore, Visconti and colleagues (Visconti et al. 2011) coupled predictions of climate-induced land use change (as assessed by IMAGE 2.4; Bouwman et al. 2007) with habitat suitability models to identify regions where local extinction of terrestrial mammals is highly likely. Resisting such indirect impacts could involve expanding or establishing new protected areas in places that are likely to be impacted by humans in the future.

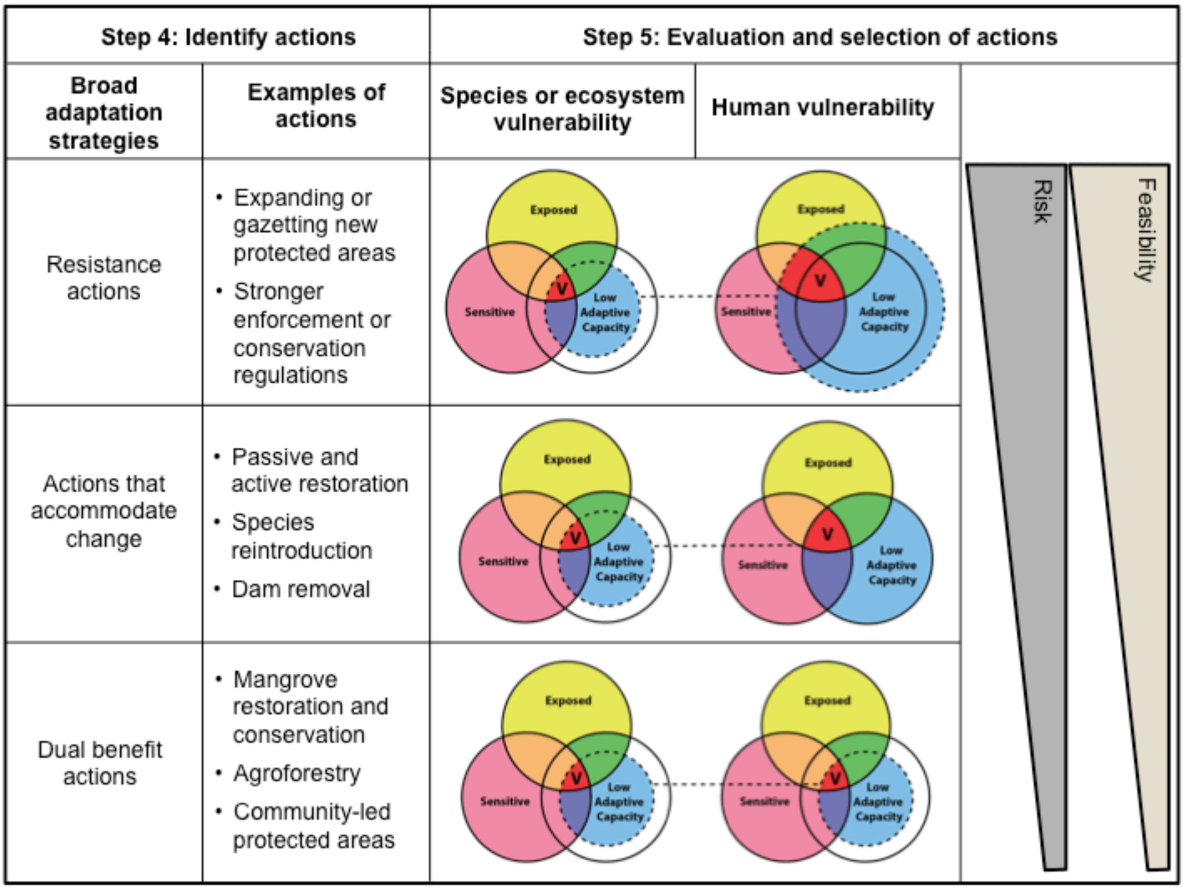


Figure 4. Schematic diagram of how indirect climate change impacts can be integrated into step four and five of the climate-smart conservation cycle – identify possible adaptation actions and evaluation and selection of actions. Colours in vulnerability diagrams reflect those in Figure 2. Vulnerability diagrams on the left represent species or ecosystem vulnerability to the indirect impacts of climate change, while circle diagrams on the right represent climate vulnerability for human communities in the same region. Solid lines in circle diagrams measure elements of vulnerability before action is taken to address indirect impacts of climate change. Dashed lines in circle diagrams measure potential changes in elements of vulnerability after action is taken to address indirect impacts of climate change. ‘Risk’ is defined as the likelihood and consequence of actions failing to achieve conservation goals and broader societal values and needs under climate change, and ‘complexity’ as the amount of knowledge and resources required to implement an action.

Accommodating change

Actions that accommodate change are designed to help move a species or ecosystem from one state to another (Morecroft et al. 2012). When used to address indirect climate change impacts, these actions essentially aim to offset losses in species and ecosystem adaptive capacity in places where humans have increased their impacts, by restoring adaptive capacity in places where humans are reducing their impacts. Forecasts show that suitable conditions for current crops are likely to shift with climate change (e.g. sugar maple - Brown et al. 2015; and wine - Hannah et al. 2013), while others predict that currently unsuitable areas will become increasingly suitable, suggesting that agriculture may intensify or shift into these regions (Ramankutty et al. 2002). Shall these shifts eventuate, they will allow for novel opportunities to restore land previously used for agriculture. Restoration can occur passively should the soil of abandoned land still house a viable seed bank, or if natural vegetation exists within the dispersal distance of the native species (Morrison and Lindell 2011). For large areas that have been farmed for a long period, more intensive active restoration action efforts will likely be required to restore a functioning native ecosystem (Smallbone et al. 2014). These restoration opportunities are not limited to terrestrial areas. For instance, as fish distribution (Sumaila et al. 2011) and associated fishing effort shifts with climate change (Pinsky and Fogarty 2012), opportunities for restoration will also arise in marine and freshwater environments that see reduced visits by destructive fishing fleets.

In regions where humans are reducing their impact, planners may choose to reintroduce a species that has previously gone been extirpated (Schwartz and Martin 2013), release individuals into an existing population of conspecifics to enhance population viability (termed ‘reinforcement’; Seddon et al. 2014), or translocate species based on their direct climate vulnerability (McDonald-Madden et al. 2011, Schwartz and Martin 2013). Other opportunities to promote change may arise from the abandonment and potential decommissioning of ecologically damaging infrastructure. For instance, changing demands for water and hydro-electric power in North America is increasingly presenting opportunities to remove dams that impede the movements of migrating salmon, though dam removal still represents a challenging undertaking (Stanley and Doyle 2003).

Dual benefits

The final strategy to combat indirect impacts of climate change on biodiversity involves working with human communities to reduce their own vulnerability to climate change, and particularly with the poorest and most vulnerable communities who have immediate adaptation needs (Chong 2014). These actions explicitly aim to increase human adaptive capacity in ways that also increase the adaptive capacity of conservation targets. A plethora of ecosystem service approaches to climate adaptation have emerged that use elements of nature to buffer human communities against the adverse impacts of climate change (e.g. ecosystem-based adaptation - Jones et al. 2012; payments for ecosystem services - Manzo-Delgado et al. 2014; integrated island management- Jupiter et al. 2014), and are heralded as promising approaches to finding dual benefit solutions when environmental problems threaten human communities.

There are many examples of dual benefit actions being used to great effect to address climate change impacts. Mangrove forests are being established and conserved in the Philippines to increase coastal resilience to storm surges, flooding and erosion (Alongi 2008). Similar actions are have been implemented around primary water sources in Haiti to reduce erosion and landslides to secure continued supply of potable water for local people (Birdlife International 2010). Fishing communities across Melanesia depend heavily on marine resources for their livelihoods, and have established locally managed marine protected areas in an effort to bolster coral diversity and likely resilience to climate change (Hughes et al. 2003, Jones et al. 2012, Weeks and Jupiter 2013). CASCADE (Central American Subsistence and Coffee farmer ADaptation based on Ecosystems) is a research project run by Conservation International that aims to help vulnerable smallholder coffee farmers adapt to climate change in Costa Rica, Honduras and Guatemala with the use of ecosystem service approaches (Figure 1G; Conservation International 2014). Dual benefit actions can be implemented at the community level, as in the previous examples, or as a top-down strategy led by governmental bodies. For example, the Chinese government offer payments to landowners to increase or restore forests on steep slopes, or in areas subject to desertification, a strategy that has led to globally significant forest expansion (Food and Agriculture Organization of the United Nations 2010).

Evaluate and select adaptation actions

The next step in the climate-smart cycle is to evaluate and select which action, or suite of actions, is most likely to deliver your revised conservation goals and objectives. We propose that actions to combat indirect climate change impacts should be evaluated across at least two broad criteria – risk and feasibility. Here we define 'risk' as the probability that actions fail to achieve conservation goals and broader societal values and needs under climate change, and the likely consequences of this failure (Burgman and Yemshanov 2013). 'Feasibility' refers to how practicable or realistic is it to implement alternative actions from a knowledge, resource and legal standpoint. These evaluation criteria are drawn from the decision science literature which has shown their consideration increases the likelihood of actions being implemented, and the capacity to measure conservation progress over time (Joseph et al. 2009, Wilson et al. 2009, Stein et al. 2014). Here we provide a hypothetical assessment of risk and feasibility levels associated with resistance, change and dual benefit actions to address indirect climate change impacts.

Risk

Perhaps the most obvious thing to consider when deciding between alternative actions is how likely an action is to achieve conservation goals and objectives. While the three broad strategies proposed in Figure 4 all have the potential to reduce species and ecosystem vulnerability to indirect climate change impacts, the realised magnitude of these effects will depend on a number of important ecological factors, including but not limited to species disease dynamics, landscape patterns and natural disturbance regimes, population size and structure of target species and the quality of habitat maintained or restored (Blaustein and Kiesecker 2002, Stein et al. 2014). However, a paradox of conservation efforts is that social variables (e.g. human wellbeing, cultural values, economic output) often underpin their effectiveness (Cowling and Wilhelm-Rechmann 2007, Stephanson and Mascia 2014, Maina et al. 2015). Actions taken to conserve biodiversity sometimes conflict with human needs and interests, and when these conflicts are ignored in climate adaptation planning, conservation actions stand little chance of being implemented effectively (Ban et al. 2013, Stephanson and Mascia 2014). Thus it is important when evaluating risk of alternative actions to also consider how well they satisfy societal values and needs under climate change.

Studies regularly identify protected areas and effective enforcement of conservation laws as being crucial to conservation success (Bruner et al. 2001, Hilborn et al. 2006, Craigie et al. 2010, Tranquilli et al. 2012, Watson et al. 2014). Where human responses to climate change are likely to erode biological values, there may be options for conservation practitioners to resist this erosion through resistance actions such as the expansion of existing protected areas or the better enforcement of existing ones. However, resistance actions such as these essentially aim to interfere with 'natural' human responses to climate change as they exclude a range of adaptation options that could have been undertaken. By doing so, these actions can inadvertently reduce human's capacity to adapt to climate change, making them more vulnerable to its impacts. Hence when used to combat indirect climate change impacts, we view resistance actions to be the most risky when compared with change-oriented and dual benefit actions. This is particularly the case for communities that are poorly equipped to cope with even short-term restrictions on resource use imposed by resistance actions (McClanahan et al. 2008). At the same time, resistance actions may be less risky when the adaptive capacity of nearby communities is high, enabling them to readily adapt to conservation restrictions and take advantage of new opportunities, such as increased tourism (McClanahan et al. 2008).

A resistance action that inadvertently increases human vulnerability to climate change can lead to perverse environmental outcomes, where climate-imperiled human communities ignore or break conservation regulations out of desperation, or simply shift the impacts of human adaptation elsewhere. Such actions are also more likely to foster hostile human communities who feel that environmental welfare was chosen over their own, undermining future engagement with conservation efforts, or more worryingly, potentially leading to cases when people intentionally jeopardise conservation efforts out of spite (West and Brockington 2006, West et al. 2006). Some resistance actions, especially those that involve expanding or gazetting new protected areas, are made more risky when they rely on uncertain predictions of climate-induced human migration or land use change. Resisting human responses requires being able to predict how they are likely to unfold without conservation intervention, which can be challenging. However, this risk can be reduced through the use of detailed human adaptation plans, or by developing more robust models of likely human adaptation actions.

Actions that accommodate change avoid some of the risk associated with resistance actions because they do not interfere with natural societal responses to climate change and do not necessarily require human responses to be predicted before they unfold.

However, permitting communities to adapt as necessary means indirect impacts on biodiversity go unchecked outside regions were conservation actions are being carried out, which makes achieving conservation goals challenging at large spatial scales. Restoration actions are often used as an accommodation oriented strategy, and imply long time delays and a low certainty of recreating 'pristine' or fully 'natural' biodiversity values needed for climate adaptation (Bekessy et al. 2010, Shoo et al. 2011, Maron et al. 2012). In the best case, ecosystem restoration can enable species richness to recover to pre-disturbance levels within a century, while enabling a similar set of species to return can take about twice as long (Curran et al. 2014). Active restoration significantly accelerates these recovery times (Curran et al. 2014), but potentially not enough to bring about timely reductions in a conservation targets' vulnerability to climate change. Despite success being more likely if individuals are released into high quality habitat, or in the centre of a species' range, reviews of reintroduction and reinforcing actions have revealed failure rates to be as high as 77%, where failure is the inability to establish a self-sustaining population (Griffith et al. 1989, Wolf et al. 1998, Seddon et al. 2014). Hence, while actions that accommodate change do not need to compete with societal needs under climate change, the strategy remains moderately risky in terms of its ability to deliver on conservation goals and objectives.

Dual benefit actions are, at least hypothetically, a relatively low risk approach to combating indirect climate change impacts because they provide practitioners with a platform to understand community needs and values under climate change, and importantly, an avenue to help shape their response (Roberts et al. 2012). The concept of ecosystems providing essential services for human survival has been successful in increasing the importance of nature conservation on policy agendas worldwide (Gomez-Baggethun et al. 2010, Skroch and Lopez-Hoffman 2010). However, dual benefit actions are still in their infancy and their ability to effectively reduce climate vulnerability for both humans and conservation targets remains uncertain (Doswald et al. 2014). Furthermore, some have argued that dual benefit actions are constrained in terms of what they can do for climate-imperilled species (McCauley 2006, Ghazoul 2007, Redford and Adams 2009). For the realised risk associated with dual benefit actions to remain low, conservation goals and objectives cannot be over-compromised or forgotten in the pursuit of societal needs under climate change.

Feasibility

Evaluating the feasibility of alternative actions is not intended to guide practitioners toward implementing only the simplest actions, but rather to help them identify barriers and obstacles to actions being effectively implemented in the real world that may have otherwise been ignored. Common criteria for assessing feasibility include technical and knowledge demands (Nichols and Williams 2006), direct costs and opportunity costs (Bottrill et al. 2008, McDonald-Madden et al. 2010), information availability (Maxwell et al. 2015b), and consistency with existing laws and policy (Stein et al. 2014). While some of these criteria can be used to compare among alternatives (e.g., the relative technical demands of each action), others may be an absolute limitation that actions can not violate (e.g. legalities; Stein et al. 2014). It is difficult to generalise on how practicable resistance, accommodation and dual benefit actions are without knowing the specific ecological and social context in which they are implemented. Nonetheless, our hypothetical assessment of the relative feasibility of these three broad strategies is as follows.

We consider a resistance strategy to be the most feasible approach to combat indirect climate change impacts because it involves actions that the conservation community have already employed across broad scales and for multiple decades. Expanding or designating new protected areas requires significant ecological information, but much of this information can be found in large, publicly available data sets (IUCN 2014). Furthermore, designing effective marine and terrestrial protected areas is made easier with free and readily available decision-support tools (e.g. Marxan with Zones - Watts et al. 2009, Segan et al. 2011, Watson et al. 2011). At the same time, the heavy financial demands to purchase and manage protected areas can reduce their feasibility in some regions (Watson et al. 2014). Improving the enforcement of conservation laws and regulations can be achieved simply by increasing on-the-ground personal, although this is expensive, and optimizing enforcement efforts to be more cost-effective presents a substantial challenge for conservation (Plumptre et al. 2014).

Using conservation actions to accommodate change is a relatively young and untested approach to climate adaptation. Although there is a large literature on restoration ecology, which includes identifying priority regions for restoration (Shoo et al. 2011), there is little consensus on what the best restoration approaches are (e.g. passive versus active restoration; Shoo and Catterall 2013), which is often site and context dependent (Suding et al. 2004, Curran et al. 2014). The lack of predictive tools and general conceptual framework to guide restoration mandates careful and precise analysis before implementation, particularly for restoration in ecologically and socially complex regions (Wang et al. 2015). Reintroduction and reinforcement efforts are also knowledge and resource intensive, and require a formal decision process to evaluate the potential benefits and risks (Schwartz and Martin 2013).

Relative to actions that promote resistance and change, we consider dual benefit actions to be the least feasible approach to addressing indirect climate change impacts because they require broad skills across not only conservation practice but also human development practice. Moreover, a variety of policy and legal barriers can pose significant challenges to operationalizing dual benefit actions (Chong 2014), as can unstable technical capacity within government departments (Hills et al. 2013). However, the success of dual benefit actions ultimately depends on the ability to effectively engage human communities with nature-based solutions to environmental problems, which demands a comprehensive understanding and analysis of human behavior, values and needs. While engaging in the needs of local communities and utilizing their traditional ecological knowledge is the norm in places like Melanesia (Jupiter et al. 2014, Gurney et al. 2015), many conservation scientists have little or no formal background in sociology, which often makes this a daunting task. However, dual benefit actions could be made more feasible with the use of negotiation tools that facilitate effective environmental agreements between conflicting stakeholders (Maxwell et al. 2015a), or learning from how numerous community conservation programs have met or failed to meet human needs in the past.

Conclusion

Conservation efforts largely target anthropogenic threats, especially those that lead to habitat loss and overexploitation of natural resources and pollution (Baillie et al. 2004, Evans et al. 2011). There has been rapidly increasing efforts to understand and plan for the direct impacts of climate change on species and ecosystems. Only recently has it become clear the climate change is shifting anthropogenic threatening processes around the land and seascape – demanding a new perspective on climate adaptation efforts. As the first real impacts of human-forced climate change are being felt across Earth (IPCC

2014a), we now need to progress to thinking about how changes in human behaviour as a result of climate change will present new threats, and also new opportunities, for conservation. Integrating these indirect impacts of climate change into conservation vulnerability assessments will require the strengths of social-ecological system models, and drawing on information from other, non-ecological sectors on likely human responses climate change. Conservation goals and objectives will need to be revised to ensure they are pragmatic and capture species and ecosystems that are vulnerable to indirect climate change impacts. Addressing indirect impacts will require a portfolio of actions that either promote resistance, accommodate change or identify dual benefits for biodiversity and human wellbeing. Here we have provided a framework and an initial assessment of the risk and feasibility associated with these alternatives. Determining actual risk and feasibility levels will require greater implementation and monitoring of how these alternatives perform in the real world. Addressing indirect impacts using the climate-smart conservation cycle outlined in this review will ultimately permit more realistic assessment and pragmatic planning for conservation needs in the near future.

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Appendix 2 – One-third of global protected land is under intense human pressure

Kendall R. Jones, Oscar Venter, Richard A. Fuller, James R. Allan, Sean L. Maxwell, Pablo Jose Negret, James E.M. Watson

Abstract

In an era of massive biodiversity loss, the greatest conservation success story has been the growth of protected land globally. Protected areas are the primary defense against biodiversity loss, but significant human activity within their boundaries can undermine this. Using the most comprehensive global map of human pressure, we show six million km^2 (32.8%) of protected land is under intense human pressure. For protected areas designated before the Convention on Biological Diversity was ratified in 1992, 55% have since experienced human pressure increases. These increases were lowest in large, strict protected areas, showing they are potentially effective, at least in some nations. Transparent reporting on human pressure within protected areas is now critical, as are global targets aimed at efforts required to halt biodiversity loss.

Main

In response to massive worldwide biodiversity loss (Barnosky et al. 2011), the global extent of protected land has roughly doubled in size since the 1992 Earth Summit in Rio de Janeiro, with more than 202,000 protected areas now covering 14.7% of the world's terrestrial area (UNEP-WCMC & IUCN 2017). The recent expansion has been closely associated with Aichi Biodiversity Target 11, which mandates inclusion of at least 17% of terrestrial areas in effectively managed and ecologically representative protected areas by 2020 (Convention on Biological Diversity (CBD) 2010). Protected areas have various management objectives, ranging from strict biodiversity conservation areas (IUCN category I-II) to zones permitting certain human activities and sustainable resource extraction (IUCN category III-VI), but the primary objective of all protected areas with an IUCN category is to conserve nature (Dudley et al. 2008). As such, maintaining the ecological integrity and natural condition of these areas is essential to ensure the protection of species, habitats and the ecological and evolutionary processes that sustain them (Convention on Biological Diversity (CBD) 2010).

The increasing growth and overall extent of protected areas is deservedly celebrated as a conservation success story (Watson et al. 2016a), and there is no doubt that well managed protected areas can preserve biodiversity (Coetzee et al. 2014; Gray et al. 2016). However, despite the clear relationship between human activities and biodiversity decline (Newbold et al. 2015), and the prevalence of these activities inside many protected areas (Laurance et al. 2012), there has been only one global assessment of multiple human pressures within protected areas (Geldmann et al. 2014). This study used low resolution human pressure data (10km^2), considered only a small subset of global protected areas (n = 8,950), and ignored many important human pressures, such as roads and navigable waterways (Laurance et al. 2009), livestock grazing (Kauffman & Krueger 1984) and urbanization (Aronson et al. 2014). A comprehensive analysis of cumulative human pressure within protected areas, and how this has changed since the Convention on Biological Diversity was ratified, is necessary to assess how human pressure inside protected areas may impede progress towards international conservation targets (Convention on Biological Diversity (CBD) 2010).

Here we use the most comprehensive global map of human pressure on the environment (the human footprint; *14*) to quantify the extent and intensity of human pressure within protected areas, and how this has changed since the Convention on Biological Diversity was ratified. The human footprint provides a single pressure metric combining data on built environments, intensive agriculture, pasture lands, human population density, night-time lights, roads, railways, and navigable waterways (Venter et al. 2016). The presence of these pressures is directly linked to constraints on and declines in biodiversity (Safi & Pettorelli 2010; Newbold et al. 2015; Tucker et al. 2018). We delineate areas of intense human pressure in protected areas (human footprint >= 4; see methods), and explore how excluding these areas would affect measurements of progress towards Aichi Target 11. We also assess the impact of protected area size and IUCN management category on patterns of human pressure within protected areas.

We find that the average human footprint score within protected areas is 3.3, almost 50% lower than the global mean of 6.16 (Venter et al. 2016). Despite this, human activities are prevalent across many protected areas, with only 42% of protected land free of any measurable human pressure (Fig. S1, S2). Areas under intense human pressure make up 32.8% (6,005,249 km^2) of global protected land (Fig. 1), and more than half (57%) of all protected areas contain only land under intense human pressure (concentrated in western Europe and southern Asia; Fig. 1). Just 4,334 protected areas (10% of analyzed areas; see methods) are completely free of intense human pressure (Fig. 1) and these primarily occur in remote areas of high latitude nations, such as Russia and Canada.

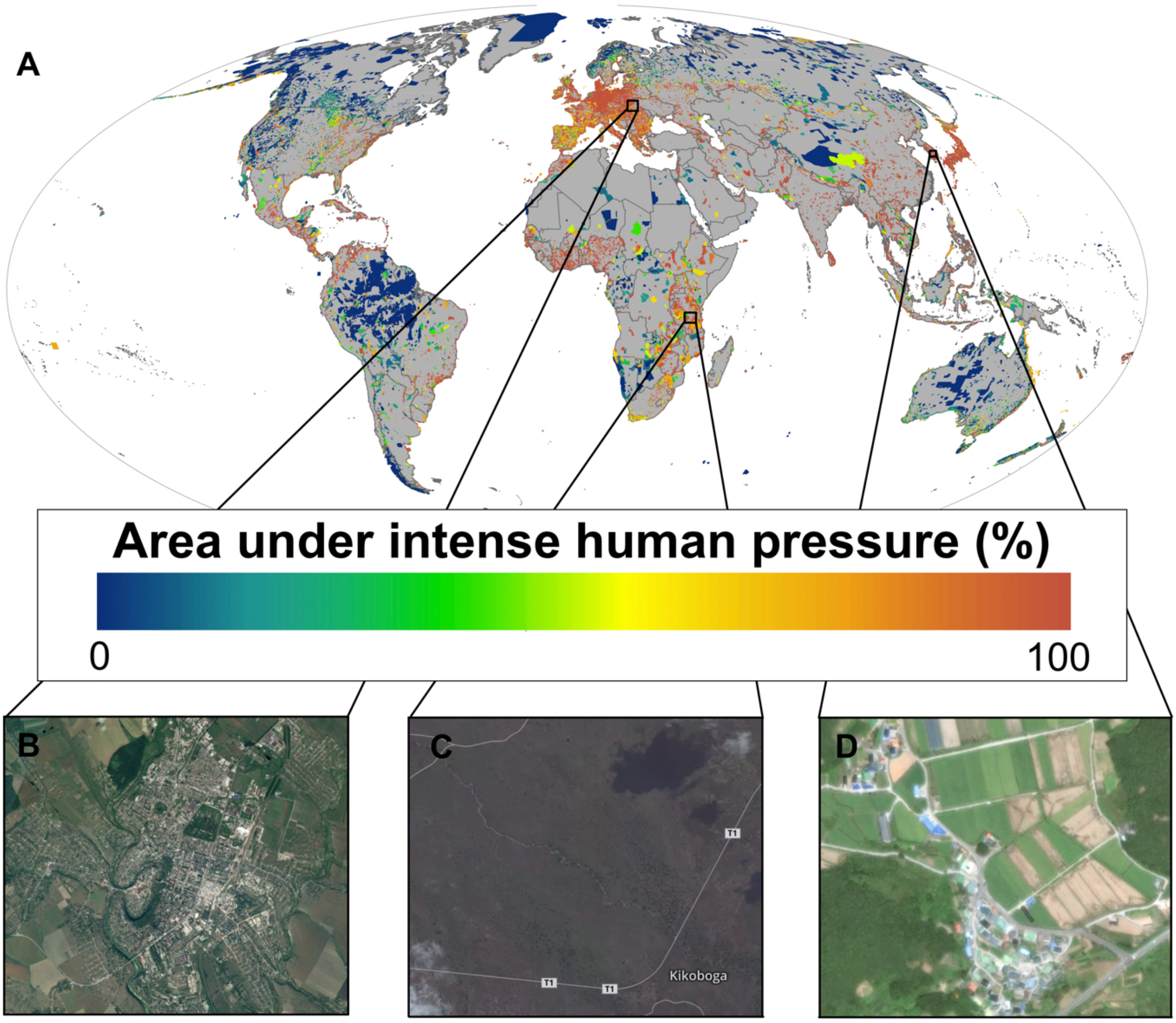

Figure 1: Human pressure within protected areas. A, proportion of each protected area that is subject to intense human pressure spanning from low (blue) to high (orange). B, Kamianets-Podilskyi, a city within Podolskie tovtry national park, Ukraine. C, Major roads fragment habitat within Kikumi national park, Tanzania. D, Agriculture and buildings within Dadohaehaesang national park, Korea. Photo Credits: Google Earth

Protected areas with strict biodiversity conservation objectives (IUCN category I-II) are subject to significantly lower levels of human pressure (Kruskal-Wallis test; $H = 5045.2$, $p < 0.001$; Fig. S3a), and a lower proportion of their area under is intense human pressure (Kruskal-Wallis test; $H = 4609.6$, $p < 0.001$; Fig. S3b), compared to those permitting a wider range of human activities (Table 1). This effect is not sensitive to the threshold used to determine intense human pressure (Fig. S4), and there are still a considerable number of less strict protected areas (IUCN III-VI) under low human pressure (Fig. S4). Smaller protected areas are much more likely to have high levels of human pressure than large protected areas (Fig. 2; linear regression; t-value = -58.02, $P < 0.001$). Nonetheless, many small protected areas contain low human pressure (Fig. 2) and they can be crucial for providing habitat in highly modified landscapes (Ricketts et al. 2005). This is especially true in protected areas where biodiversity has persisted under high human influence, and traditional management practices (IUCN VI) can maintain biodiversity values (Moguel & Toledo 1999).

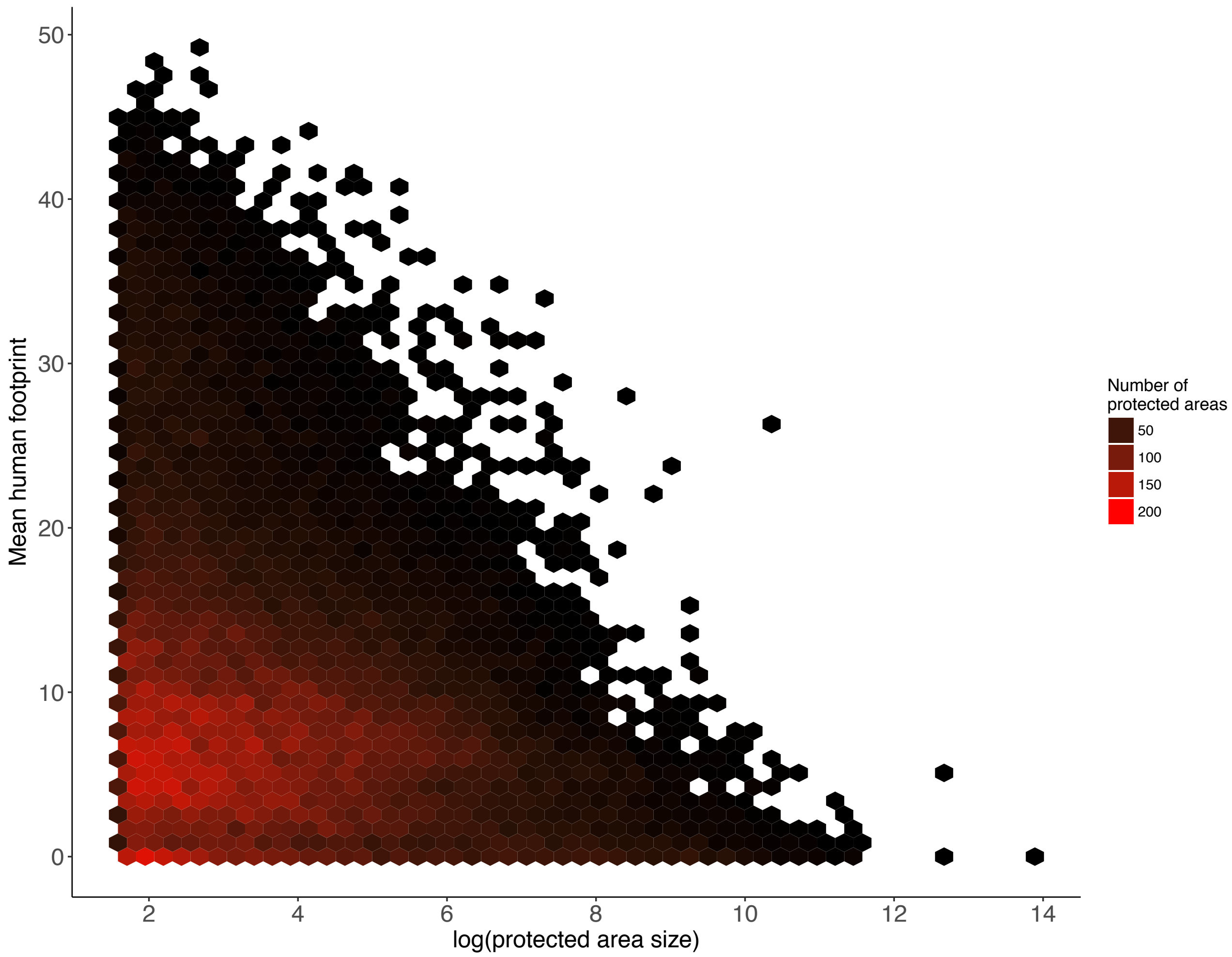

Figure 2: Influence of protected area size on human pressure intensity. Size of protected area (x-axis) versus mean Human Footprint scores within each protected area (y-axis). Due to the large number of overlapping points, values have been grouped into hexagonal bins, with brighter red bins containing more protected areas.

Mean human pressure has increased substantially since the Earth Summit, both worldwide (9% increase; Venter et al. 2016) and within protected areas (6% increase; Table S1). Human pressure increased in 55% (n = 11390) of protected areas designated in or before 1993, with substantial increases (mean human footprint increase > 1) occurring in 10%

(n=3966; Fig. S5). While strict protected areas (IUCN I-II) have the lowest current levels of human pressure, IUCN management category does not appear to affect the rate at which human pressure has increased (Table S1). Protected areas designated after 1993 have a lower level of intense human pressure within their borders, compared to those designated in or before 1993, suggesting that recent protected area establishment may be targeting a higher percentage of area under low human pressure (Table 1).

Table 1. Influence of protected area category on current human pressure. Strict biodiversity conservation areas (IUCN category I-II) contain lower levels of human pressure than protected areas which permit a broader range of activities (e.g. non-industrial resource use; IUCN category III-VI). NA represents those protected areas without an assigned IUCN category. Protected areas smaller than 5km^2 are excluded.

IUCN category	# of protected areas (area km^2)	Mean human footprint	Area under intense pressure (%)
I	3992 (2,089,560)	1.27	12.4
II	3628 (4,529,337)	2.12	24.1
III	1672 (199,062)	2.42	24.0
IV	7412 (2,410,055)	3.68	36.6
V	8378 (2,557,816)	5.21	45.8
VI	2365 (2,859,949)	2.4	26.4
NA	14481 (4,502,128)	4.38	44.2
All protected areas	41928 (19,147,911)	3.26	32.8
Protected areas est. pre 1993	22046 (11,048,058)	3.36	34.9
Protected areas est. post 1993	19882 (8,099,852)	3.13	29.7

The most concerning increases in human pressure are in those landscapes that were intact when a protected area was designated. Within protected areas designated during or before 1993, 280,000km^2 of land has changed from a low to an intense human pressure category (Table S1). Strict protected areas (IUCN I-II) lost far less of their low-pressure land than non-strict protected areas (3.6% vs 8%; Fig. S6), and by far the largest losses occurred in those without an IUCN category (17%; Fig. S6).

Human pressure inside protected areas is likely compromising national progress towards Convention on Biological Diversity obligations. Almost three quarters of nations (n = 137, 70%) have > 50% of their protected land under intense human pressure (Fig. S7; Table S2). If one assumes that protected land under intense human pressure does not contribute towards conservation targets, we show that 74 of the 111 nations that have reached a level of 17% protected area coverage would drop out of that list (Fig. S7; Table S2).

Moreover, the protection of some biomes (e.g. mangroves and temperate forests) would drop by >70% (Fig. 3a). While 301 (38%) ecoregions (ecologically similar areas) currently have more than 17% coverage inside protected areas (Fig. 3b), excluding land subject to intense human pressure would almost halve this (n= 167, 21%, Fig. 3c). These results make a clear case that nations reporting solely on the area of protected land may be overestimating the true level of protection for biodiversity, and highlight the need for international reporting on protected areas to include robust, reproducible measures of human pressure and ecological condition (Watson et al. 2016a). It is also important to note that we are unable to capture the full range of human impacts on biodiversity, such as ecological shifts associated with changing climate and disturbance regimes (Scheffers et al. 2016), which should also be incorporated into measures of protected area condition.

While we show that human pressure may be compromising the conservation value of protected lands worldwide, we are not suggesting that high pressure protected areas be degazzetted or defunded. To the contrary, it is crucial that nations recognize the profound conservation gains that can be realized by ‘upgrading’ (increasing the strictness of protection zones) and restoring degraded protected areas, while respecting the needs of local people (Pringle 2017). A crucial part of this will be combatting the chronic underfunding of protected areas worldwide, which will require recognizing and quantifying the return on investment that well-managed protected areas provide, through protection of cultural heritage, improvements in economic and social well-being, and the natural capital they hold (Balmford et al. 2002; Watson et al. 2014). Funding could also be increased through mechanisms which allow nations to trade or offset conservation funding and commitments, so wealthy nations can support conservation in poorer nations (Lindsey et al. 2017). Our finding that there is no relationship between the degree of human pressure and IUCN categories III-VI points to a need for nations to categorize protected areas based on consistent classifications of permitted human activities, which would ensure that IUCN categories better reflect the actual impacts of human activities within protected areas (Horta e Costa et al. 2016).

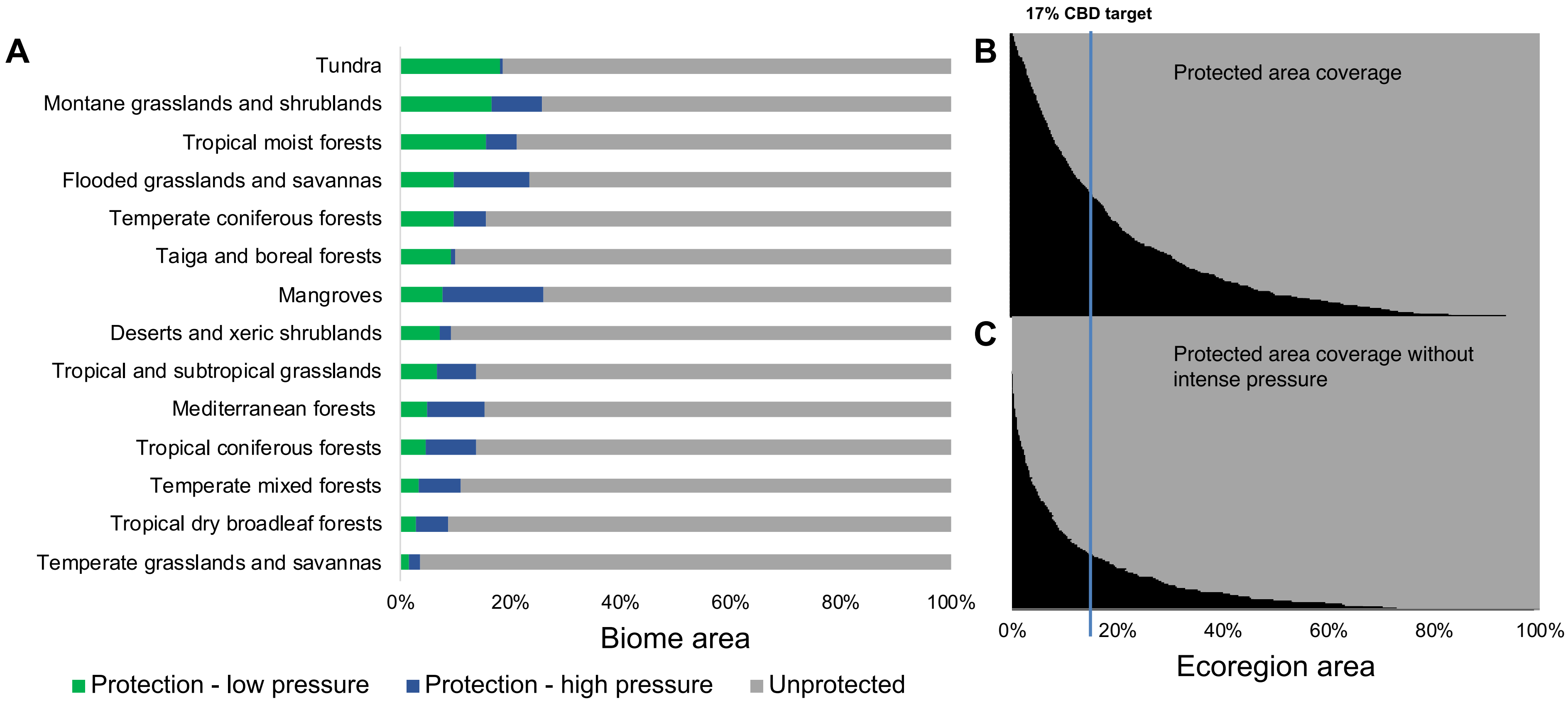

Figure 3: Human pressure compromises protection of biomes and ecoregions. A, Biome area contained in protected areas with low human pressure (Protection – Low Pressure), contained in protected areas subject to intense human pressure (Protection – Intense Pressure) and not protected (Unprotected). B, Over one-third (38%) of ecoregions have >17% (vertical blue bar) of their area protected. C, When protected land under intense human pressure is excluded, the number of ecoregions meeting the 17% CBD target is almost halved (21%).

We show that human pressure is prevalent within many protected areas, but our work is subject to three caveats. First, while we explore a scenario where land under intense human pressure does not contribute towards conservation targets, some aspects of biodiversity can persist in areas of high human pressure (e.g. mixed agricultural land (Phalan et al. 2011)), and some protected areas are intentionally placed in high-pressure areas. Second, the human footprint does not account for all pressures affecting biodiversity, such as poaching or climate change. This is especially true for developing regions, where activities such as small-scale shifting agriculture and poaching are exerting significant pressure on biodiversity in many protected areas (Laurance et al. 2012). Third, the human footprint measures the pressure humans place on the environment, not the realized state or impact on biodiversity. Further studies investigating how natural systems within protected areas respond to specific human pressures, or assessing the impacts of human pressure on biodiversity within protected areas at a local scale, would provide valuable additional information for measuring progress towards CBD commitments.

The Convention on Biological Diversity provides a unique opportunity to overcome one of society’s grandest challenges – halting global biodiversity loss. Many nations report being on track to meet their commitments (UNEP-WCMC & IUCN 2017), but our analysis suggests this progress may be undermined by widespread human pressure inside protected areas. As nations continue to expand their protected area estates, there is clearly an urgent need for them to undertake objective assessments of human pressure and habitat condition within protected areas. These efforts must be combined with better management practices in land beyond protected areas, to ensure nature conservation goals can be more fully achieved across diverse landscapes in the long-term.

Materials and Methods

Protected Area Data

Data on protected area location, boundary, and year of inscription were obtained from the 2016 World Database on Protected Areas (*2*). Following similar global studies (*26*), we extracted protected areas from the WDPA database by selecting those areas that have a status of "designated", "inscribed", or "established", and were not designated as UNESCO Man and Biosphere Reserves. We included only protected areas with detailed geographic information in the database, excluding those represented as a point only. Many protected areas overlapped spatially, but contained different IUCN categories. To eliminate these overlaps and avoid double counting protected areas, we followed WDPA best practice guidelines (https://www.protectedplanet.net/c/calculating-protected-area-coverage) and previous studies (*26*) and 'dissolved' overlapping areas into a single polygon, assigning overlapping areas the strictest IUCN category of all protected areas in that location. To reduce computational burden, we used the simplify polygon tool in ArcGIS 10.4 to remove redundant vertices (tolerance was set at 1000m). We then used a layer of terrestrial country boundaries (http://datadryad.org/resource/doi:10.5061/dryad.6gb90.2) to clip protected area polygons to only include terrestrial areas. From this base dataset, we selected only those protected area polygons > 5km^2 in an attempt to minimise miscalculations due to data resolution issues. Excluding protected areas < 5km^2 eliminated 73% of individual protected areas (mostly in Europe). However, because most protected land is contained in a small number of very large protected areas, and three-quarters of eliminated protected areas were < 1km^2 in overall size, this only reduced the total area of protected land analyzed by 0.5%.

As the year of establishment was unknown for ~10% of this processed protected areas layer, we followed recent research (*27*, *28*) and assigned an establishment date by randomly selecting a year (with replacement) from all protected areas within the same country with a known date of establishment. For countries with fewer than five protected areas with known year of establishment, a year was randomly selected from all terrestrial protected areas with a known date of establishment. The random assignment was repeated 1,000 times, to identify the median and year of establishment, which we assigned to each protected area without an establishment date.

Human Pressure Data

We used the recently revised human footprint map (*29*, *30*) to measure human pressure and habitat modification within protected areas. The revised human footprint map is a globally-standardized and temporally comparable measure of cumulative human pressure on the terrestrial environment at a 1km^2 resolution. The human footprint provides a cumulative score of eight in-situ anthropogenic pressures: urban centers, intensive agriculture, pasture lands, human population density, night-time lights, roads, railways and navigable waterways. To create the human footprint map, individual pressures were placed within a 1 – 10 scale based on their contribution to human influence on the natural environment. The standardized scores were then summed, giving a cumulative score of human pressure ranging from 0- 50 for each 1km^2 cell (some pressures are mutually exclusive while others can co-occur). A human footprint score below four indicates land which is predominantly free of permanent infrastructure, but may hold sparse human populations. A pressure score of 4 is equal to pasture lands, and considered a reasonable threshold of when land faces significant human activity and species are likely to be threatened by habitat conversion (*28*, *31*). For this analysis, we followed previous studies (*28*) and set a Human Footprint value of 4 or greater as a threshold criterion for intense human activity. This threshold value was set for the cumulative human footprint score, not for each stressor individually. We conducted this thresholding using both the 1993 and 2009 human footprint layers, to allow for calculations of change over time.

To explore the sensitivity of our results to the threshold used to define intense human activity, we calculated the area of intense human pressure within protected areas from each IUCN category using two additional definitions of intense human pressure:

1) A human footprint threshold of one or greater, which corresponds to any level of mapped human pressure (*32*). This identifies areas as under intense human pressure if they had any mapped human activity at all, and represents a highly sensitive threshold for mapping intense human pressure.

2) A human footprint threshold of seven or greater, which is equivalent to intensive agriculture (*30*, *33*). This identifies areas as under intense human activity if they contain intensive agriculture, or more intense pressures such as urban areas and roads, but allows pasture lands and low levels of human activity. This represents a more conservative threshold for mapping intense human pressure.

While the Human Footprint does not directly assess habitat condition via in situ measurements, the dataset was extensively validated through visual interpretation of satellite imagery (*29*,*30*), finding 88.5% agreement between Human Footprint data and visual interpretation scores. This validation process found that the human footprint is sometimes susceptible to false negatives, where pressures are actually present in locations where the Human Footprint map shows them as absent, and therefore the Human Footprint is likely a conservative estimate of human pressures.

Ecoregions

For ecoregional and biome analysis, we followed previous global studies (*28*, *34*) and used spatial distributions of 827 terrestrial ecoregions, grouped into 14 biomes or major habitat types (*35*). We excluded ecoregions which contain no human footprint data, leaving 790 for analysis. Ecoregion boundaries delimit areas within which ecological and evolutionary processes interact most strongly (*35*), and are used by international funding institutions and conservation organizations to guide broad-scale conservation investments (*36*).

Analysis of spatial data

All spatial data were processed using ESRI ArcGIS v10 in Mollweide equal-area projection. To analyze human pressures within protected areas, we first calculated the mean Human Footprint value, and the area of land under intense human pressures (Human Footprint ≥ 4), within all individual protected areas. We then repeated this analysis, treating all protected areas of the same IUCN category (IUCN I – VI) as one, rather than doing calculations at the individual protected area level. We repeated this analysis once more, treating all protected areas as one group, regardless of IUCN category. As outlined above, to explore the sensitivity of our results to different definitions of intense human pressure, we repeated these analyses using two different human footprint thresholds (Human Footprint ≥ 1 & Human Footprint ≥ 7) to define intense human pressure.

To assess change in human pressure since 1993, we followed previous studies (*37*, *38*) and extracted all protected areas which were established in or before 1993, as those established post 1993 could potentially have been impacted before their designation. We then calculated the mean Human Footprint value, and the area of land under intense human pressures (Human Footprint ≥ 4), within all individual protected areas, using both the 1993 and 2009 human footprint layers. We repeated this analysis, treating all protected areas of the same IUCN category (IUCN I – VI) as one, rather than doing calculations at the individual protected area level. We then repeated this analysis once more, treating all protected areas as one group, regardless of IUCN category.

To analyze how human pressure affects protected areas across countries and ecoregions, we extracted all 1km^2 cells from the Human Footprint that overlap with a protected area polygon. For country scale analysis we used a layer of terrestrial country boundaries recommended by the WDPA (http://datadryad.org/resource/doi:10.5061/dryad.6gb90.2), and then calculated the extent of protected land under intense pressure for each country. Because we exclude protected areas smaller than 5km^2, using our dataset to calculate protected area coverage would underestimate the true extent of national protected area networks. Therefore, we obtained country protected area coverage data from the WDPA (https://www.protectedplanet.net/c/protected-planet-report-2016/protected-planet-report-2016--data--maps-figures), which includes all protected areas regardless of size. To analyze how intense human pressure would affect progress towards the 17% CBD target, we subtracted the area of our refined protected area dataset that is under intense human pressure from total protected area coverage data obtained from the WDPA. This implicitly assumes that all protected areas smaller than 5km^2 are not under intense human pressure, so our estimates are likely conservative. To analyze how human pressure compromises protection of biomes and ecoregions, we repeated the above analysis, using biomes and ecoregions as the unit of calculation, rather than countries.

Statistical Analysis

To analyze the relationship between protected area IUCN category and human pressure, we calculated the mean human footprint of each protected area, and the proportion of each protected area under intense human pressure. We then conducted two separate Kruskal-Wallis tests, with IUCN category as our predictor variable in both tests, and mean human footprint or proportion of protected area under intense human pressure as our response variable. The Kruskal-Wallis test is a nonparametric (distribution free) test, and was used as our data violated the assumption of normality required by a one-way ANOVA. To analyze the relationship between protected area size and human pressure, we conducted a linear regression using protected area size as our predictor variable, and mean human pressure of each protected area as our response variable.

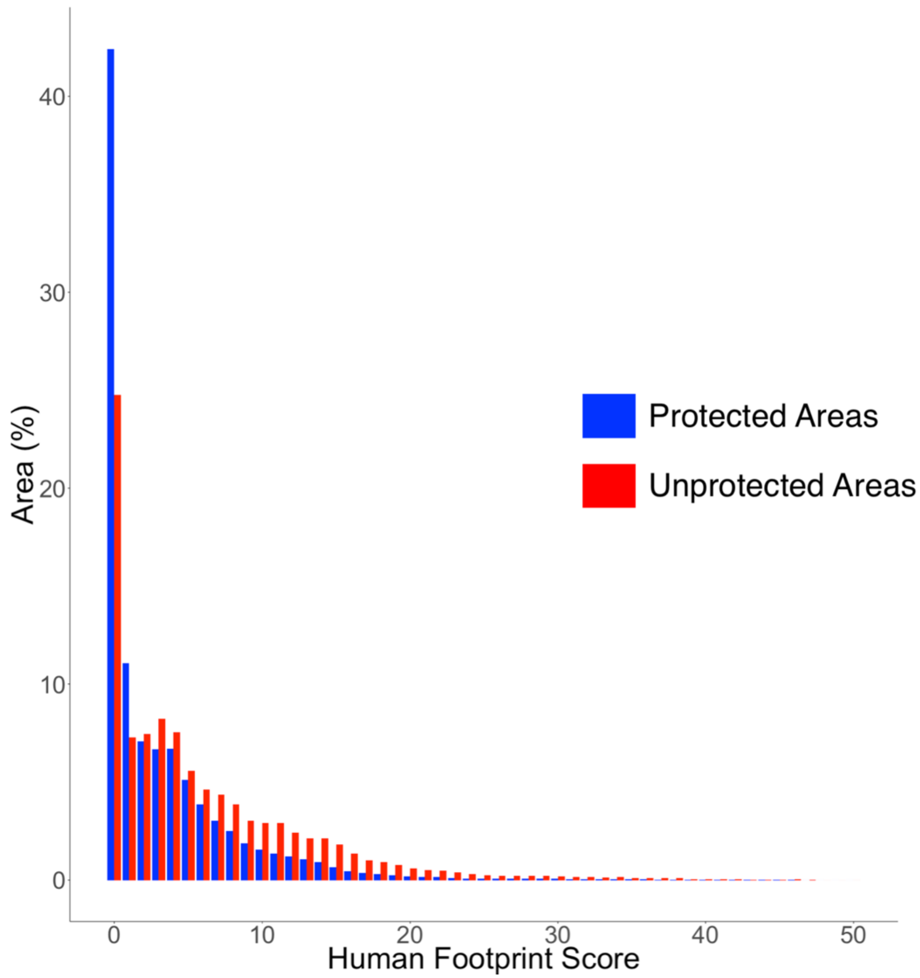

Figure S1. Frequency distribution of human footprint scores for Protected Areas (green bars) and unprotected areas (red bars). Area on the y-axis represents the total area of protected areas (green bars) and unprotected areas (red bars). The sum of all bars equals 100%.

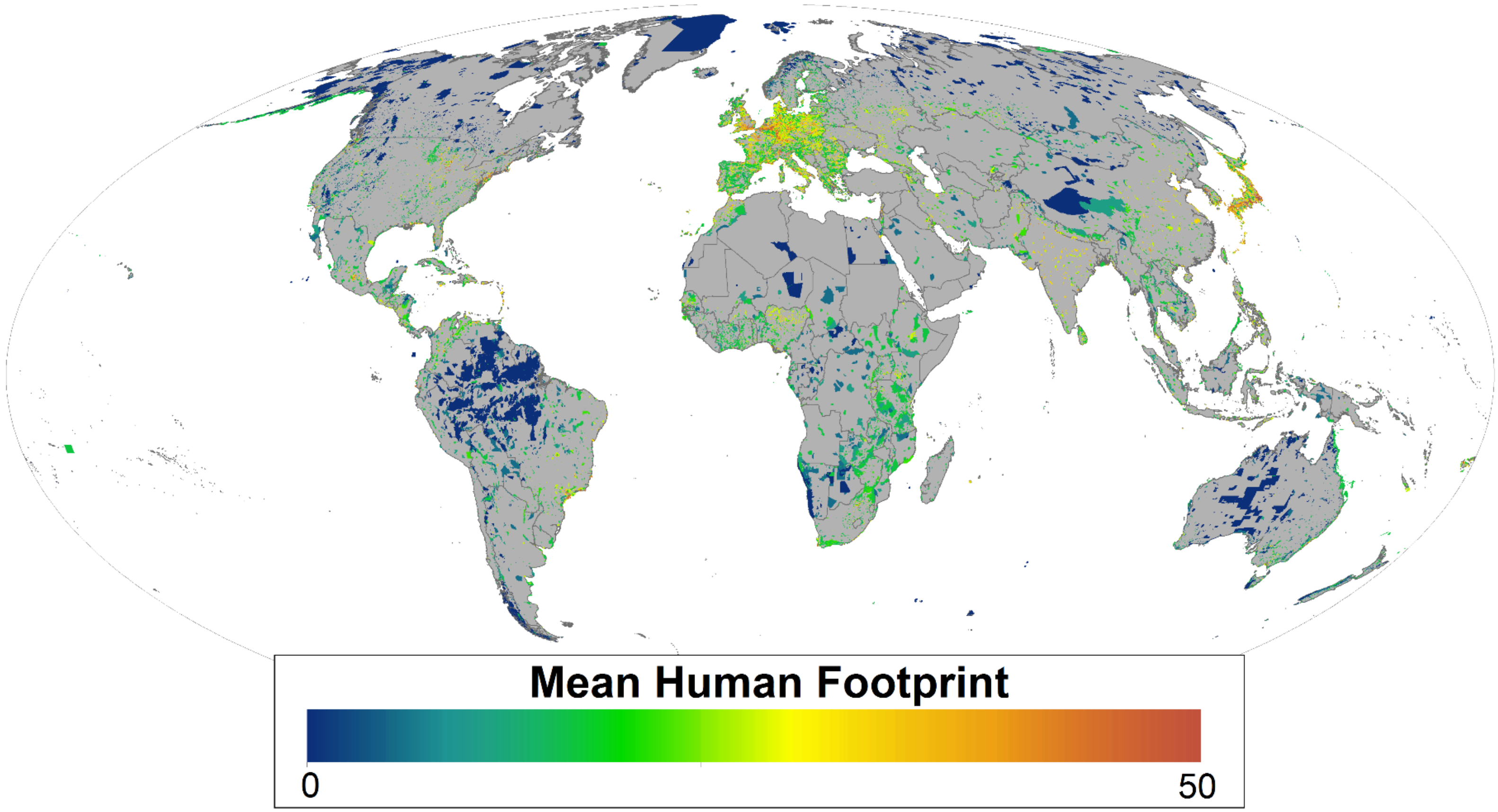

Figure S2. Current mean human footprint scores in protected areas. Protected areas with a mean human footprint of zero are shown in blue.

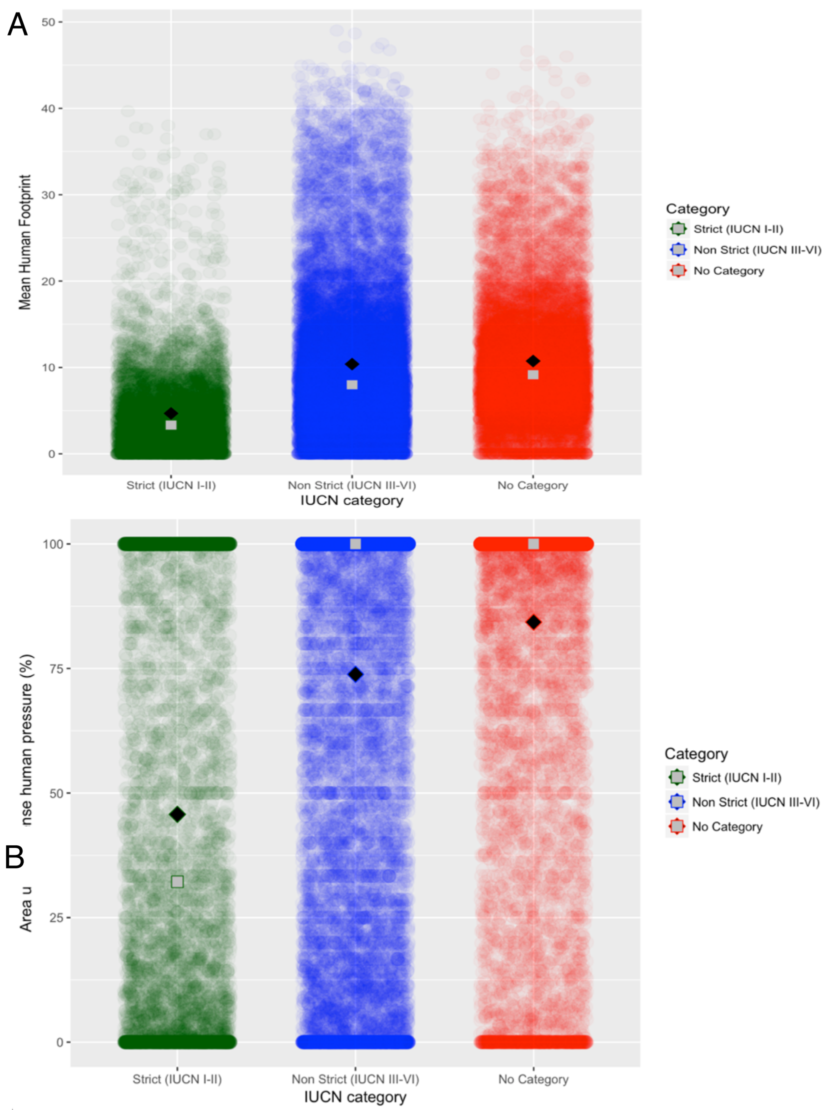

Figure S3. A, Percentage of protected area under intense human pressure, using three different human pressure thresholds to define intense human pressure. A, intense human pressure defined by human footprint scores >= 1. B, intense human pressure defined by human footprint scores >= 4 (equivalent to grazing land, with low human population densities). C, intense human pressure defined by human footprint scores >= 7 (equivalent to agricultural land). Mean values for all protected areas in each IUCN category are represented as a black diamond, and median values are represented by a grey square. Point color is darker where more points overlap. There are a large number of PAs with either 0% of area under intense human pressure, for example those in central Australia and the Arctic, or with 100 of area under intense human pressure, such as those in Europe. Colors correspond to IUCN management category.

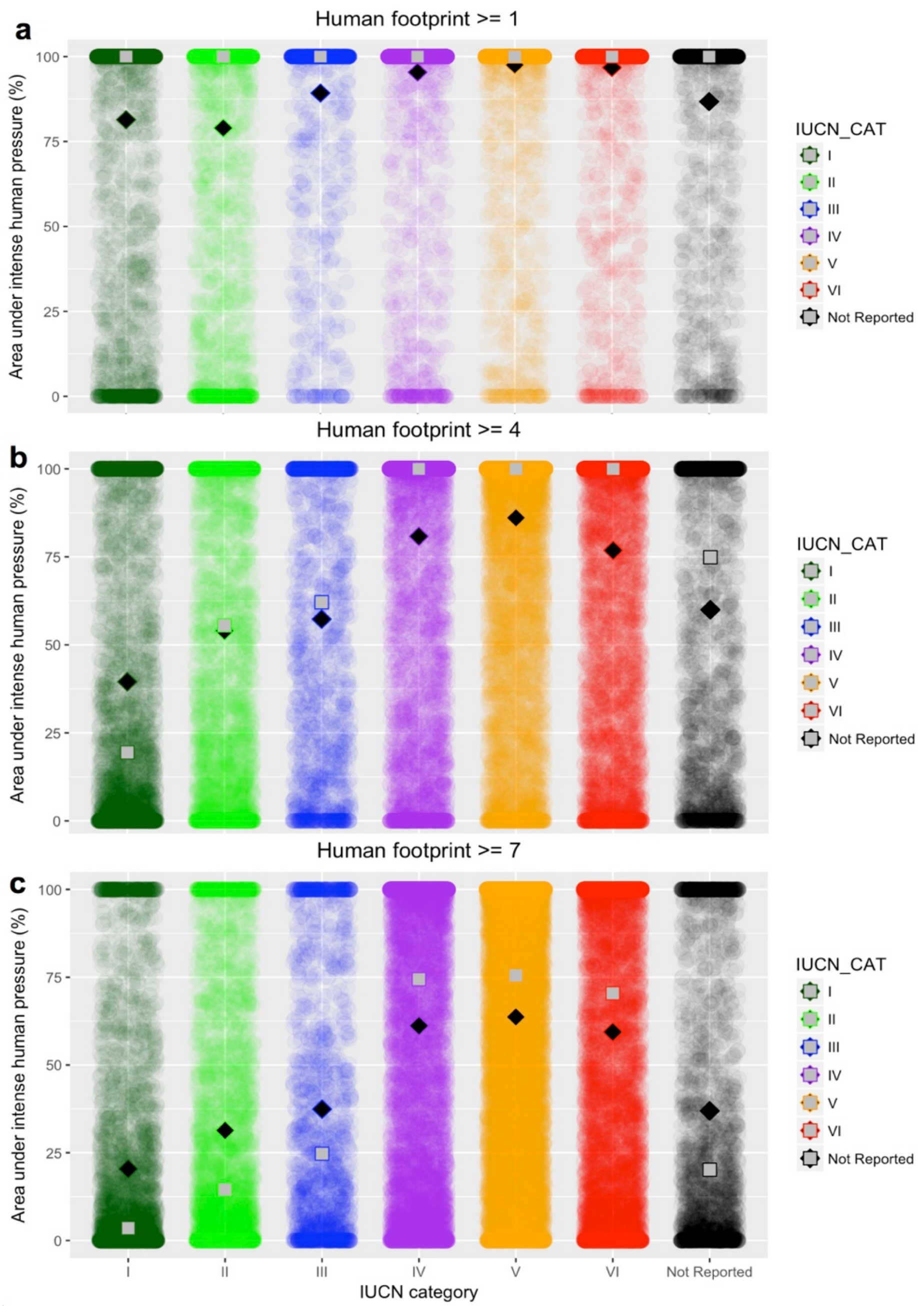

Figure S4. A, Average human footprint values within individual protected areas and B, percentage of protected area under intense human pressure, for Strict protected areas (IUCN categories I-II), Non-Strict protected areas (IUCN categories III-VI), and protected areas with no IUCN category (No Category). Mean values for all protected areas in each group are represented as a black diamond, and median values are represented by a grey square. Point color is darker where more points overlap (e.g. at 0% and 100%). There are a large number of PAs with either 0% of area under intense human pressure, for example those in central Australia and the Arctic, or with 100 of area under intense human pressure, such as those in Europe.

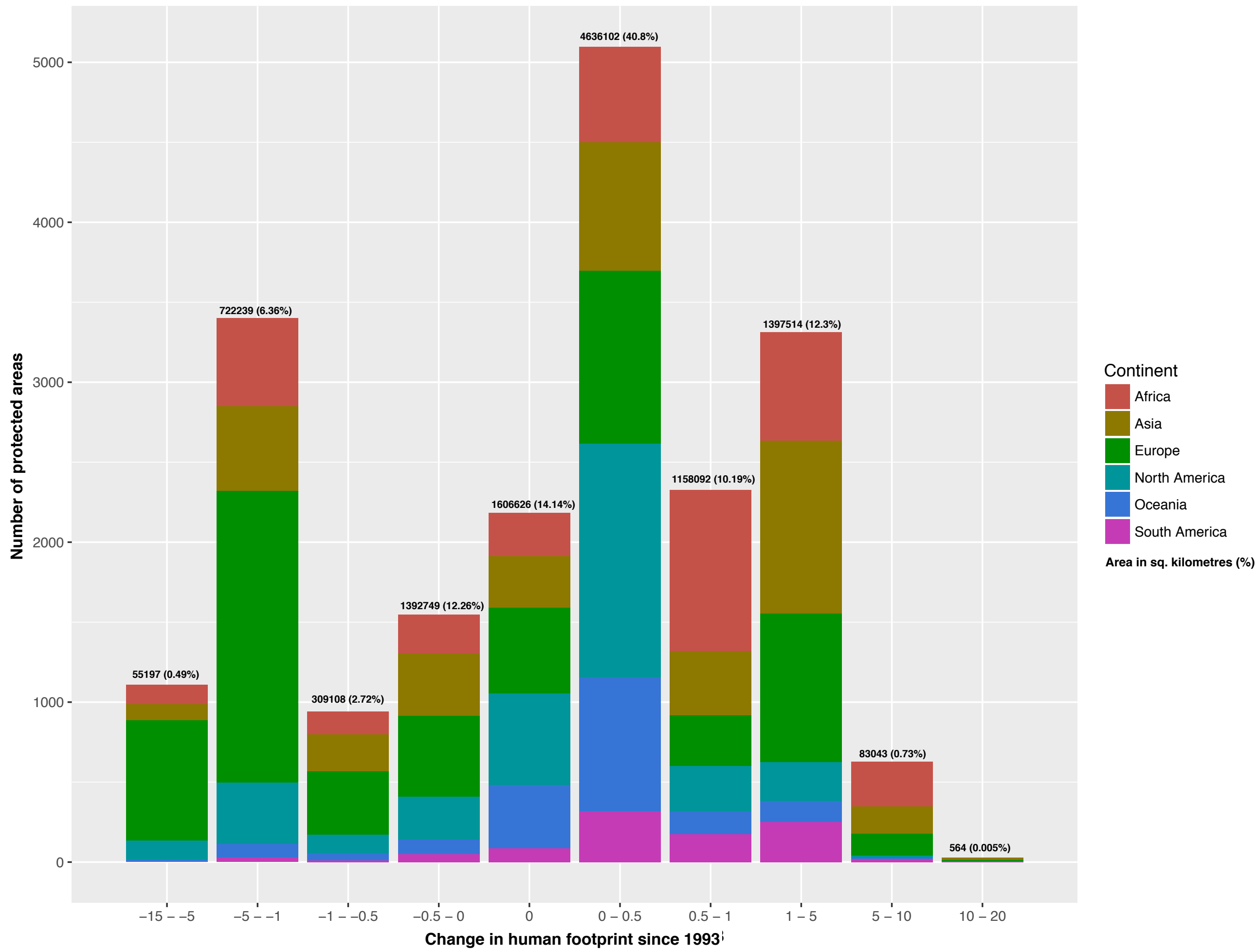

Figure S5. Frequency distribution of mean human footprint change since 1993 in protected areas. Colors specify the continent in which the protected area is situated

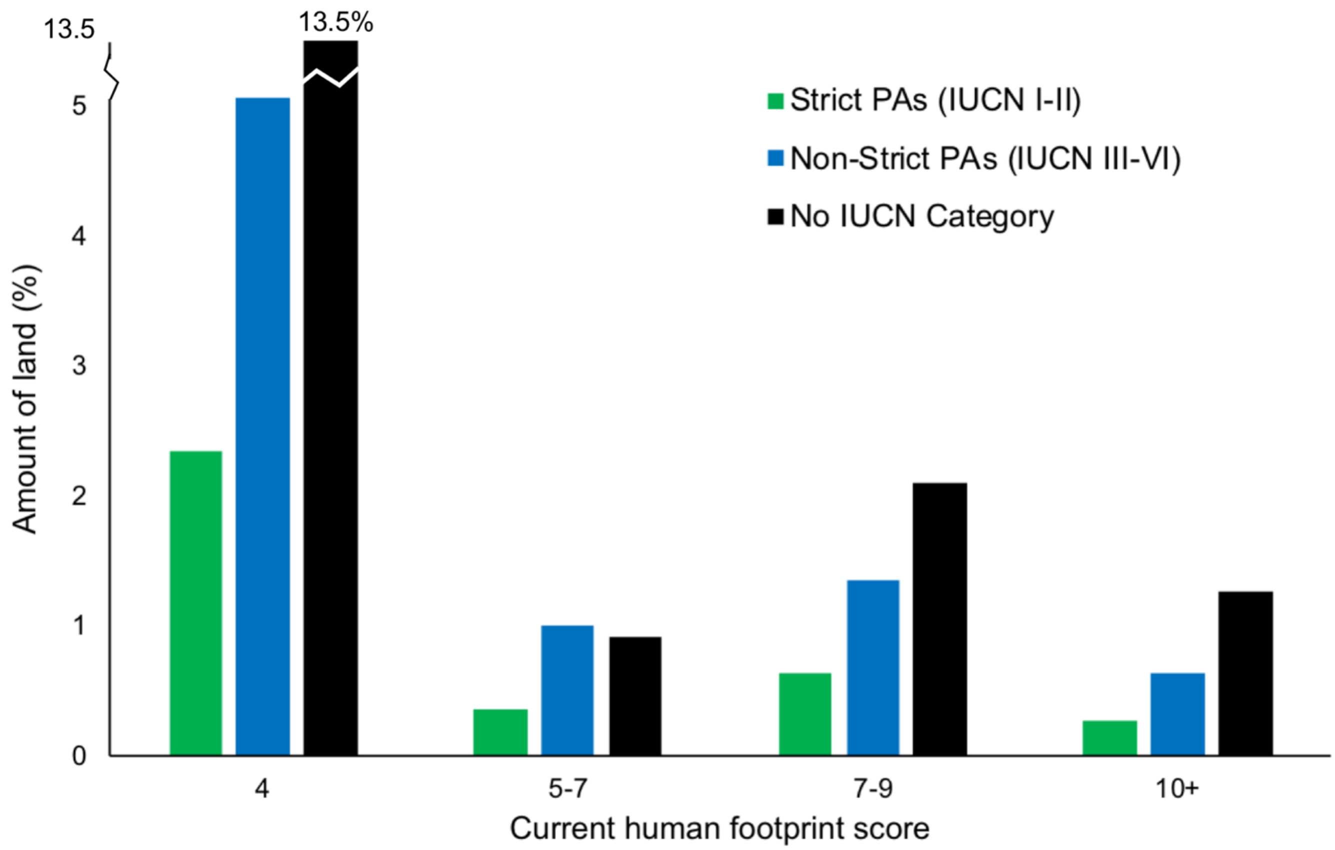

Figure S6. Conversion of low pressure land (HFP < 4) within protected areas since 1993. Frequency distribution of current human footprint scores for protected land that was under low human pressure (HFP < 4) in 1993, but is now under intense human pressure (HFP > 4). Colors specify the IUCN category of protected areas.

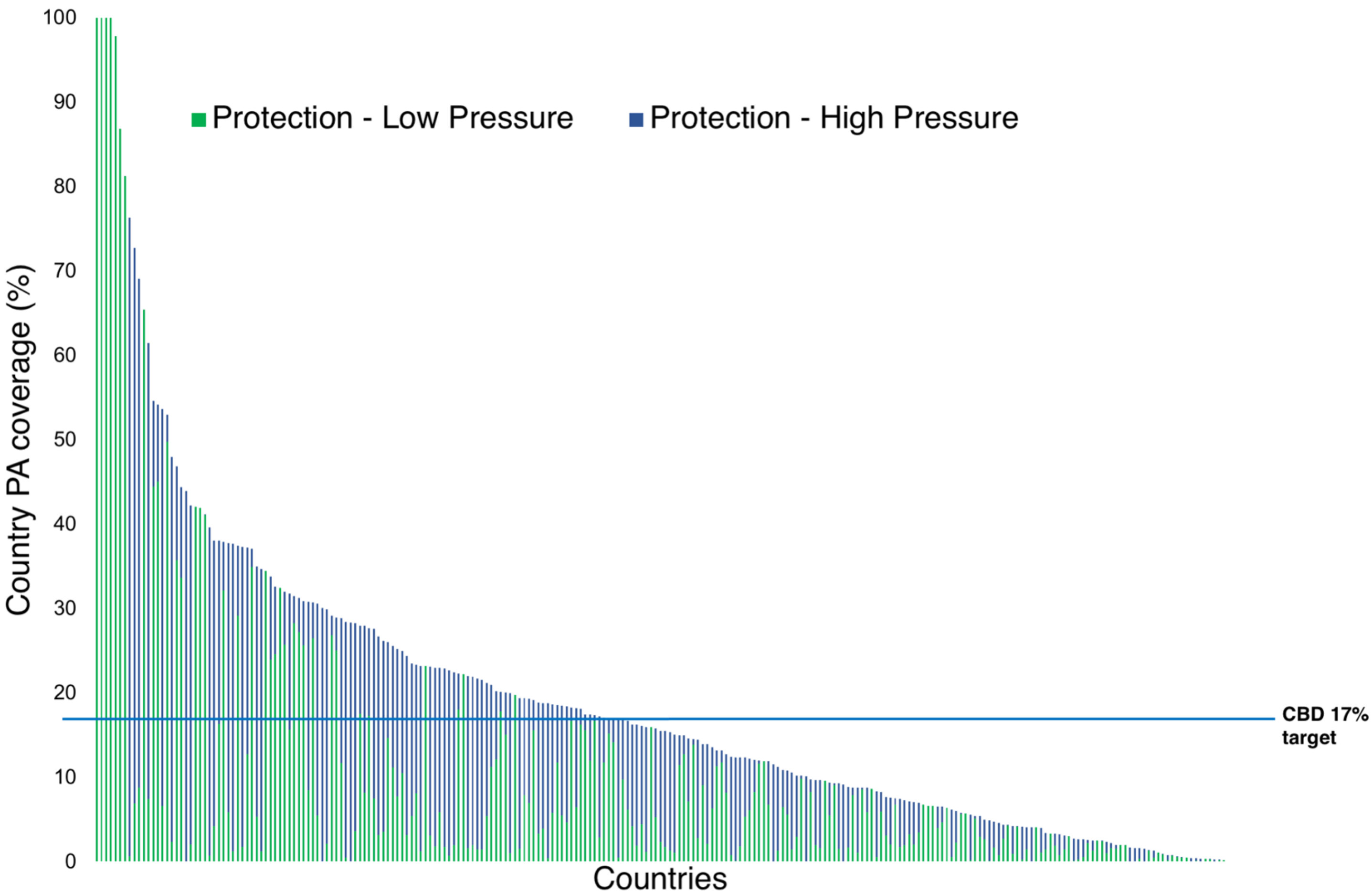

Figure S7. Percentage of country area contained in protected areas with low human pressure (Protection), and contained in protected areas subject to intense human pressure (Protection under pressure). Blue line represents the minimum 17% protected area coverage target set by the CBD. Countries with a green bar above the blue line have met their 17% obligation. Countries with an orange bar above the blue line would fail to meet the CBD 17% target if areas under intense human pressure were removed from calculations.

Table S1. Influence of protected area category on change in human pressure since 1993. Protected areas established after 1993 are excluded from this analysis as they may have been impacted by human pressure before their designation.

IUCN category	Mean human footprint			Area of intense human pressure (km^2)		
	1993	**2009**	**Change since 1993 (%)**	**1993**	**2009**	**Change since 1993 (%)**
I	1.13	1.20	6.19	158774	173495	1.01
II	2.03	2.12	4.43	690422	745946	1.81
III	3.59	3.55	-1.11	28348	30072	2.02
IV	3.58	3.87	8.10	646014	699042	2.97
V	4.66	4.96	6.44	789412	819131	1.61
VI	3.18	3.45	8.49	400788	467484	5.64
NA	5.19	5.44	4.82	791243	856389	4.62
All PAs	3.13	3.32	6.07	3505001	3791559	2.64