Socio-ecological drivers of fish biomass on coral reefs : the importance of accessibility, protection and key species

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Abstract

Coral reefs have the greatest biodiversity of any ecosystem on the planet and support ecosystem goods and services to million people who depend directly on them for food, economic income, coastal protection and cultural values. There is a clear consensus that accessibility through road networks and infrastructure expansion is a main driver of ecosystem conditions, with the most accessible resources being most at risk. Yet to date measuring the extent to which coral reefs are accessible to humans is strictly limited to examining the linear distance between fishing grounds and markets or ports. However, linear distance ignores ragged coastlines, road networks and other features that can affect the time required to reach fishing grounds from a human settlement. This thesis presents a double challenge: *(i)* developing new metrics of accessibility that account for seascape heterogeneity to better assess human impacts on coral reefs; and *(ii)* evaluating the importance of coral reef accessibility, in interactions with their management, to explain variations of fish biomass. First, I estimated the travel time between any given coral reef and human populations and markets based on the friction distance which is related to transport surfaces (paved road, dirt road, water) influencing transportation costs and the effective reach from human settlements. Then travel time was used to build a human gravity index, defined as human population divided by the squared travel time, to assess the level of human pressure on any reef of the world. I found that both travel time and gravity are strong predictors of fish biomass globally. Second, gravity was used to assess the effectiveness of marine reserves given the level of human pressure. The results highlighted critical ecological trade-offs in conservation since reserves with moderate-to-high human impacts provide substantial gains for fish biomass while only reserves located where human impacts are low can support populations of top predators like sharks which are otherwise absent from coral reefs. Third, using a downscaling of the travel time approach I illustrated how market proximity can affect the behaviour of fishermen and, ultimately, trigger changes in marine resource exploitation in North-Western Madagascar. Market access appears as a critical step toward a long-term management of coral reef fisheries. Fourth, I developed a new Community-Wide Scan (CWS) approach to identify fish species that significantly contribute, beyond the socio-environmental and species richness effects, to fish biomass and coral cover on Indo-Pacific reefs. Among about 400 fishes, I identified only a limited set of species (51), belonging to various functional groups and evolutionary lineages, which promote biomass and coral cover; such key species making tractable conservation targets. Within the context of global changes and biodiversity loss, the thesis challenges the sustainable and efficient management of coral reef socio-ecological systems with accessibility being the cornerstone but also the main danger in a near future where roads will expand and coastal human populations will grow.

Key words: fish community, fish biomass, ecosystem functioning, ecosystem services, human pressure, accessibility, gravity, Marine Protected Areas, coral reefs, socio-ecological systems, conservation.

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1. General introduction

1.1. Tropical coral reefs

1.1.1. Biodiversity hotspots in the middle of an oceanic desert

Corals appeared about 500 million years ago and first coexistence between fishes and coral reefs dates from the Devonian (420-359 Ma) (Bellwood *et al.* 2015). The vast majority of modern coral reefs as we know them today are less than 10,000 years old (Seard 2010), are located in shallow waters (< 50m water depth) within a tropical zone between 29° N and 31° S latitude so within an annual mean temperature range of approximately 22° to 29°C. Modern coral reefs are estimated to cover about 284,000 km^2 (Spalding *et al.* 2001) or less than 0.1% of the world's ocean surface.

Coral reefs support the world's greatest biodiversity of marine organisms (Roberts *et al.* 2002) with almost 1,000,000 (95% credible limits: 550,000– 1,330,000) of multi-cellular species worldwide (Fisher *et al.* 2015). In fact, coral reefs host no less than 6,000 fish species which represent the major group of vertebrates (Kulbicki *et al.* 2013). The group of Acanthomorphs comprises 92% of the reef fish species and its origin was estimated at -130 million years (Near *et al.* 2013) while several waves of colonization of coral reefs by fishes have been identified about 44 million years ago (Price *et al.* 2014). The distribution of reef fish biodiversity in the oceans has raised the interest of several generations of researchers (Bellwood & Meyer 2009) and still presents uncertainties (Cowman *et al.* 2017). Indeed, reef fish richness is distributed along a latitudinal gradient from the tropics to the poles, but also according to a longitudinal gradient, centered on the Indo-Australian Archipelago. The distribution of reef fish richness has been related to variables such as sea surface temperature and available reef area (Tittensor *et al.* 2010; Parravicini *et al.* 2013), as is proposed for the great land clades (Davies *et al.* 2007; Buckley & Jetz 2008; Kreft & Jetz 2010). However, taking into account historical and paleo-environmental factors seems also essential to explain the distribution of current reef fish biodiversity (Tittensor *et al.* 2010; Parravicini *et al.* 2013; Pellissier *et al.* 2014).

Almost 200 years ago, Charles Darwin first asked how the dazzling biodiversity of coral reefs could flourish in relatively barren oceans (Darwin 1842). In fact, phytoplankton production is paradoxically enhanced near an island-reef ecosystem by the Island Mass Effect (IME). This phenomenon is caused by nutrients that result from decomposing reef animals, upwellings of nutrient-rich colder waters toward the surface, mixing effects of waves and currents, sedimentation from land erosion and human-derived runoffs from agriculture and urban development (Gove *et al.* 2016). Such ocean oases or hotspots increase nearshore phytoplankton biomass by up to 86% over oceanic conditions, providing basal energetic resources to higher trophic levels that support great fish biomass for example (Gove *et al.* 2016). A healthy and well-managed coral reef can yield between 0.2 and 40 tons of fish and seafood per square kilometer per year (Dalzell 1996; Newton *et al.* 2007). These estimates lead to an annual yield of 0.056 - 11.36 million tons of fish and seafood per year (for the 284,000 km^2 of reefs) while total global landing was estimated at 1.4 - 4.2 million tons per year (Pauly *et al.* 2002). Preserving the biodiversity of healthy reefs is the key to maintaining sustainable reef fisheries that provide an important, almost irreplaceable, source of animal protein to the populations of many developing countries (FAO 2000; Kawarazuka & Béné 2011; Teh *et al.* 2013; Charlton *et al.* 2016).

1.1.2. The entwined relationship between reef fish and coral complexity

Tropical reef ecosystems strongly rely on Scleractinian corals which have long been recognized as providing essential habitat for reef-associated organisms (Luckhurst & Luckhurst 1978; Roberts & Ormond 1987; Stella *et al.* 2011). Naturally, coral reefs provide high structural complexity, defined as the physical three-dimensional configuration of a reef, which can shape the abundance and diversity of reef fish assemblages across both large and small spatial scales (McCormick 1994; Nash *et al.* 2013; Ferrari *et al.* 2016). Indeed, corals and fishes are closely entwined since corals offer extensive prey refugia that support greater densities of small-bodied and fast-growing fish species that feed most of higher trophic levels while, as a positive feedback, some fishes favor coral growth through herbivory, bioerosion and nutrient recycling (Holmlund & Hammer 1999; Wilson *et al.* 2010; Alvarez-Filip *et al.* 2011; Bellwood *et al.* 2012; Rogers *et al.* 2014). Eutrophication, bleaching and storms continuously shape coral reef systems and can lead to coral complexity loss (Graham 2014; Rogers *et al.* 2014). The last 2015–2016 bleaching event was extreme where 75% of the coral reefs monitored globally

were affected while the likelihood of annual bleaching may keep increasing in the coming decades (Hughes *et al.* 2018). The fish species that feed exclusively on live coral (most numerous within the Chaetodontidae) are the prime species affected by both live coral cover and habitat complexity loss (Findley & Findley 2001). Beyond the mere obligate coral feeders, top predators, herbivores and planktivores are also affected through shelters and resources loss (Emslie *et al.* 2014; Rogers *et al.* 2014). Ainsworth & Mumby (2015) show that when corals are removed, annual reef fish landings decline by 39%. Destructive fishing practices such as dynamite and cyanide fishing, or trawling are threatening coral reef habitats thus limiting the long-term productivity of reef-related fisheries since complex reefs produce much more fish biomass than flat rocky reefs. Indeed, habitat loss induces trophic cascade which reduces the productivity of predatory fish by almost half (Figure 1.1 A), and of herbivorous fish by more than two and a half times (Figure 1.1 B). As a result, the impact of a loss of complexity on productivity of combined predator and herbivore targeted by fishing (> 25 cm) was more than 3-fold (Rogers *et al.* 2014).

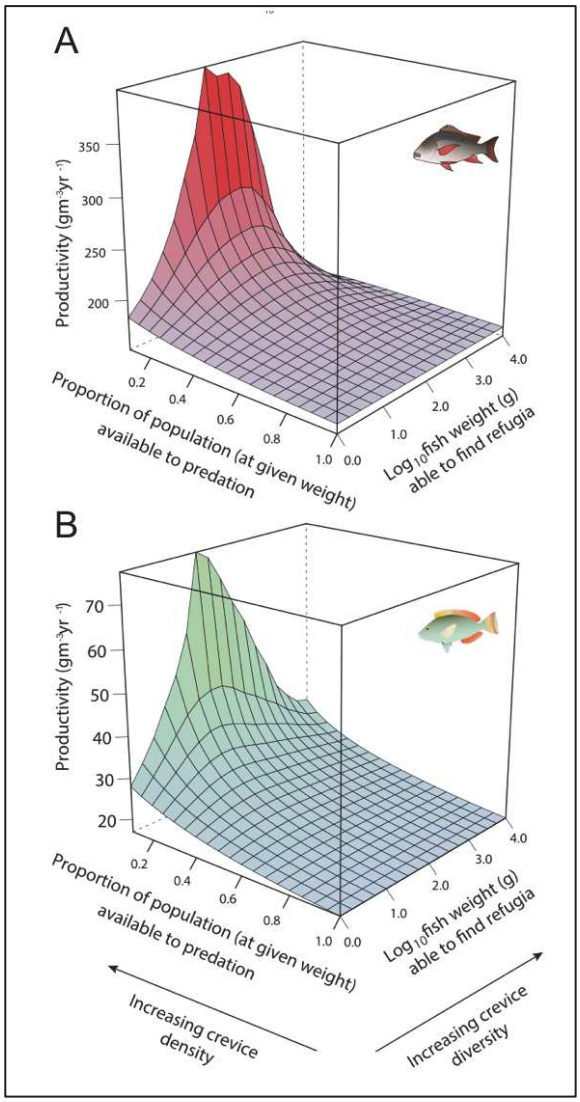

Figure 1.1 | Relationships between productivity and complexity of coral reef. *Model predictions show how declining habitat structural complexity influences predatory (A) and herbivorous (B) fish productivity (g m^{-3} yr^{-1}; measured as the rate at which biomass fluxes through fish size classes). Roger et al. (2014).*

1.1.3. Importance of fish biodiversity on coral reefs

1.1.3.1. The multiple facets of biodiversity and their relation with ecosystem functioning

The functioning of ecosystems is based on i) physical, chemical and biological processes which insure an efficient circulation of matter and energy through various levels of biological organizations (primary, secondary producers and decomposers), ii) energy and matter storage and iii) the stability of energy and matter storage over time (Boero & Bonsdorff 2007). In the face of worldwide declines in biodiversity in early 1990s, many studies have been interested in quantifying the importance of biodiversity on ecosystem functioning and consequences in the supply of ecosystem goods and services to human populations (Chapin *et al.* 2000; Cardinale *et al.* 2012). A recent study used empirical measurements of biodiversity and functioning of natural ecosystems to prove that increase in biomass production with biodiversity is much higher in nature than has previously been documented in experiments and at least comparable or higher than climate and nutrient availability (Duffy *et al.* 2017).

However, if many experimental studies have showed a saturating (concave-down) relationship (Figure 1.2 A) between ecosystem functioning (standing stock and productivity) and biodiversity (species and functional richness) (Cardinale *et al.* 2006); more recent studies have yielded non-saturating (concave-up, Figure 1.2 B) patterns (Danovaro *et al.* 2008; Mora *et al.* 2011). Mora *et al.* (2014) have developed theoretical framework to support concave-up biodiversity-ecosystem functioning relationships in natural ecosystems and thus, proved that consequences of biodiversity loss could be substantially more dramatic than previously predicted.

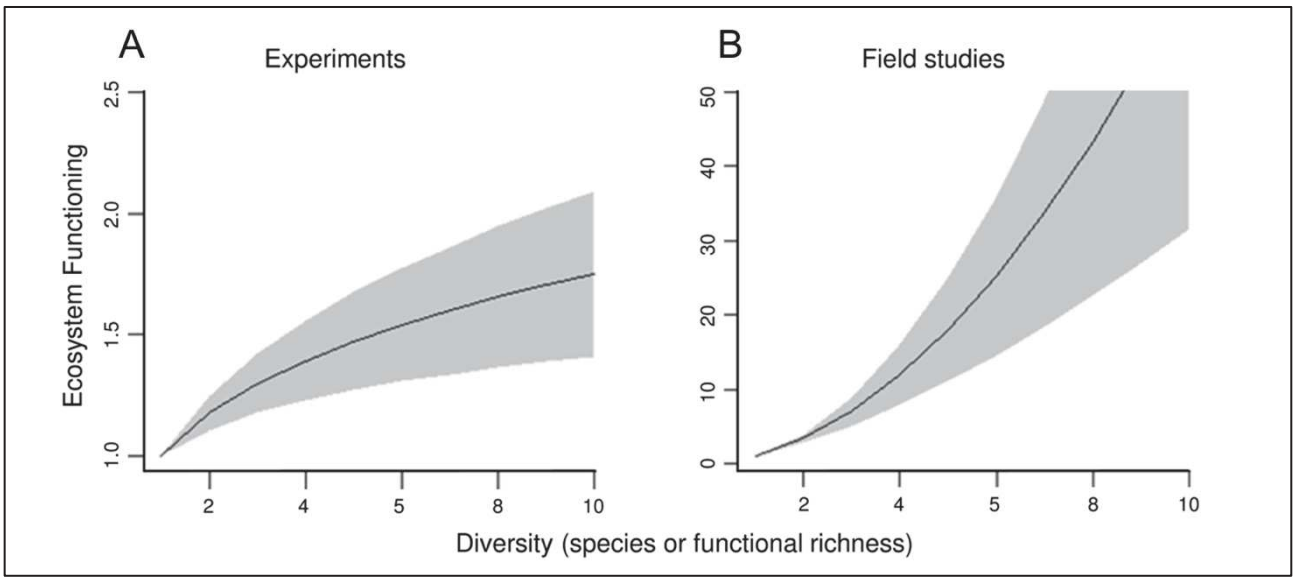

Figure 1.2 | Experimental (A) and natural (B) ecosystems relationships between biodiversity and ecosystem functioning. *(Mora et al. 2014)*

Scientists estimate that coral reef biodiversity could reach around 1,000,000 (550,000-1,330,000) species of multi-cellular plants and animals while only 8% of them are currently named (Fisher *et al.* 2015). From the 1980s, scientific community has been interested in better understanding the role of biodiversity and more specifically of the number of species on ecosystem functioning (Cardinale *et al.* 2012). First studies have mainly been conducted in controlled terrestrial ecosystems and have showed a positive but rather weak ($r^2 < 0.5$, $p<0.001$) relationship between plant species richness and their biomass or nutrient recycling (Naeem *et al.* 1994; Tilman & Downing 1994; Tilman *et al.* 1996; Loreau & Hector 2001). The relative weak explanatory power of species richness to ecosystem functioning comes from simplistic assumption that each species would have the same contribution to ecosystem functioning. However, natural selection and speciation processes confer various morphological, biological (life history traits) and ecological traits to species, which enable them to perform various functions, most being similar or redundant (Rosenfeld, 2002) while some are unique (Petchey *et al.* 2008). Redundancy or unicity of functions realized by species are strongly linked to life history traits which motivates the use of functional diversity instead of the mere species richness to explain ecosystem functioning (Mora *et al.* 2011).

Functional diversity is a powerful, important component of biodiversity, but also rather complex to measure and define (Petchey & Gaston 2006). Functional diversity can be defined as "the value and the range of those species and organismal traits that influence ecosystem functioning" (Tilman 2001) meaning that functional diversity focuses on understanding communities and ecosystems based on what organisms do, rather than on their evolutionary diversification (Petchey & Gaston 2006). Beyond the mere loss of species, the loss of particular functions insured by species is the main threat that jeopardize functioning (Bellwood *et al.* 2012; Naeem *et al.* 2012). Especially in complex systems such as coral reefs, functional redundancy (e.g. several species can support similar functions) may preserve ecosystem functioning even under species decline (Yachi & Loreau 1999; Fonseca & Ganade 2001). However, Mouillot et al. (2014) have showed that in coral reefs, higher levels of redundancy in functions are packed into a few functional entities whereas 38% of the functions are highly vulnerable since without functional insurance with only one species. Therefore, some species performing unique roles, appear to be irreplaceable (Bellwood *et al.* 2006) and imperil ecosystem functioning if extinct.

Evaluating functional diversity relies on biological traits (called functional traits) that embodies various life history traits and processes. For example, body size reflects the metabolism but also informs about the trophic level and the mobility of the specie. Size, mobility, period of activity, schooling, vertical position in the water column and diet are functional traits commonly used to describe coral reef fishes (Mouillot *et al.* 2014). If the species description using functional traits intends to simplify our vision of the functions performed by the whole fish community, the critical step remain the traits choice which can influence the measure of functional diversity (Petchey & Gaston 2006). In richer ecosystems such as coral reefs, functional traits may capture only a restricted number of functions supported by species because of the wide range of traits observed (Petchey & Gaston 2006).

Given these limitations, phylogenetic diversity e.g. the sum of phylogenetic branch lengths (measured on phylogeny) connecting species together, has been proposed as alternative. Phylogenetic diversity may capture the whole range of functions even those not measured by functional traits (Flynn *et al.* 2011) and may be able to predict biomass production often better

than specific richness or functional diversity (Cadotte *et al.* 2008; Cadotte *et al.* 2009; Harmon *et al.* 2009; Cadotte *et al.* 2012; Cadotte 2013; Milcu *et al.* 2013).

1.1.3.2. Are all fish species necessary for coral reef functioning? identifying key fish entities.

Coral reefs have the greatest biodiversity of any ecosystem on the planet, even more than a tropical rainforest (Wilkinson 2000) and contain the most diverse fish assemblages to be found anywhere across the oceans, with at least 6000-8000 species (Lieske & Myers 2002) spread in more than 200 families, yet coral reefs cover less than one percent of the ocean floor (Spalding *et al.* 2001). Over 25% of the world's fish biodiversity, and between 9 and 12% of the world's total fisheries, are associated to coral reefs (Spalding *et al.* 2001). Fisheries management must thus preserve balance between fish harvesting and ecosystem functioning so need a reconciliation between exploitation and conservation. Tackling this issue can be challenging in complex ecosystems, particularly if the target species by fisheries also support key roles in ecosystem functioning.

It is now clear that biodiversity promotes higher productivity of fish biomass and higher resilience of that ecosystem service in the face of climate change (Duffy *et al.* 2016). Identifying functionally important or key species is particularly challenging in biodiverse ecosystems, due largely to the complexity of interactions between species and with their environment including human disturbances. For example, despite the large body of research on coral reefs, the identification of fish species that disproportionally drive ecosystem functioning is still in its infancy (Hoey & Bellwood 2009; Bellwood *et al.* 2012). The functional importance of most coral reef fishes is still poorly understood, and no study has scanned entire fish communities to detect potential links with ecosystem functioning and services at large scale. The critical issue is whether the extraordinary species diversity on coral reefs matters for ecosystem functioning or whether a smaller proportion of species is enough to perform most of the key functions (Mouillot *et al.* 2013).

The integrity of coral reef ecosystems thus critically depends on the interaction between corals and fishes with fish biodiversity being the cornerstone. In the last few decades, the concept of biodiversity has become multifaceted starting with taxonomic richness and then integrating functional and phylogenetic relatedness between species. Biodiversity is a major

determinant of ecosystem productivity, stability, invasibility, and nutrient dynamics. Concerns about the ongoing loss of biodiversity and degradation of coral reefs have motivated scientists to *(i)* better understand how anthropogenic threats imperil coral reef ecosystems and their associated biodiversity and *(ii)* to identify which fish species, functional groups and phylogenetic lineages disproportionally sustain coral reef functioning and services.

1.2. Coral reefs in the Anthropocene

1.2.1. Socioeconomic benefits from coral reefs

The world population is expected to increase from the current 7.2 billion to 9.6 billion in 2050 and 10.9 billion people in 2100 with the highest growth in Africa (Gerland *et al.* 2014). More than 40% of the world's population live within 150 kilometers of the coast (UN 2002; Neumann *et al.* 2015) and a disproportionate number lives in the biodiversity hotspots and tropical remote areas (Williams 2013). Those millions of people in coastal areas depend directly on the ecosystem goods and services provided by coral reefs which sustain from food and economic income through artisanal subsistence fisheries, commercial fisheries, aquaculture, and live reef-fish for the ornamental industry (Kittinger *et al.* 2012; Teh *et al.* 2013; Cinner 2014). Coral reef fisheries supply more than half of the protein consumed by human populations in coastal regions (Moffitt & Cajas-Cano 2014) and are still the major source of protein for many people in some small islands (Kawarazuka & Béné 2011; Teh *et al.* 2013; Charlton *et al.* 2016). Coral reefs do not support only livelihood of people they also offer coastal protection, medicines, recreational and touristic opportunities (Ferrario *et al.* 2014; Harris *et al.* 2018). Additionally, coral reefs contribute to aesthetic, cultural and spiritual values of coastal societies (Kittinger *et al.* 2012; Cinner 2014).

1.2.2. Climate change impacts

Since the 1980s, rising sea surface temperatures, owing to human-induced global warming, has been a major concern for coral reefs. Indeed, unprecedented mass bleaching of corals, including three pan-tropical events in 1998, 2010 and 2015-2016 (Figure 1.3), which often leads to high levels of coral mortality (Heron *et al.* 2016), is imperiling the future of coral reefs.

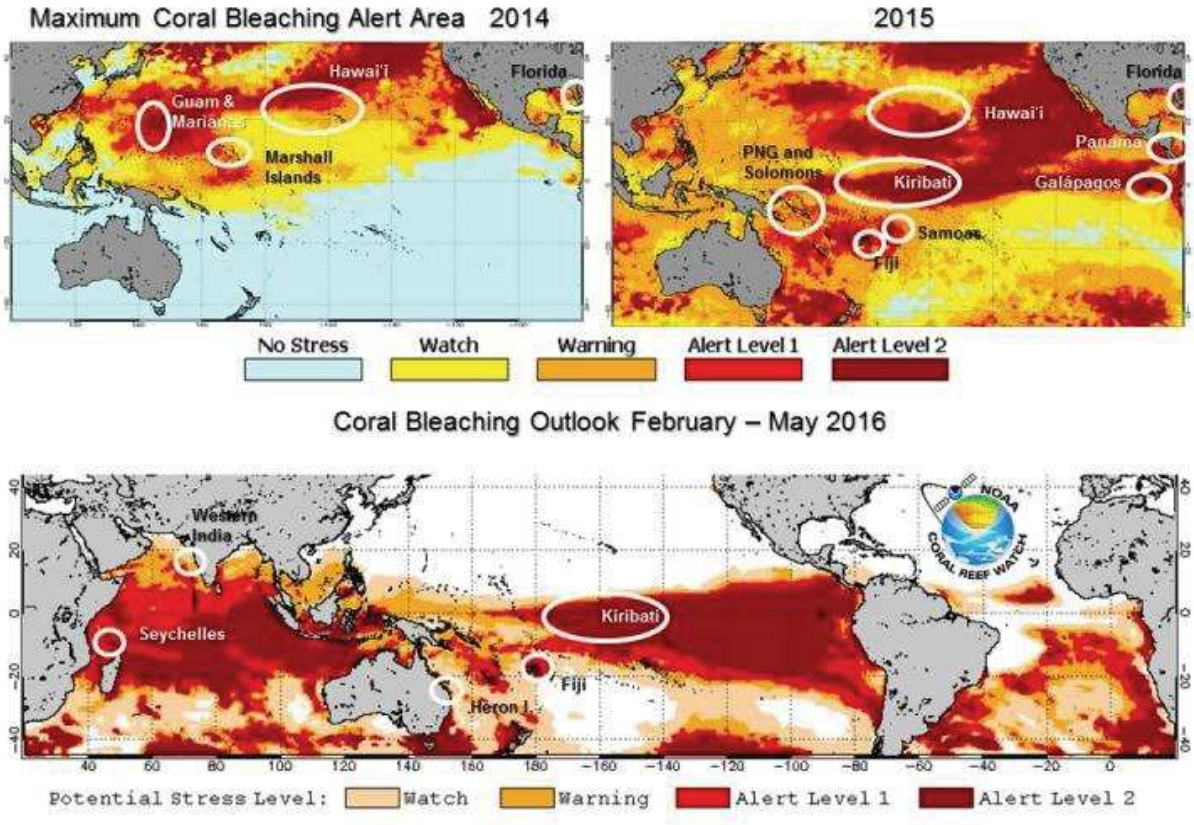

Figure 1.3 | Recent massive coral bleaching. *The top images show the maximum thermal stress levels measured by NOAA satellites in 2014 and 2015 along with locations where the worst coral bleaching was reported. The bottom image shows the Four Month Bleaching Outlook for February-May 2016 based on the NOAA Climate Forecast System model along with locations. Source: NOAA.*

Recent studies lead by Pr. Terry P. Hughes (2017, 2018) have showed that severe recurrent heat waves, boosted by more and more severe El Nino events, are the major threat on coral reefs and that local resistance (fisheries management and water quality) cannot provide any "magic shield" to extreme heat. Indeed, even highly protected and near pristine areas in the Great Barrier Reef (GBR) have experienced massive bleaching in 2016 (Figure 1.4), leaving very few potential refugia on the GBR since only 9% of reefs repeatedly surveyed have never bleached (Hughes *et al.* 2017b). Moreover, these warming events are getting warmer and are occurring more frequently than previously leaving a too short time interval for a full recovery of coral reefs (Hughes *et al.* 2018). Global warming is behind the recent acceleration of sea level rise with major repercussions on coastal regions. In fact, many coral reefs would be unable to keep growing fast enough to keep up with rising sea levels, leaving tropical

coastlines and low-lying islands exposed to increased erosion and flooding risk (Perry *et al.* 2018).

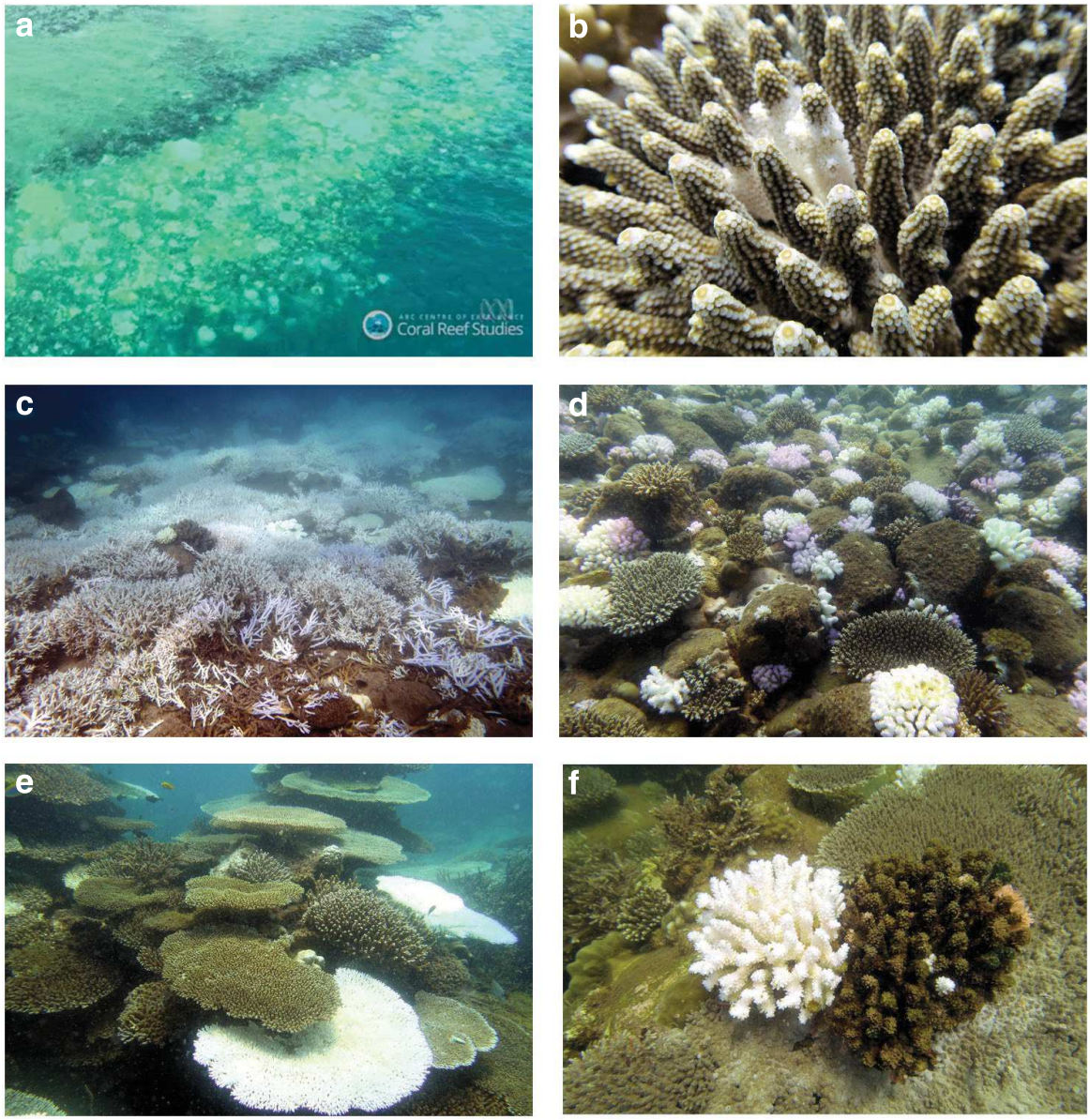

Figure 1.4 | Severe coral bleaching. a, *Aerial view of severe bleaching in Princess Charlotte Bay, northeast Australia in March 2016 where almost 100% of corals are bleached on the reef flat and crest.* ***b,*** *Bleaching occurs when algal symbionts (Symbiodinium spp.) in a coral host are killed by environmental stress, revealing the white underlying skeleton of the coral.* ***c, d, e,*** *Mature corals were extirpated by heat stress and* ***f,*** *rapidly colonized by algae. Photo credits: a, James T. Kerry.; b-f, Eva Maire.*

Impacts of global change are already underway, with an average global temperature increase of nearly 1°C since pre-industrial conditions (<1900). There is overwhelming evidence that 1.5° or 2°C of warming above preindustrial conditions will inevitably contribute to further degradation of the world's coral reefs (Heron *et al.* 2016). Securing a future for coral reefs requires urgent and rapid actions to reduce global warming and a clearer understanding of multiple drivers and ecosystem responses under these new scenarios in the Anthropocene (Hughes *et al.* 2017a).

1.2.3. Anthropogenic direct impacts

Anthropogenic changes have become the dominant force shaping all ecosystems on Earth, a new era termed the Anthropocene (Steffen *et al.* 2011). Social and ecological processes are closely intertwined (Halpern *et al.* 2008; Rockström *et al.* 2009; Österblom *et al.* 2017) particularly on coral reefs ecosystems where humans have historically depleted marine resources (Jackson *et al.* 2001; Pandolfi *et al.* 2003; Bellwood *et al.* 2004; Norström *et al.* 2016). For instance, a high-resolution 3,000-year record of reef accretion rate and herbivore (parrotfish and urchin) abundance (Cramer *et al.* 2017) shows that historical fishing may have been significantly affecting Caribbean reefs for over two centuries, initiating ecosystem declines from which they have never recovered. Declines in fish and coral abundance become detectable in the Caribbean since the mid-18th century with the increasing exploitation of coastal marine resources from indigenous inhabitants, European traders, and pirates engaging in intensive harvesting and land clearing for industrial-scale banana agriculture (Cramer *et al.* 2017).

Scientific understanding of human impacts on reef systems has mainly demonstrated negative relationships between local human populations and the condition of coral reefs (Mora *et al.* 2011; Bellwood *et al.* 2012), the term 'condition' referring to many aspects from the quality of habitat to fish biomass and biodiversity. More specifically, fishing activities impact trophic pyramid at all levels and the famous 'fishing down the food web' tenet implies that fishing starts at the highest-valued species at the top of the pyramid and then moves down the pyramid as predators collapse with exploitation (Pauly *et al.* 1998). For coral reefs, fishing through entire trophic pyramids (Branch *et al.* 2010) may be a common practice since all trophic levels have market value. Previous studies have showed that reef fish biomass is

constrained by the density of local human populations (Mora *et al.* 2011) but the linear distance to the nearest market is also a strong explanatory variable for the condition of reef fisheries (Cinner *et al.* 2013). One major point is that even low human settlement or population densities can deplete resources on close reefs and have great impacts on fish abundance. Indeed, Bellwood and colleagues (2012) show that 16 people per square kilometer is enough to make bigger parrotfishes (*Bolbometopon muricatum, Chlorurus sp.*) locally extinct (Figure 1.5).

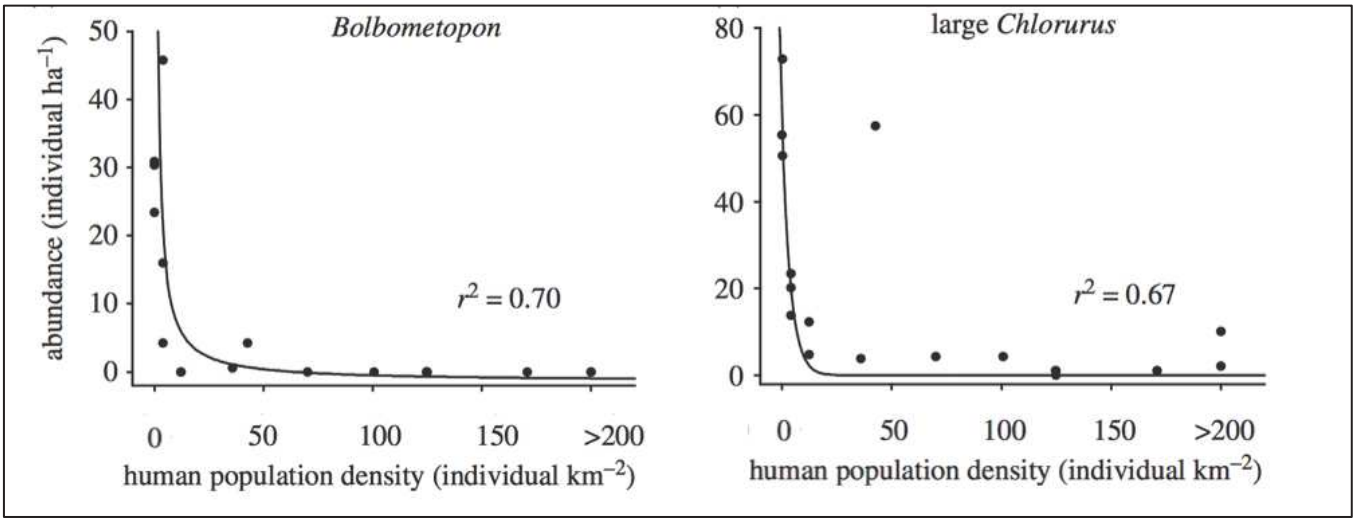

Figure 1.5 | Relationships between human density (inhabitants per km^2) and the abundance of Green humphead parrotfishes (Bolbometopon) and large Chlorurus parrotfishes. *(Bellwood et al. 2012).*

Parrotfishes sustain bioerosion and coral predation which are key functions for coral reef resilience, thus abrupt ecosystem shift can be observed as soon as fishing reduces parrotfish size and abundance (Bellwood *et al.* 2012; Bozec *et al.* 2016). Coral reefs integrity can be disrupted by human activities and over-exploitation, leading to social-ecological traps (Cinner 2011) where fish extraction reduces the wide diversity of functions provided to the ecosystem and induces coral habitat degradation. It results a more heavily human pressure on remaining fishes and ultimately, coral reef systems are not able to support services that people depend on anymore.

Ever increasing coastal population growth, with associated demands on natural resources may compromise the capacity of coral reefs to keep providing human societies with fisheries and other socioeconomic benefits.

1.2.4. Management actions to counteract human impacts

Numerous approaches can be used to sustain marine resources (Costello *et al.* 2008; Gelcich *et al.* 2008; Worm *et al.* 2009; Cinner *et al.* 2012). Since the 1960s, Marine Protected Areas (MPAs) and Marine Reserves (MRs), the latter being defined as no-take MPAs where fishing activities are prohibited (Costello & Ballantine 2015), have become popular tools for conserving biodiversity and managing marine resources (Gaines *et al.* 2010; Veitch *et al.* 2012; Watson *et al.* 2014; MacNeil *et al.* 2015). MPAs are more and more popular across the oceans to preserve biodiversity but also to reduce poverty, build food security, create employment and protect sustain fisheries (Van Beukering & Lea 2013; Ferrario *et al.* 2014; Brander *et al.* 2015). There is now a large body of evidence supporting positive effects of MRs within their boundaries and in their vicinity. MRs unambiguously increase fish abundance (Lester *et al.* 2009) and biomass (Costello 2014) and host larger, and thus more fertile, fish individuals (Abesamis & Russ 2005; Evans *et al.* 2008). These benefits typically appear after 2 to 5 years of protection (Claudet *et al.* 2008) and continue to grow even after 40 years for some fish groups like predators (MacNeil *et al.* 2015).

Rapid degradation of the world's coral reefs (Hughes *et al.* 2003; Pandolfi *et al.* 2003; Bellwood *et al.* 2004; Hughes *et al.* 2017a) jeopardizes their ecological functioning and ultimately imperils the wellbeing of the millions of people with reef-dependent livelihoods (Teh *et al.* 2013). There is an urgent need to understand the context under which conservation gains can be maximized (Devillers *et al.* 2015; Pressey *et al.* 2015) and where conservation outcomes (e.g. fish biomass) can be maximized. Increased fish biomass inside marine reserves provides higher levels of ecosystem functioning (McClanahan *et al.* 2011) but also results in spillover of adults and larvae to surrounding areas (Abesamis & Russ 2005), which can benefit fishers (Harrison *et al.* 2012; Januchowski-Hartley *et al.* 2012; Andrello *et al.* 2017). Thus, conservation gains are beneficial for both people and ecosystems

Securing a future for coral reefs under these multiple Anthropogenic forcing factors (Hughes *et al.* 2017a) requires urgent alternatives to sustain coral reef socio-ecological systems. We thus need to *(i)* better understand, quantify and map the level of interactions between reefs and humans and *(ii)* define how the intensity of human impacts in the surrounding seascape affects the ability of MPAs to achieve conservation objectives.

1.3. Accessibility as a cornerstone of the multiple interactions in social-ecological systems

1.3.1. Accessibility as a key driver of the conditions of ecosystems

Natural resources, such as forests and fisheries, are becoming severely depleted; especially those that are more accessible to people (Mora *et al.* 2011; Cinner *et al.* 2013; Barber *et al.* 2014). For example, numerous studies have linked increased accessibility through road building to deforestation (Laurance *et al.* 2009) and avian biodiversity erosion (Ahmed *et al.* 2014). Accessibility is also shown to be a main driver of ecosystem recovery. Distance to primary roads enhances recovery of secondary forests after abandonment of agriculture in Puerto Rico (Crk *et al.* 2009). In terrestrial systems, there is thus considerable attention on accessibility management, mainly via road networks at both local (Dobson *et al.* 2010) and global scales (Laurance *et al.* 2014).

In contrast, considerably less research has focused on accessibility in marine ecosystems, though it has been shown to strongly determine their conditions (e.g. fish biomass and biodiversity) and functioning (Morato *et al.* 2006; Cinner *et al.* 2013). For example, in Nicaragua, the development of a road to reach a former remote fishing area altered both price and price variability of fish, which led to more intensive overexploitation (Schmitt & Kramer 2009). Likewise, several studies have demonstrated that proximity to market, measured as a linear distance, is the strongest predictor of overfishing on coral reefs (Cinner & McClanahan 2006; Cinner *et al.* 2012; Cinner *et al.* 2013).

Measuring the extent to which global marine resources are accessible to humans has been generally limited to examining the linear distance between fishing grounds and markets, villages or ports (Watson *et al.* 2015). However, for most coastal ecosystems and artisanal

fisheries, this linear distance ignores ragged coastlines, road networks and other features that can affect the time required to reach fishing grounds. The availability of new analytical tools and high-resolution geo-referenced landscape data now allows for estimating reef accessibility, through travel time, by taking account the heterogeneity of the seascape. Yet, such calculation routines remain to be built and optimized to obtain large scale assessment.

1.3.2. Moving beyond the Malthusian perspective

Researchers have classically turned toward the Malthusian perspective suggesting that human population size is a major driver of ecological conditions of ecosystems where population grows exponentially and will always exceed food production that grows linearly, leading to increasing poverty and inducing inevitable collapse of human societies (Malthus 1798). Applied to fisheries, the causes of overfishing are driven by "too many fishers chasing too few fish" (Pauly 1990) and as fishing effort grows proportionately to human population growth, which is often exponential particularly in coastal cities, policy interventions that reduce fisher access, the number of fishers, or the human population are needed (Pauly 1990; Roberts 1995). Regions in the world characterized by positive population growth, high level of poverty and strong dependence on marine resources fall within this context. However, there is still little empirical evidence that global or local population growth has more impacts on coral reefs than other socio-economic aspects (de Sherbinin *et al.* 2007). Many coral reef studies revealed that other drivers such as technology, market access and development often provide better explanation of the conditions of coral reefs fisheries than human population size or density (Cinner & McClanahan 2006; Cinner *et al.* 2009a; Brewer *et al.* 2012; Cinner *et al.* 2013; Finkbeiner *et al.* 2017).

Focusing only on human population density may lead to biased human impact assessment because other important drivers may be at played while ignored by most managers and policy makers (Berkes *et al.* 2006). Assessing accessibility of coral reefs from human settlements seems to be a complementary and useful tool to better explain the status and dynamics of coral reef socio-ecological systems.

1.3.3. Scaling down the link between coral reef accessibility and resource exploitation

Earth's ecosystems have come under increasing pressure as globalization connects the world (Liu *et al.* 2013). Expanding trade, transportation, migration, and technology are altering intertwined dynamics between human and natural ecosystems across space and time (Rockström *et al.* 2009; Liu *et al.* 2015). Global trade through interconnected markets or new access to markets heavily shape the exploitation of natural resources and has raised serious ecological and management issues (Berkes *et al.* 2006; Rockström *et al.* 2009; Steffen *et al.* 2011). Accessibility is an important determinant of people's ability to use natural resources. In particular, in both terrestrial and marine biomes, accessibility through road networks and infrastructure expansion has been shown to be a main driver of the conditions of the ecosystems, with the most accessible resources being most at risk (Laurance *et al.* 2009; Dobson *et al.* 2010; Mora *et al.* 2011; Ahmed *et al.* 2014; Barber *et al.* 2014; Alamgir *et al.* 2017). Previously remote regions of the world have become more accessible and thus, more integrated with the global economy which may profoundly affect previously remote or even pristine ecosystems (McCauley *et al.* 2013; Mora *et al.* 2016). Yet the mechanisms through which the level accessibility influences social and ecological conditions are still unknown and certainly not so straightforward.

To date, research on market accessibility has mainly examined how increased market access affects resources users through trade and price changes (Delgado 2003; Schmitt & Kramer 2009; Thyresson *et al.* 2011; Thyresson *et al.* 2013), and changes in livelihood diversification (Cinner & Bodin 2010; Chaves *et al.* 2017; Kramer *et al.* 2017) (composition effect) as well as technology introductions or changes (Brewer 2013; Stevens *et al.* 2014) (technique effect). Lack of knowledge on how market access shapes local human communities remains largely under-estimated and could hide crucial dynamics at local scale.

Understanding how accessibility from human societies affects the exploitation of natural resources is a critical step toward a long-term management of the ecosystems where actions are needed to enhance their ecological and economic sustainability. Given that the human-environmental interrelations are dependent on the social context, a scaling-down of reef accessibility to highlight the drivers of resource use and governance at fine scale is needed.

1.4. Aims and thesis outline

The present thesis has two main objectives: i) developing new metrics of accessibility to better account for human impacts on coral reefs in an heterogenous seascape; and ii) evaluating the importance of these new metrics, in interaction with management, to explain variations of fish biomass on coral reefs.

These aims are addressed in four separate studies focusing on distinct research questions (RQ) that remain unsolved (Figure 1.6):

RQ 1. Is travel time from human settlements a good predictor of reef fish biomass at the global scale?

RQ 2. How the intensity of human impacts affects the effectiveness of marine reserves in the context of coral reefs?

RQ 3. How travel time from market affect resource use at local scale?

RQ 4. Which and how species are necessary to maintain fish biomass and coral cover on coral reefs?

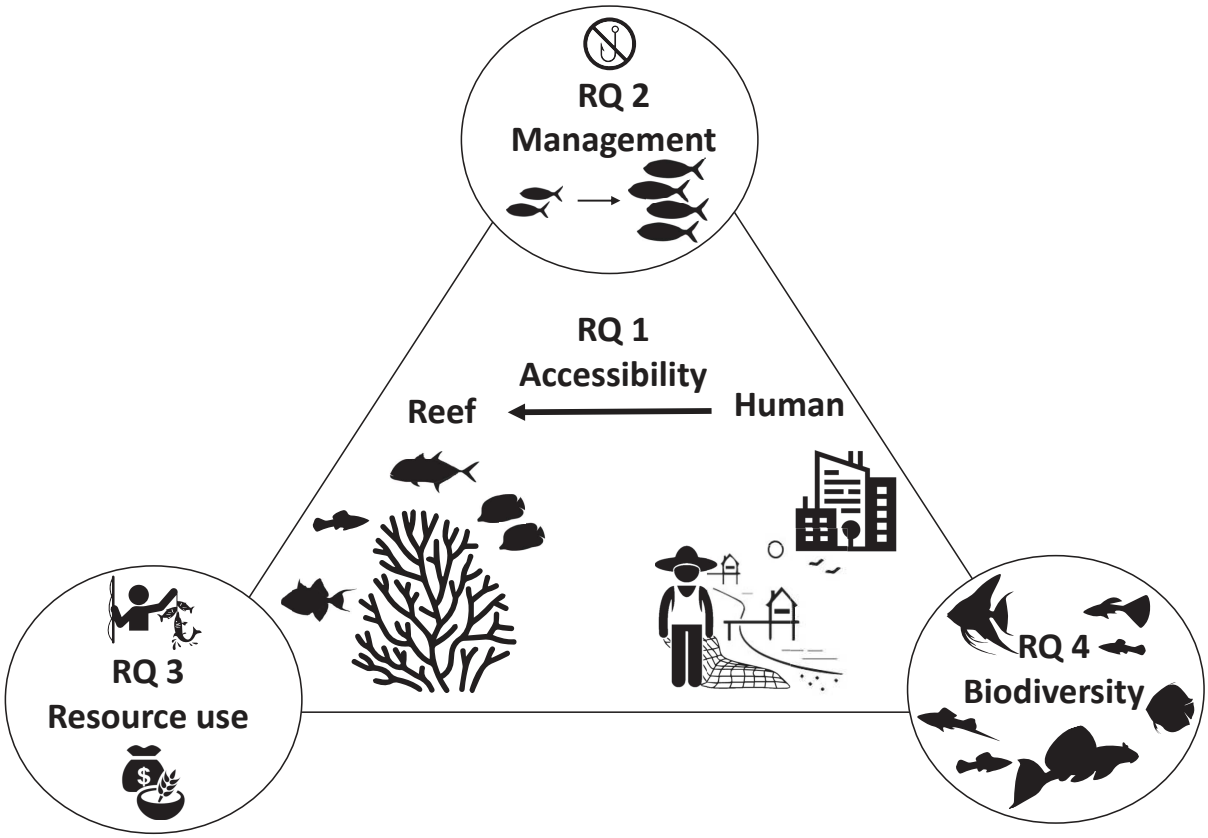

Figure 1.6 | Key aims of the thesis through 4 distinct research questions (RQ 1-4).

The research questions are addressed in the four studies briefly described below and fully developed in introduction of each corresponding chapter.

After this general introduction **(Chapter 1)**, I first provide the methodological and theoretical basis of my PhD: **Chapter 2** exposes the global dataset I used during the thesis which is one of the largest sets available for tropical reefs that compiles coral reef conditions and socioeconomic drivers from more than 2,500 reefs worldwide; **Chapter 3** explains the framework I developed to assess travel time between any reef and human settlements through land (road and vegetation) and water (navigable river, lake and ocean) at global scale. It also shows that travel time is a major driver of reef fish biomass. It also describes how to combine travel time and human population into an integrative metric of human gravity.
Secondly, I highlight the importance of these new metrics in reef conservation and management with three dedicated chapters: **Chapter 4** explore how the intensity of human impacts, measured as a function of human population size and accessibility to reefs, affects the effectiveness of marine reserves in tropical reefs; **Chapter 5** explores how travel time from market can affect resource use at local scale through a study case in Northwest Madagascar, where I participated in the collection of social and ecological data; and **Chapter 6** exposes the framework I developed to define which species are necessary to maintain fish communities and their associated services.
Lastly, **Chapter 7** consists on a synthetic analysis presenting the main conclusions and limitations of the thesis. It also provides perspectives and future applications.

2. Global dataset on coral reefs

2.1. Introduction

My PhD is integrated into the *Cinner Research Group* led by Dr. Joshua E. Cinner that focuses on the interface between social science and ecology to develop solutions for a wide range of issues facing coral reefs and the millions of people who depend on them. The major part of my PhD (Chapter 4 and 6) has been conducted at large scale and uses one of the largest sets of reef data available that compiles coral reef conditions and socioeconomic drivers from more than 2,500 reefs worldwide. This part aims to describe the variables included in the dataset that I have used in my PhD.

2.2. Nested scales of data

The global dataset was organized at three spatial scales: reef site, reef cluster, and nation/state described below:

(i) Reef site (hereafter 'reef') is the smallest scale and represents a pool of surveys (transects).

(ii) Reef cluster have been obtained by clustering reefs together that were within 4km of each other and used the centroid to estimate reef cluster-level social and environmental covariates. To define reef clusters, the linear distance between all reef sites was first estimated, then a hierarchical analysis with the complete-linkage clustering technique based on the maximum distance between reefs was used. A cut-off at 4 km was set to select mutually exclusive sites where reefs cannot be more distant than 4 km. The choice of 4 km was informed by a 3-year study of the spatial movement patterns of artisanal coral reef fishers, corresponding to the highest density of fishing activities on reefs based on GPS-derived effort density maps of artisanal coral reef fishing activities (Daw *et al.* 2011).

(iii) Nation/state (nation, state, or territory) which are jurisdictions that generally correspond to individual nations (but could also include states, territories, overseas regions).

2.3. Reef Fish biomass

Reef fish biomass can reflect a broad selection of reef fish functioning and benthic condition (McClanahan *et al.* 2011; Mora *et al.* 2011; Edwards *et al.* 2014; MacNeil *et al.* 2015), and is a key metric of resource availability for reef fisheries. The initial dataset gathers more than 24,000 visual counts collected from 7,328 reefs between 1992 and 2013 in 63 nations, states or territories. All surveys used 3 census methods (standard belt-transects, distance sampling and point-counts). Where data from multiple years were available from a single reef site, only data from the year closest to 2010 were considered.

For the purposes of the research questions, only parts of this dataset have been selected to extract targeted fish (Chapter 4), top predators presence (Chapter 4) and Indo-Pacific fish biomass (Chapter 6) described below:

- Targeted Fish Biomass: 4,164 surveys collected from 1,798 tropical reef sites between 2004 and 2013 were retained. Only 14 fish families were considered since were consistently studied, commonly targeted, and were above a minimum size cut-off even if targeting of reef fishes can vary by location due to gear, cultural preferences, and a range of other considerations. Thus, counts of >10cm diurnally-active, non-cryptic reef fish that are resident on the reef were retained, excluding sharks and semi-pelagic species (Table I).

-Top Predators: 8 families of fish were considered as top predators (Table I). In Chapter 4, only presence/absence was used instead of biomass because biomass was heavily zero inflated.

-Indo-Pacific Fish Biomass: 4,694 surveys collected from 1,824 reefs located in the Indo-Pacific were retained. Those surveys used only two census methods (belt-transects or distance sampling) and were conducted between 2004 and 2013. Then, all counts of non-cryptic reef fish species >10cm in total length, that are reef-associated (30 families, 748 species, see Appendices Chapter 6) were considered. Sharks were not included in the study as they were often excluded from visual surveys.

Within each survey area, reef associated fishes were identified to species level, abundance counted, and total length (TL) estimated, with the exception of one data provider who measured biomass at the family level. Fish biomass on each selected reef has then been

estimated using published species-level length-weight relationship parameters or those available on FishBase (Froese & Pauly 2012). When length-weight relationship parameters were not available for a species, the parameters for a closely related species or genus were used. To make estimates of biomass from these transect-level data comparable among studies, differences among census methods were directly taken into account by including each census method (standard belt-transects, distance sampling, or point-counts) and sampling area for each reef (m^2) as a covariate in the analysis.

2.4. Socio-economic drivers

Many social drivers that are thought to be related to the condition of reef fish biomass have been included in my thesis. Full description of each variable is described below.

Local Population Growth: a 100 km buffer was created around each site and was used to calculate human population within the buffer in 2000 and 2010 based on the Socioeconomic Data and Application Centre (SEDAC) gridded population of the world database. Population growth was the proportional difference between the population in 2000 and 2010. A 100 km buffer was chosen as a reasonable range at which many key human impacts from population (e.g., land-use and nutrients) might affect reefs (MacNeil & Connolly 2015).

Human Development Index (HDI): HDI is a summary measure of human development encompassing: a long and healthy life, being knowledgeable, and having a decent standard of living. In cases where HDI values were not available specific to the State (e.g. Florida and Hawaii), the national (e.g. USA) HDI value were used.

Population Size: For each nation/state, the size of the human population was estimated. Data were derived mainly from national census reports the CIA fact book (https://www.cia.gov/library/publications/the-world-factbook/rankorder/2119rank.html), and Wikipedia (https://en.wikipedia.org).

Tourism: Tourist arrivals relative to the nation/state population size (above) were examined. Tourism arrivals were gathered primarily from the World Tourism Organization's Compendium of Tourism Statistics.

Management: For each observation, the prevailing type of management was determined, including: (i) marine reserve- whether the site fell within the borders of a no-take marine reserve. Data providers were asked to further classify whether the reserve had high or low levels of compliance; (ii) restricted fishing- whether there were active restrictions on gears (e.g. bans on the use of nets, spearguns, or traps) or fishing effort (which could have included areas inside marine protected areas that were not necessarily no take); or (iii) openly fished - regularly fished without effective restrictions. To determine these classifications, the expert opinion of the data providers was used, and validated with a global database of marine reserve boundaries (IUCN & UNEP-WCMC 2016). Size and age of each reserve were calculated.

National reef fish landings: Catch data were obtained from the Sea Around Us Project (SAUP) catch database (http://www.seaaroundus.org), except for Florida, which was not reported separately in the database. In total, 200 reef fish species and taxon groups were identified in the SAUP catch database (Teh *et al.* 2013). Reef-associated pelagics such as scombrids and carangids normally form part of reef fish catches. However, these species were not included because they are also targeted and caught in large amounts by non-reef operations.

Voice and accountability: This metric, from the World Bank survey on governance, reflects the perceptions of the extent to which a country's citizens are able to participate in selecting their government, as well as freedom of expression, freedom of association, and a free media. In cases where governance values were not available specific to the nation/state (for example, Florida and Hawaii), national (for example, USA) values were used.

2.5. Environmental Drivers

Depth: The depth of reef surveys was grouped into the following categories: <4m, 4-10m, >10m to account for broad differences in reef fish community structure attributable to a number of inter-linked depth-related factors. Categories were necessary to standardize methods used by data providers and were determined by pre-existing categories used by several data providers.

Habitat: The following habitat categories were included: *(i*) Slope: The reef slope habitat is typically on the ocean side of a reef, where the reef slopes down into deeper water; *(ii)* Crest:

The reef crest habitat is the section that joins a reef slope to the reef flat. The zone is typified by high wave energy (i.e. where the waves break). It is also typified by a change in the angle of the reef from an inclined slope to a horizontal reef flat; *(iii)* Flat: The reef flat habitat is typically horizontal and extends back from the reef crest for 10's to 100's of meters; *(iv)* Lagoon / back reef: Lagoonal reef habitats are where the continuous reef flat breaks up into more patchy reef environments sheltered from wave energy. These habitats can be behind barrier / fringing reefs or within atolls. Back reef habitats are similar broken habitats where the wave energy does not typically reach the reefs and thus forms a less continuous 'lagoon style' reef habitat. Due to minimal representation among our sample, other less prevalent habitat types were excluded, such as channels and banks. The Millennium Coral Reef Mapping Project (MCRMP) hierarchical data (Andréfouët *et al.* 2006), Google Earth, and site depth information were used to verify the sites' habitat information.

Productivity: Ocean productivity for each of our sites in mgC / m^2 / day (http://www.science.oregonstate.edu/ocean.productivity/) was examined. Using the monthly data for years 2005 to 2010 (in hdf format), those data were imported and converted into ArcGIS. Yearly average and finally an average for all these years was calculated. A 100 km buffer around each of our sites was chosen and the average productivity within that radius was examined. Note that ocean productivity estimates are less accurate for nearshore environments, but the best available data were used.

Climate stress: An index of climate stress for corals was included, developed by (Maina *et al.* 2011), which incorporated 11 different environmental conditions, such as the mean and variability of sea surface temperature.

2.6. Overview of the data

The next table summarizes the data used during the PhD. This includes ecological, social and environmental variables collected at different scales and from various sources.

Variable	Description	Scale	Key data sources
Habitat	Whether the reef is a slop, crest, flat, or back reef/lagoon	Reef	Primary data
Depth	Depth of the ecological survey (<4m, 4-10m, >10m)	Reef	Primary data
Protection status	Whether the reef is openly fished, restricted (e.g. effective gear bans or effort restrictions), or unfished	Reef	Expert opinion, global map of marine protected areas.
Local population growth	Difference in local human population (i.e. 100km buffer around our sites) between 2000-2010	Site	Socioeconomic Data and Application Centre (SEDAC) gridded population of the work database (CIESIN 2005)
Climate stress	A composite metric comprised of 11 different environmental variables that are related to coral mortality from bleaching	Site	(Maina *et al.* 2011)
Ocean productivity	The average (2005-2010) ocean productivity in mgC / m2 / day	Site	http://www.science.oregonstate.edu/ocean.productivity/
Human Development Index (HDI)	A summary measure of human development encompassing: a long and healthy life, being knowledgeable and have a decent standard of living	Nation/state	United Nations Development Programme
Population Size	Total population size of the jurisdiction	Nation/ state	World Bank, census estimates, Wikipedia

Tourism	Proportion of tourist visitors to residents	Nation/ state	World Tourism Organization's Compendium of Tourism Statistics, census estimates
Voice and accountability	Perceptions of the extent to which a country's citizens are able to participate in selecting their government.	Nation/ state	World Bank
Fish landings	Landings of reef fish (tons) per km^2 of reef	Nation/ state	(Teh *et al.* 2013)
National fisheries poaching	Results from survey of national fisheries managers about levels of compliance with national fisheries regulations	Nation/ state	(Mora *et al.* 2009)

2.7. Variable selection

A broad number of social, ecological and environmental variables were initially available in the dataset. For each study, the pool of variables retained as covariates was defined under the same procedure. Given the pool of reef sites and the response variable considered (targeted fish biomass and predators in Chapter 4 or total biomass in Chapter 5), collinearity among all the possible variables was checked using bivariate correlations and Variance Inflation Factor (VIF) estimates, and variables having correlation coefficients greater than 0.7 and VIF scores greater than 5 were not considered in the study.

This led to the systematic exclusion of several covariates (not described above): *(i)* Biogeographic Realm (Tropical Atlantic, western Indo-Pacific, Central Indo-Pacific, or eastern Indo-Pacific); *(ii)* Gross Domestic Product (purchasing power parity); *(iii)* Rule of Law (World Bank governance index); *(iii) Control of Corruption* (World Bank governance index); and *(iv) Sedimentation*. Other covariates had correlation coefficients and VIF scores indicating multicollinearity was not a serious concern.

The same procedure was repeated for each study (Chapters 4 & 5) to determine the most appropriate pool of covariates given the reef sites and the response variable considered. The complete methodological procedures and the covariates used for each study will be fully developed in the “Methods” section of the corresponding chapter.

3. Redefine accessibility of coral reefs to better predict their biomass[1]

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[1] *Published as Maire, E., Cinner, J., Velez, L., Huchery, C., Mora, C., Dagata, S., Vigliola, L., Wantiez, L., Kulbicki, M., & Mouillot, D. (2016). How accessible are coral reefs to people? A global assessment based on travel time. Ecology Letters. 19, 351:360, doi: 10.1111/ele.12577.*

3.1. Travel time to reach a reef from human settlements

"The journey not the arrival matters […] Only those who will risk going too far can possibly find out how far one can go" – Thomas S. Eliot, 20th century English author.

3.1.1. Travel time calculation

3.1.1.1. Generalities on travel time

Accessibility of a given location is defined as the travel time for humans to reach this location using land (road and land cover) or/and water (navigable river, lake and ocean) based travel. Then, the 'cost' of travelling to reach a location of interest can be computed on a regular grid using a cost-distance algorithm. The cost of travelling is expressed in units of time per unit of distance (e.g. 10 $min.km^{-1}$) and represents the cost required to travel across a specific surface (road, land, water) hence this grid is often termed a friction-surface. Thus, each cell on the cost grid contains a unique value depending of land use and infrastructures. More precisely, the friction-surface grid integrates information on the transport network, environmental and political factors that affect travel time between locations. Transport networks can include road and rail networks, navigable rivers and shipping lanes. Environmental factors generally contribute to travel speeds off the transport network, such as land cover and slope. Political factors - such as national boundaries and border crossings - can act as barriers or travel delays.

In the present study, accessibility is defined as the potential time it takes to travel between two locations of interest, here, between a given reef and either its nearest human settlement or its nearest market.

3.1.1.2. Creating a global friction-surface grid

The friction-surface grid is simply a 'raster' Geographic Information System (GIS) data layer where each cell contains a unique cost value.

The friction-surface grid computation requires combining spatial datasets i) on roads (2 data layers), and ii) land cover. These data include:

- The Global Roads Open Access Data Set, Version 1 (gROADSv1) provided by the Centre for International Earth Science Information Network (CIESIN), Columbia University, and

Information Technology Outreach Services (ITOS). This dataset combines the best available data by country into a global road network using the UN Spatial Data Infrastructure Transport (UNSDI-T) version 2:

- The Vector Map Level 0 (VMap0) which is an updated, improved and free version of the National Imagery and Mapping Agency's (NIMA) Digital Chart of the World (DCW®). VMap0 provides worldwide coverage of vector-based geospatial data of major roads and tracks.
- Land cover data extracted from the Global Land Cover 2000 (GLC 2000). GLC 2000 is a global land cover for the year 2000 produced by an international partnership of 30 research groups coordinated by the European Commission's Joint Research Centre (http://forobs.jrc.ec.europa.eu/products/gam/).

Suitable resolution and projection systems are therefore required. So I defined the spatial resolution at 1km and used the Behrmann projection which is an equal area projection (e.g. no area distortion across latitude). Confronting land cover data from GLC 2000 and road networks showed a mismatch near coastlines. Nevertheless, accurate calculation of travel time based on land-water differential is grounded on a high-resolution shoreline dataset. I used the GSHHS (Global Self-consistent, Hierarchical, High-resolution Shoreline) database version 2.2.2, a high-resolution shoreline dataset, to adjust land-water boundaries (Wessel & Smith, 1996) to finally obtain a global grid at 1km-resolution.

I then assigned a travel speed or crossing time to each class of friction surface considered so to each 1km grid cell. I based these values on Travel Time to Major Cities: A global map of Accessibility. This map was produced by the cooperation between the European Commission's Joint Research Centre and highlights the connectivity and the concentration of economic activities around the world (Nelson 2008). For simplification I considered only road networks, land cover, and water bodies while slope and elevation were considered as negligible factors in coastal areas. Land cover from GLC2000 has some missing values that need to be filled to avoid errors in cost-distance assessment. Missing values were set to a mean value of travel time across the various surfaces of vegetation (1.6 $km.h^{-1}$, see details in Table II).

3.1.1.3. Graph theory in geography

Distances and routes are closely related concepts in geography. The most commonly used geographic distance measure is the great-circle distance, which represents the shortest line between two points, taking into account the curvature of the earth. The great-circle distance could be conceived of as the distance measured along a route of a very efficient traveler who knows where to go and has no obstacles to deal with. In common language, this is referred to as a distance ‘as the crow flies'.

When travel is less goal-directed and is affected by the environment but also land use or political constraints, grid-based distances and routes become relevant. The least-cost distance is implemented in most GIS softwares taking into account obstacles and the local `friction' of the landscape (roads, land cover, water, slope etc.). So, calculations of distances and routes rely on raster data. In geospatial analyses, rasters are rectangular, regular grids that represent continuous data over geographical space. Cells are arranged in rows and columns and each has a value. A raster is accompanied by metadata that indicate the resolution, extent and other properties.

Distance and route calculations on rasters rely on graph theory. So as a first step, rasters are converted into graphs by connecting cell centers to each other, which become the nodes in the graph. This can be done in various ways (Figure 3.1).

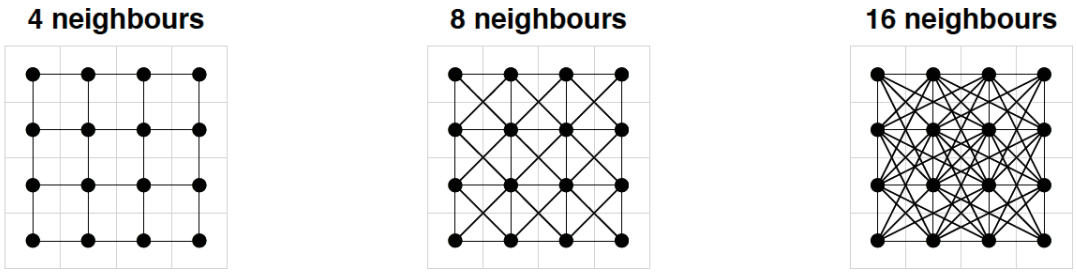


Figure 3.1 | The three ways to traduce connectivity between cells within grids. *Cells can be connected (i) orthogonally to their four immediate neighbors, which is called the von Neumann neighborhood (left panel), (ii) with their eight orthogonal and diagonal nearest neighbors, the Moore neighborhood. The resulting graph is called the 'king's graph’ because it reflects all the*

legal movements of the king in chess. This is the most common and often only way to connect grids in GIS softwares. (middle panel) or (iii) in 16 directions combines king's and knight's moves and may increase the accuracy of the calculations but increase calculation time (right panel) (Van Etten 2012).

The cost to travel between one node to another is dependent on the spatial orientation of the nodes. How the cells are connected also impacts the travel cost. Here, I describe how the cost to travel between two adjacent nodes is calculated in two different cases: a perpendicular or a diagonal move.

Cost calculation with horizontal and vertical moves only

Moving from a cell to one of its four directly connected neighbors (a1 distance represented as the red line) is equivalent to travel between the two nodes e.g. cross half of the cell 1 et half of the cell 2 (Figure 3.2). If we consider cell with a length of 1, which means the cost between 2 adjacent cells in perpendicular travel is the mean of the costs of the cells 1 and 2.

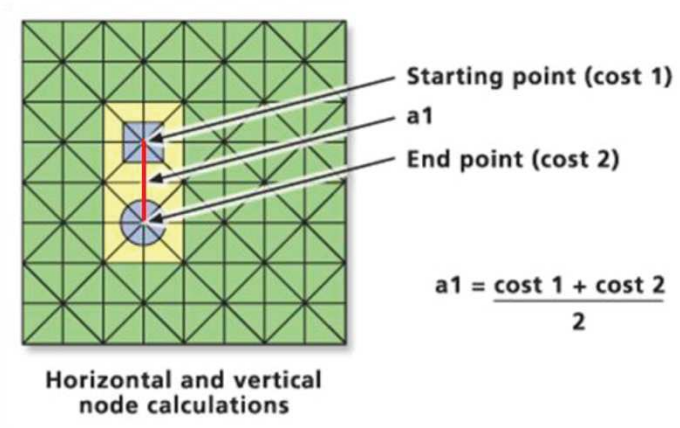


Figure 3.2 | The accumulative perpendicular cost between 2 cells with a length of 1 represents the mean of the costs of the two cells *(source: ArcGIS Resources).*

In the usual case, cost in perpendicular travel between two adjacent cells with a length of r is:

$$cost_{perpendicular} = r.\frac{cost\ 1 + cost\ 2}{2}$$

Cost calculation with diagonal moves allowed

If the movement can be diagonal, the cost to travel over the distance a1 (Figure 3.3) depends on the square root of two times the square cells length and the mean of the costs of the cells 1 and 2.

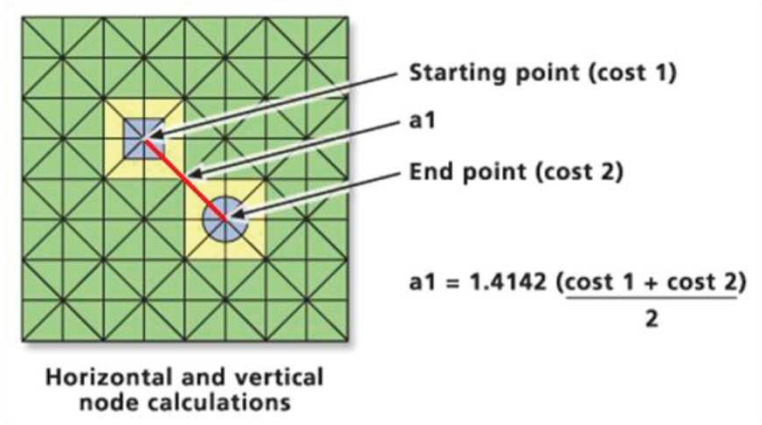


Figure 3.3 | The accumulative diagonal cost between 2 cells with a length of 1 represents the mean of the costs of the two cells multiplied by the square root of 2 or approximately 1.4 *(source: ArcGIS Resources).*

In the usual case, cost in diagonal travel between two adjacent cells with a length of r is:

$$cost_{diagonal} = \sqrt{2r^2}.\frac{cost\ 1 + cost\ 2}{2}$$

Cumulative cost is therefore, calculated from the origin cell passing by one adjacent cell to another to the destination cell using diagonal or vertical movement as described above.

3.1.1.4. Estimating the least-cost distance

The objective of the present study is to calculate travel time, or say, accumulated cost (in time) from strategic human settlements (major markets and the nearest human settlement) to reef sites taking into account obstacles and the local `friction' of the landscape (roads, land cover, water, etc.). I used the accCost function of the 'gdistance' package in the R environment (R Development Core Team 2014) to automate calculation for any reef location. This function

requires the origin and destination points as inputs and a transition matrix describing the 8 connections between cells across the friction-surface grid (Van Etten 2012). The function uses the Dijkstra's algorithm which is the most commonly used algorithm to calculate least-cost distance (Dijkstra 1959).

3.1.1.5. Assessment of human accessibility for any coral reef globally

World database on Coral Reefs

The Global Distribution of Coral Reefs (UNEP 2010) is the most comprehensive global dataset showing the global distribution of coral reefs in tropical and subtropical regions. I overlapped a global 10 km x 10 km resolution grid across the oceans with the Global Distribution of Coral Reefs (UNEP-WCMC 2010). Then I checked the presence of coral reefs within each cell (1) or the absence (0). Globally, 27,212 coral reef cells were found. A finer resolution grid would have required higher computational capacity not available for this project. Each of the 27,212 reef cells has been considered as a potential origin point in travel time calculation.

Defining markets and the nearest human settlement

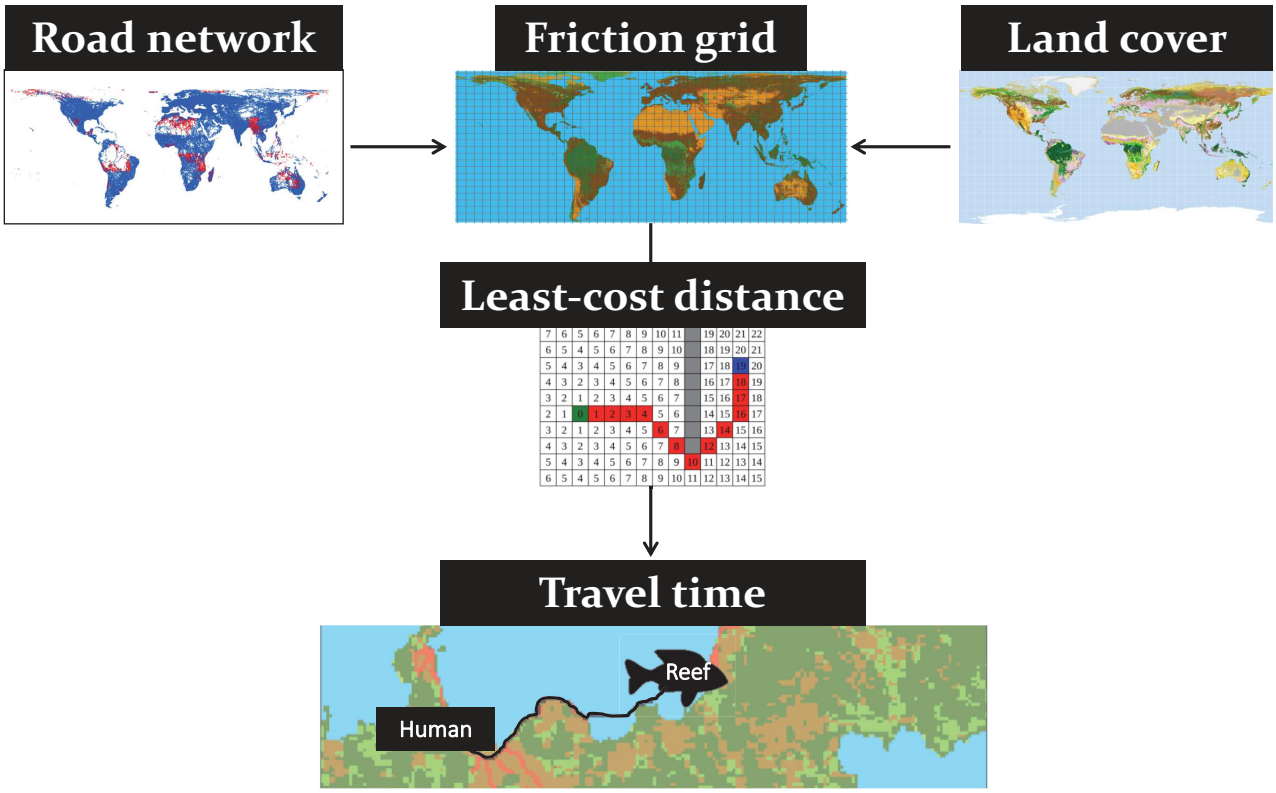
The key goal was to determine how far coral reefs were from both major markets and the nearest human settlement (destination points). Following standard convention in agricultural economics, the nearest city was defined as the market. I built the list of major markets using the World Cities map layer given by Esri™ (sources: ESRI, CIA World Factbook, GMI, NIMA, Times Atlas 10th) which includes national capitals, provincial capitals, major population centers, and landmark cities.

To define the nearest human settlement, I also assessed human density per unit of surface using the LandScan™ 2011 database developed by the Oak Ridge National Laboratory (ORNL). This is the finest resolution for global population distribution. It integrates daytime movements and collective travel habits into a single measure to produce a better representation of where people are located during an average day at approximately 1km resolution. I considered any populated cell as a human settlement.

3.1.1.6. Calculation of travel time between humans and coral reefs

I developed a script in R 3.0.3 (R-Development-Core-Team 2014) to automate the calculation of travel time to reach the nearest major market and the nearest populated pixel within a 500km-buffer from any coral reef cell. A 500 km-buffer surrounding the coral reef pixel was chosen as it encompasses the majority of coral reefs. The rationale for 500 km was a compromise between balancing the intensive computational requirements and coverage of coral reef cells. When coral reef cells were further than 500 km from any population settlement, travel time calculation would have been extremely time consuming so linear path from human settlements was considered, assuming that most of the distance travelled is on water. The amount of time was obtained by dividing the total linear distance by the speed on water bodies. For cells which are in the same pixel as human settlements (major market or populated pixel), the calculation of potential travel time was not possible, so I set a minimum value of 1 minute.

Box 1. Overview of the methodological procedure developed to assess travel time between any coral reef and its nearest human settlement



Step 1. Combination of GIS data to create a friction-distance grid

Road network and land cover were combined to create a global regular grid (raster layer) at 1km-resolution called a friction grid where each cell had a unique value corresponding to the time required to cross the given surface (paved road, track, forest, water body, etc.)

Step 2. Processing the least-cost distance algorithm **to assess potential travel time**

The Dijkstra's algorithm was used to calculate least-cost distance (Dijkstra 1959) between the origin (each reef) and the destination points (the nearest market and the nearest human settlement) across the friction-surface grid (Van Etten 2012) to obtain the potential travel time from each human population settlement. This procedure has been automated in R 3.0 (R Development Core Team 2014) for every coral reef in tropical and subtropical regions (27,712 cells).

3.1.2. Potential travel time as a new measure of accessibility – more than linear distance

Linear distance between coral reefs and human settlements can fail to capture landscape and seascape heterogeneity that create differences in accessibility depending on road networks and coastline tortuosity among others. The existence of a road along the coast, for instance, facilitates faster access to a given reef than the direct travel by boat (Figure 3.4). To account for all these drivers of differential accessibility, the geographical concept of 'friction of distance' was adapted to develop a metric referred as 'potential travel time'. This metric integrates speeds required to cross 24 different types of land cover for each cell of our global 1km-resolution grid and represents the minimum travel time required to cross each type of surface, assuming that road and maritime travels are made by motorized vehicles. Road speed depends on road type while off road travel is foot based. Since these values can vary depending on available technology, infrastructures and vehicles this new metric can be called 'potential travel time'. As an average scenario, I considered 60 $km.h^{-1}$ on a road, 30 $km.h^{-1}$ on a track and 20 $km.h^{-1}$ on the ocean (see details in Table II).

Here, I determined the minimum cumulative cost in time between every coral reef in the world (27,212 coral reef cells) and *(i)* the nearest human settlement of any size (any populated pixel given by the finest resolution global human distribution grid, see Figure I), and *(ii)* the nearest major market (considered as a national capital, a provincial capital, a major population center, or landmark city) since both have been shown to impact reef resources, conditions and functioning (Cinner *et al.* 2013; Advani *et al.* 2015).

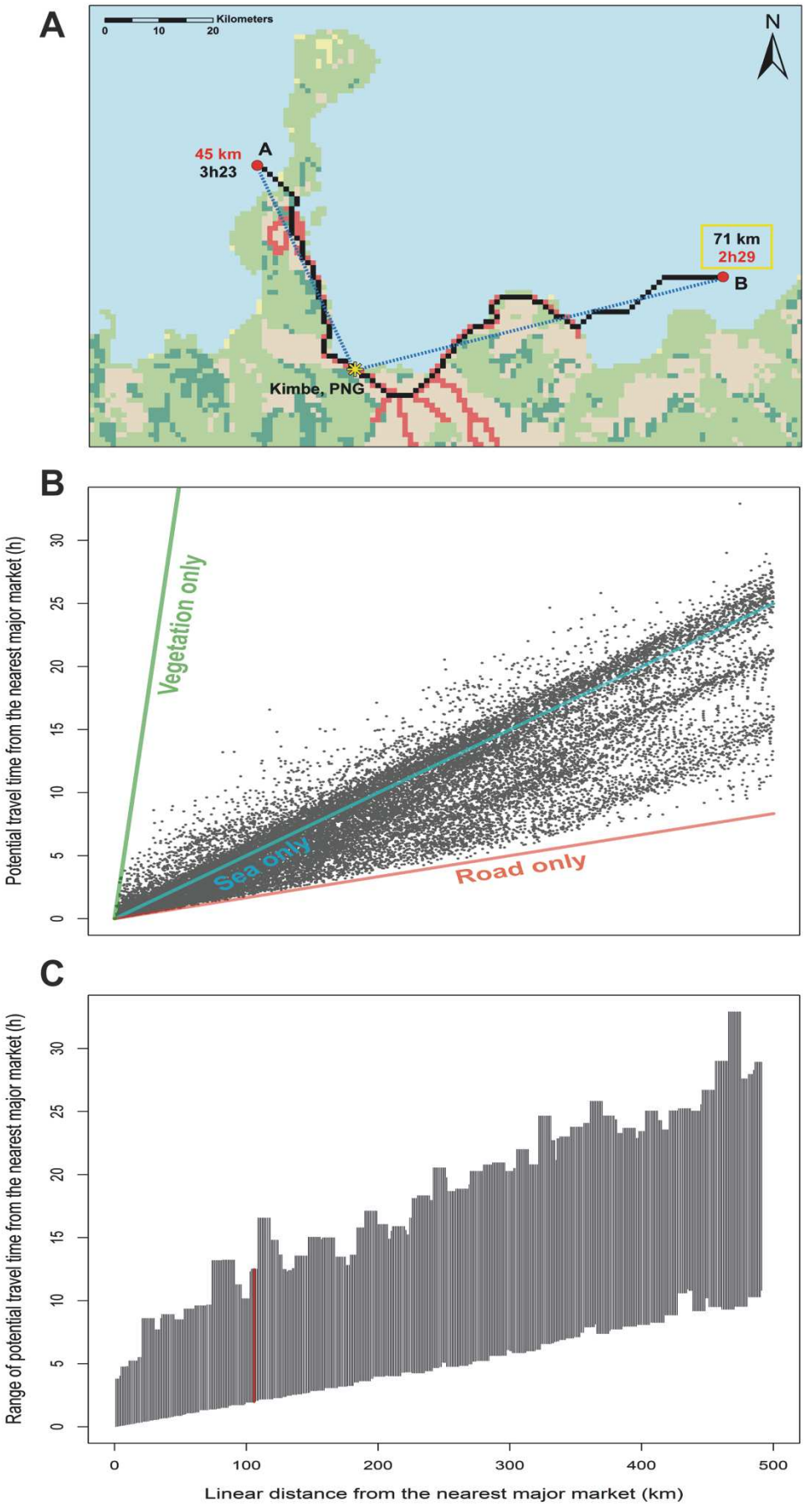

A
Kilometers
0
10
20
N
45 km
3h23
A
71 km
2h29
B
Kimbe, PNG
B
Potential travel time from the nearest major market (h)
Vegetation only
Sea only
Road only
C
Range of potential travel time from the nearest major market (h)
Linear distance from the nearest major market (km)

Figure 3.4 | Potential travel time as a measure of accessibility. *Accessibility is defined as the travel time to a location using land (road and land cover) or water (navigable river, lake and ocean) based travels and represents the 'cost' of travelling in time across a specific surface (e.g. land, sea, forest, etc.). As an illustration, the major market in Papua New Guinea, Kimbe (yellow asterisk), and two reef sites (red points) were considered (a). I calculated the linear distance and the travel time from the nearest market for 23,940 cells of coral reefs globally (b). Linear distance and travel time are highly correlated ($R^2 = 0.9$) but a small range of linear distance values (10 kilometers) may correspond to a wide range of potential travel time values (c). Travel time is a combination of road (red line), off road (green line) and maritime (blue line) travels*

The linear geographic distance and potential travel time from the nearest major market can be related (Figure 3.4B). Not surprisingly, linear distance and travel time are correlated globally ($R^2 = 0.9$); a reef far from people cannot be reached with limited travel time while a reef close to people (<10km) is always accessible with less than 4h travel time. However, a given linear distance value may correspond to a wide range of potential travel times (Figure 3.4C). For any 10km-window along a whole linear distance gradient from 0 to 500 kilometers between a given reef and the nearest market, the range of travel time is highly variable. For example, a range of linear distance to market between 105 and 115 kilometers (represented as red bar in Figure 3.4C) corresponds to potential travel time ranging from 2 to 13 hours. This result highlights the importance of integrating the landscape heterogeneity in accessibility assessments since considering travel on a unique surface may produce a coarse and unrealistic estimation of time required to reach reefs. Travelling only off-road, i.e. through the vegetation, only on road or only on the ocean provide over-simplified scenarios that are almost never met (Figure 3.4B). Most of the pathways to reach the reefs combine road and maritime travel, preventing any simplification. Even if linear distance may appear to be a good surrogate for estimating potential travel time to reach the reefs globally (Figure 1B), a map of residuals from predicted values shows that, relative to potential travel time, linear distance tends to underestimate accessibility in populated areas where roads are present and overestimates accessibility in more remote places (Figure II). This likely has to do with the potential travel time metric's recognition of reduced travel time on roads.

3.1.3. Travel time as a predictor of fish biomass on coral reefs

3.1.3.1. The New Caledonian case study

There is considerable effort to better understand the multi-scale drivers of change in coral reef ecosystems through predictive modelling from local to global scales. For instance, patterns of fish biomass and biodiversity across coral reefs have been explained by several non-mutually exclusive processes that involve the roles of energy (Tittensor *et al.* 2010), climate (Pellissier *et al.* 2014), habitat (Rogers *et al.* 2014), biogeography (Parravicini *et al.* 2013), humans (Mora *et al.* 2011), and environmental stochasticity (Dornelas *et al.* 2006). A key goal of this body of research is to identify drivers of change that can be used as policy levers to positively influence the future conditions of coral reefs (Cinner & Kittinger 2015). The availability of travel time estimation to reach the reefs from markets or populations may help to decipher the many dimensions of human influence on ecosystem conditions when integrated to models in combination with other commonly used predictors (e.g., environment and habitat). Coral reef conditions (biomass or biodiversity) and functioning (e.g. herbivory) are classically related to the density of local human populations (Bellwood *et al.* 2012; Williams *et al.* 2015b) and more recently to the linear distance to humans (Advani *et al.* 2015) or markets (Brewer *et al.* 2012; Cinner *et al.* 2013). To assess if travel time is a better predictor of reef fish biomass than local human density and linear distance to market, I used data from New Caledonia which is located in the South Pacific, approximately 1200 km off eastern Australia. This archipelago comprises a main high island and several smaller islands. One third of the human population lives in Noumea the main city (~ 98,000 people) considered as the regional capital hosting the main market.

I used 1,357 Distance Sampling Underwater Visual Census (UVC) surveys of fish communities (Figure 3A) to quantify the relative influences of environment, habitat, and human impact on fish biomass (Table III, Figure III).

3.1.3.2. Fish sampling

Reef fishes and the associated coral reef habitats were surveyed from 1986-2013 across New Caledonia. Description of the sampling campaigns can be found in Andréfouët & Wantiez (2010), D'Agata *et al.* (2014), Kulbicki (1997; 2006), Letourneur *et al.* (2000) and Wantiez (2010). Data were collected along 1,357 Distance Sampling Underwater Visual Census (UVC)

transects collected along a gradient of human pressures (e.g. highly populated (2,135 people.km-²) to isolated and uninhabited sites).

The main reef types (biotope) included: *(i)* sheltered coastal reef, *(ii)* lagoon reef, *(iii)* inner barrier reef, and *(iv)* outer reef. For each reef, transects were performed on both the reef flat and slope, when feasible. To decrease the bias due to diver attraction and repulsion, UVC datasets were truncated at a distance of 7 m on each side of transects. This incorporated approximately 95% of sighted commercially important species and all apex predators, and allowed for the calculation of fish biomass over a 700 m² area (2 sides x 7 m width x 50 m long). Sharks and rays were removed from the main species list due to the difficulties in assessing their abundance with UVC. The dataset comprises 352 species belonging to 33 different families.

The biomass of individual fishes was estimated using the allometric length-weight conversion: $W = aTL^b$, where parameters a and b are species-specific constants, TL is the individual total fork length in cm, and W is the weight in grams. Biomass was log-transformed for statistical analyses.

3.1.3.3. Human impact variables

I combined data on three human impact variables (Table III). These were: 1) the human population occurring within a 20 km radius of each UVC for the sampling year (already calculated in previous studies); 2) the linear distance between each UVC and the market Noumea; 3) the travel time between each UVC and Noumea.

3.1.3.4. Habitat and environmental variables

Several habitat and environmental variables were also collected (Table III). The Medium Scale Approach (MSA) was used to record substrate characteristics along transects where finfish were counted by UVC. MSA has been developed by Clua *et al.* (2006) to specifically complement UVC surveys. The method consists in recording depth, habitat complexity, and 23 substrate parameters (% coral cover, % macro algae, etc.) within ten 5x5 m quadrats on each side of 50-m transects, for a total of 20 quadrats per transect. Habitat characteristics of each transect are then calculated by averaging over the 20 quadrats each habitat parameter potentially relevant to explain the structure of finfish communities.

Island type was included and is characterized by three categories: high island (island without lagoon, which include tectonically uplifted reefs), low island (island with a large lagoon) and atoll (no island except reef islands which are islands created by the accumulation of reef sediments). Weekly average Sea Surface Temperature (SST) (1998-2008 in a 5 km pixel) was available from AVHRR (Advanced Very High Resolution Radiometer; http://oceanwatch.pifsc.noaa.gov/). For each UVC transect, the temperature within that pixel was calculated.

3.1.3.5. Models and importance of variables

I first ran a series of Generalized Linear Models (GLM) models that predict fish biomass using different sets of predictor variables (human, habitat and environment, Table III). Fish biomass was log-transformed to obtain a normal distribution. Travel time, linear distance, and depth were log-transformed prior analyses, because theses variable showed a power relationship with log-biomass of fish. I first built a base model without any human impact variables (only habitat and environment variables). Then I added to this model only one human variable to provide three new models each corresponding to one aspect of human impact. I compared the performance of each of these three models to the base model using the likelihood-ratio (LR) test. Then, using a backward selection procedure, I identified the most parsimonious model using the Akaike Information Criterion (AIC), a model coined as “best” model.

To determine the importance of each variable in explaining variations in fish biomass I built all sub-models (containing a subset of variables) from the full model (all variables) using the dredge function from package ‘MuMin’ in R 3.0.3 (R Development Core Team 2014). Then for each sub-model, I calculated the Akaike weight (AICw) that can be interpreted as the probability that a specific model is the best. The relative importance of each predictor variable at explaining variation of fish biomass was estimated by summing Akaike weight values across all models that include this predictor variable. These summed Akaike weights (AICw) range from 0 (useless variable) to 1 (essential variable), hence providing a means for ranking the predictor variables in terms of information content.

As a complementary analysis I ran a Boosted Regression Tree (BRT) model to predict fish biomass using all predictor variables. BRT have the advantage, over GLM models, to cope with

interacting factors and non-linear relationships (Elith *et al.* 2008). In BRTs, contributions of each explanatory variable (%) are the proportion of each variable selected to split the data among all the trees, weighted by the squared improvement to the model as a result of each split, and averaged over all trees. The variables with the highest contributions are the most important variables contributing to the model.

3.1.4. Travel time from market as the key driver of coral reef conditions

Humans shape the level of reef fish biomass since each proxy of human impact has a significant effect beyond that of habitat and environment (Table 3.1).

Table 3.1 | Comparison of candidate models predicting reef fish biomass as a function of environmental, habitat, and human impact variables across the coral reefs of New Caledonia. *The Aikaike Information Criterion (AIC) and the total adjusted R-squared (R^2) for each model and sub-model were calculated. A likelihood ratio test (LR-test and F-value) between the "Environment+Habitat" model and each enriched model with one aspect of human influence (population, linear distance, or travel time) shows the significance of adding human impact variables. The "Best" model is the most parsimonious according to the AIC criterion containing only travel time and some selected environmental variables (mean depth, surface cover of live coral, surface cover of macroalgae, the reef type, and island type).*

Model	*AIC*	*R^2*	*F*
Null	2085	0	
Environment + Habitat	1544	0.37	LR-test
Environment + Habitat + Human density	1449	0.41	98.854*
Environment + Habitat + Linear distance	1413	0.43	138.3*
Environment + Habitat + Travel time	1352	0.45	206.2*
Best	1350	0.45	

** p-value<0.001*

However, potential travel time from the market is the strongest predictor of fish biomass since its AICw is 1 (essential variable in all best GLM sub-models) and its relative contribution to the BRT model is 28% surpassing that of all other competing variables (Figure 3.5B). By contrast, human density and linear distance to market have lower AICw values (0.33 and 0.44 respectively) and contribute to BRT models at, respectively, the fourth (11%) and third rank (13%) suggesting their marginal influence on fish biomass compared to travel time. Finally, the most parsimonious model ('best' in Table 3.1), based on variable selection using the AIC criterion, only retains potential travel time from the market as the sole human driver of fish biomass on New Caledonian reefs. This GLM model explains 45% of variation in fish biomass across reefs. However, the BRT model, which takes into account variable interactions and thresholds effects, explains up to 70% of this variation highlighting potential interplay between human, environmental, and habitat drivers. When extracting the 'pure' effect of travel time from the market on fish biomass using a partial plot from the GLM a saturating relationship was observed (Figure 3.5C). Low biomass values (<100 $kg.ha^{-1}$) are mostly found when travel time is lower than 10h (Figure 3.5C). All remote reefs (Figure 3.5A) have a fish biomass higher than 500 $kg.ha^{-1}$, which has been suggested as a potential threshold to maintain healthy and functioning coral reefs (McClanahan *et al.* 2011; MacNeil *et al.* 2015).

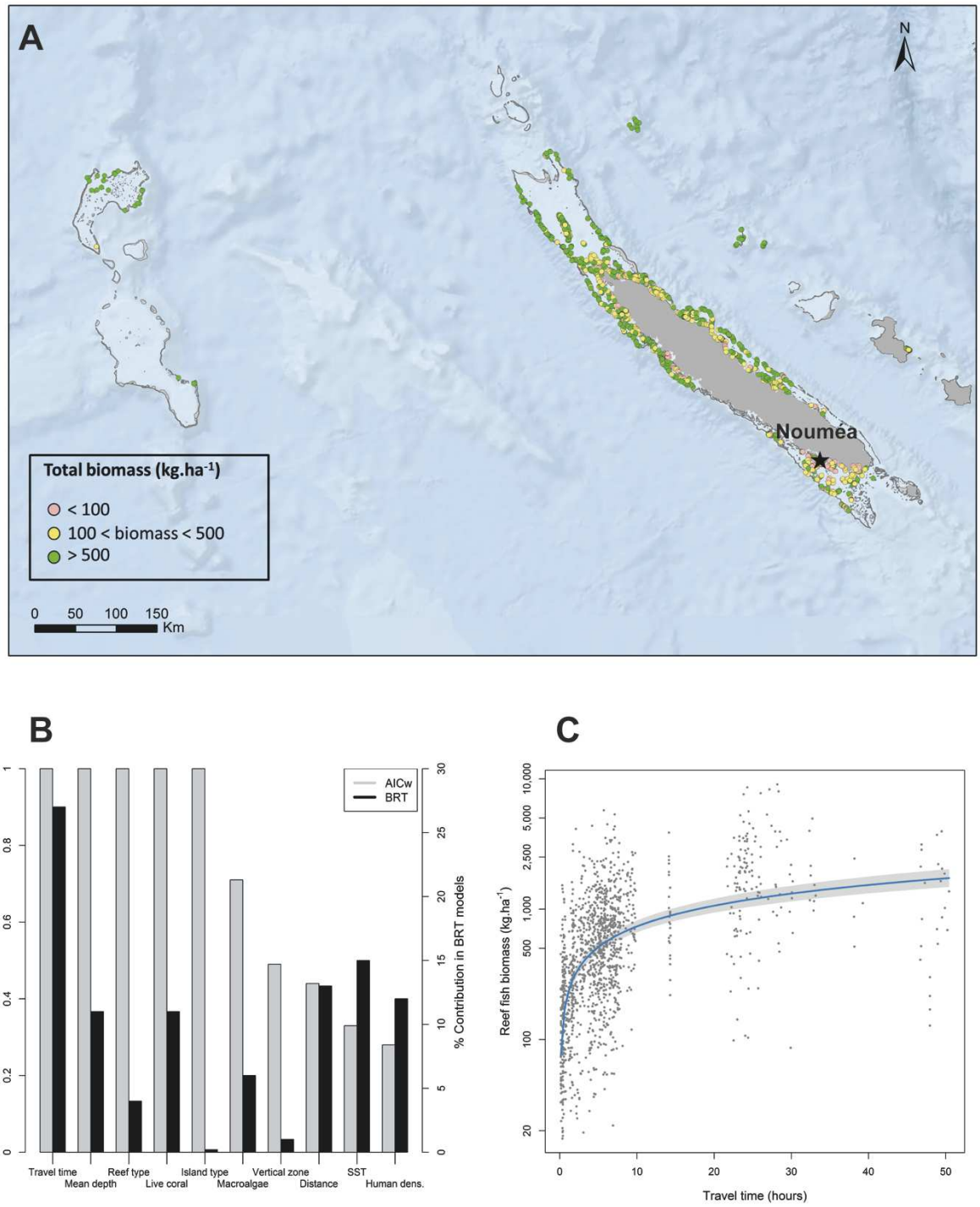


Figure 3.5 | Potential travel time as the main driver of fish biomass. *Fish biomass estimates from 1,357 Underwater Visual Census (UVC) surveys performed across coral reefs of New Caledonia (a). The relative influences of predictor variables (environment, habitat and human impact) are assessed using the weighted Akaike Information Criterion (AICw) from generalized linear models and the relative contribution from boosted regression tree models (b). The*

partial plot (c) shows the 'pure' relationship between potential travel time and reef fish biomass, i.e. while considering the other predictor variables.

3.1.5. High but variable accessibility of coral reefs around the world

The global assessment of coral reefs accessibility shows that 58% of coral reefs (15,609 out of 27,212 coral reef cells) are located at less than 30 minutes travelling time from the nearest human settlement (Figure 3.6). On average, each reef can be reached within 1h50 (SD = 4h15). The bulk of reefs are highly accessible in the Caribbean, the Coral Triangle, the Western Indian Ocean, and the Pacific Islands. However, some areas like the Chagos Archipelago, the Spratly Islands, the Chesterfield Islands, the northwest Hawaiian Islands, and the Coral Sea have reefs at more than 12h travel time from the nearest human settlement. None of Caribbean coral reefs are more than 13 hours from people (Figure 3.6 A1 & B1).

Accessibility of coral reefs from major markets is high relative to the nearest human settlement (mean = 10h) but is highly variable around the world (SD = 9h). This analysis shows that 25% (6,790 pixels) of reefs are located at less than 4 hours from the nearest major market while 31% (8,428 pixels) of reefs are more than 12 hours from the nearest market. Caribbean coral reefs appear much more accessible from markets than their Indo-Pacific counterparts (Figure 3.6 A2 & B2).

To take into account the variability of available boat technology, I re-assessed global accessibility using slow (10 $km.h^{-1}$) and fast (40 $km.h^{-1}$) boat speeds. Accessibility of coral reefs from the nearest population ranges between 3h40 (SD = 8h30) and 1h10 (SD = 3h), and from the nearest market between 17h (SD = 17h30) and 6h10 (SD = 4h40) using slow vs. fast boats, respectively (Figures IV & V). Future applications should consider variable travel speeds according to per capita Gross Domestic Product in order to reflect different levels of infrastructure and technology in developed versus developing countries. Yet this country-scale assessment was beyond the scope of our initial exploration of travel time.

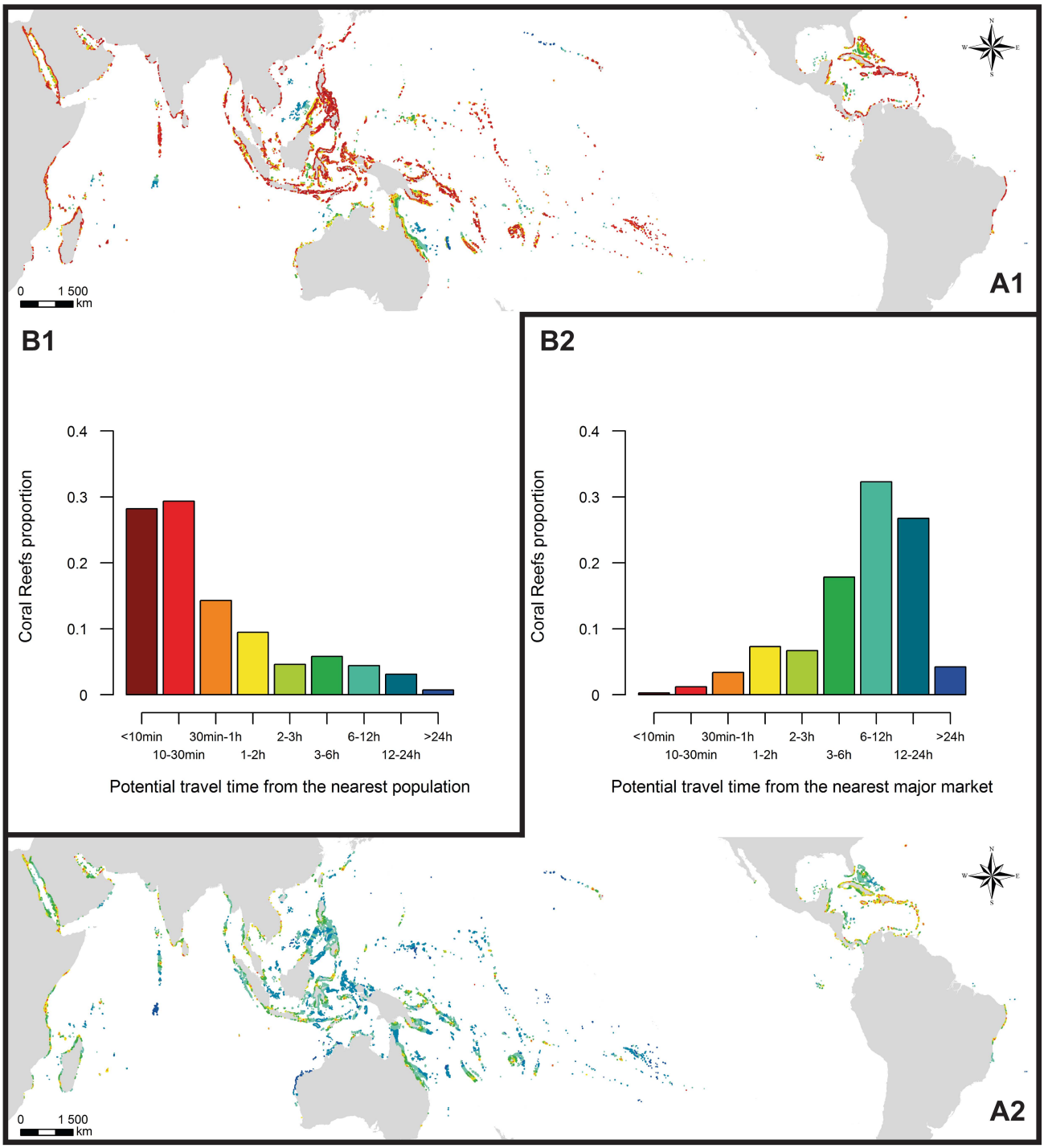


Figure 3.6 | Accessibility of any coral reef from people (nearest market and nearest human settlement) around the world. *Global coral reefs are extremely close to people (A1 & B1); 58% of reefs located at < 30 min travelling from the nearest human settlement while 25% of reefs are located at < 4 h from the nearest major market (A2 & B2). Only few areas appear as remote reefs (further away than 12 h travelling from human settlements) like the Chagos Archipelago, the Spratly Islands, the Chesterfield Islands and the Hawaiian Islands.*

3.1.6. Conclusion and perspectives

Better understanding the dynamics of coral reef social-ecological systems is one of the most critical challenges that scientists and managers are facing today (Cinner 2014). To sustain coral reef ecosystems, there is an urgent need to model the complex interactions between people and reefs. The development of a global measure of potential travel time is an important step toward this objective.

Indeed, the New Caledonian study case proved that travel time from market is the strongest predictor of fish biomass and outperforms linear distance and human population density that were commonly used. The global assessment of coral reefs accessibility revealed which coral reefs are particularly at risk as more accessible to people. Travel time calculations may help to develop news solutions that could preserve coral reefs while meeting socioeconomic development goals.

Nonetheless, our global assessment of coral reefs accessibility presents two major limitations: *(i)* travel time from a given human settlement does not accurately reflect human impacts on reefs since it does not include the population size of this settlement and *(ii)* our framework assumes that road and maritime travels are made by motorized vehicles while many reefs are located in developing countries where wooden canoes are commonly used.

Indeed, one further step consists on assessing human impact on reefs as a function of how large and far away the surrounding human population is. The next part proposes one alternative to the first limitation by describing how to combine travel time and human population density into an integrative metric of human impact.

The second limitation will be discussed in Chapter 5 which considers a study case in Northwest Madagascar and where travel time calculation integrates the local levels of infrastructure and technology.

3.2. The gravity of human settlements

"Gravity has long been one of the most successful empirical models in economics. Incorporating deeper theoretical foundations of gravity into recent practice has led to a richer and more accurate estimation and interpretation of the spatial relations described by gravity. Wider acceptance has followed. Recent developments are reviewed here, and suggestions are made for promising future research." - James E. Anderson, Professor of Economics at Boston College.

3.2.1. Combining travel time and human density: the gravity concept

Many variables related to human pressure were calculated based on markets or human population density while other take into account the distance from human settlements (Mora *et al.* 2006; Mora *et al.* 2011; Bellwood *et al.* 2012; Williams *et al.* 2015b). Very few combine these both aspects and the gravity concept can fill this gap. This is a concept commonly used in geography which uses a modified version of the Isaac Newton's Law of Gravitation to predict movement of people, information, and commodities between cities and even continents. The gravity model, as social scientists refer to, is based on the modified law of gravitation that predicts that interactions between two places (e.g. cities) are positively related to their mass (i.e. population) and inversely related to the distance between them (Anderson 2011). Since *(i)* larger places attract people, ideas, and commodities more than smaller places and *(ii)* places closer together have a greater attraction, the gravity model combines these two key aspects in a single metric. Application of the gravity concept in a coral reef context posits that the strength or magnitude of human interactions with a reef is a function of the population size divided by the squared time it takes for this population to reach a given reef as:

$$\frac{population\ size}{travel\ time^2}$$

Therefore, gravity is a balance between human population size and accessibility, it reflects potential human pressure and is expressed in inhabitants per square hour. For example, a gravity value of 10,000 inhab/h² can be reached in three different cases:

-at small scale, a human settlement of 2,500 inhabitants 30 minutes away from the reef.

-at medium scale, a market of 40,000 inhabitants located 2 hours travelling.
-at large scale, a market of 1,000,000 inhabitants located 10 hours travelling.

It is also possible to calculate aggregated gravity within a buffer by adding up gravity of each human settlement considered. For example, aggregated gravity of total population within a spatial buffer requires calculation of travel time from reef to each cell from LandScan™ dataset where population density is positive, then, gravity of each populated pixel is summed.

3.2.2. Reef fish biomass is primarily related to the gravity of human settlements

3.2.2.1. Calculation of gravity metrics

If gravity seems to be good candidate to disentangle complex relationships between human populations and the conditions of coral reefs, empirical evidence is still needed.
My PhD is integrated into the *Cinner Research Group* led by Dr. Joshua E. Cinner that focuses on the interface between social science and ecology to develop solutions for a wide range of issues facing coral reefs and the millions of people who depend on them. One current centerpiece of this research theme is the "Bright Spots" project, which seeks to identify and learn from the outliers in this case, places with more fish than expected, given the socioeconomic and environmental conditions they are exposed to.
The first paper developing the idea was published in July 2016 and aimed to explore how standing stocks of reef fish biomass are related to 18 socioeconomic drivers (including gravity) and environmental conditions using data from more than 2,500 reefs worldwide and a Bayesian hierarchical model (Cinner *et al.* 2016).
My contribution to this project was to calculate, for each reef, the gravity of the nearest market and the gravity of the nearest human settlement and then to integrate them in the model.

To compute the gravity to the nearest market, I calculated the population of the nearest major market and divided that by the squared travel time between the market and the reef, I used the squared travel time (previously calculated).
To determine the gravity of the nearest settlement, I located the nearest populated pixel, determined the population of that pixel, and divided that by the squared travel time between that cell and the reef site.

Although other exponents can be used (Black 1973), we used the squared travel time, which is relatively common in geography and economics. This decay function could be influenced by local considerations, such as infrastructure quality (for example, roads), the types of transport technology (that is, vessels being used), and fuel prices, which were not available in a comparable format for this global analysis but could be important considerations in more localized adaptations of this study.

3.2.2.2. Importance of gravity to explain variations in reef fish biomass

We found that reef fish biomass decreased as the size and accessibility of markets increased (Figure 3.7).

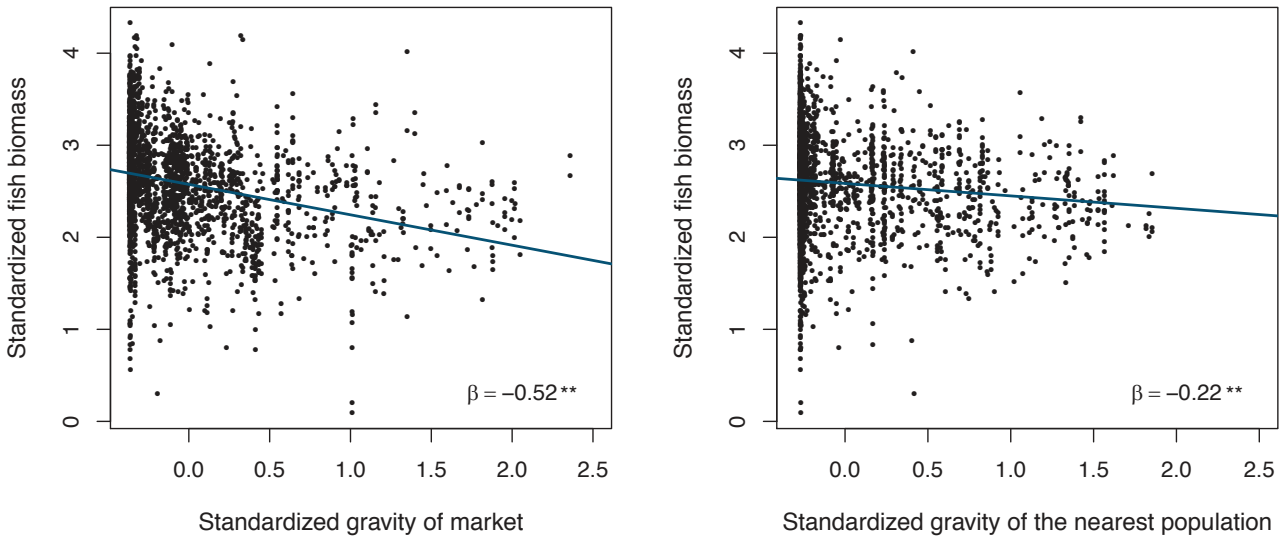


Figure 3.7 | Marginal relationships between reef fish biomass and gravity indices. *Standardized effect size of the gravity of market (left panel) and the gravity of the nearest human settlement (right panel). Parameter estimates (β) are Bayesian posterior.* (Cinner *et al.* 2016)

Specifically, the key finding from our global analysis is that the gravity of market more so than local or national population pressure, management, environmental conditions, or national socioeconomic context, had the strongest effect on reef fish biomass (Figure 3.8).

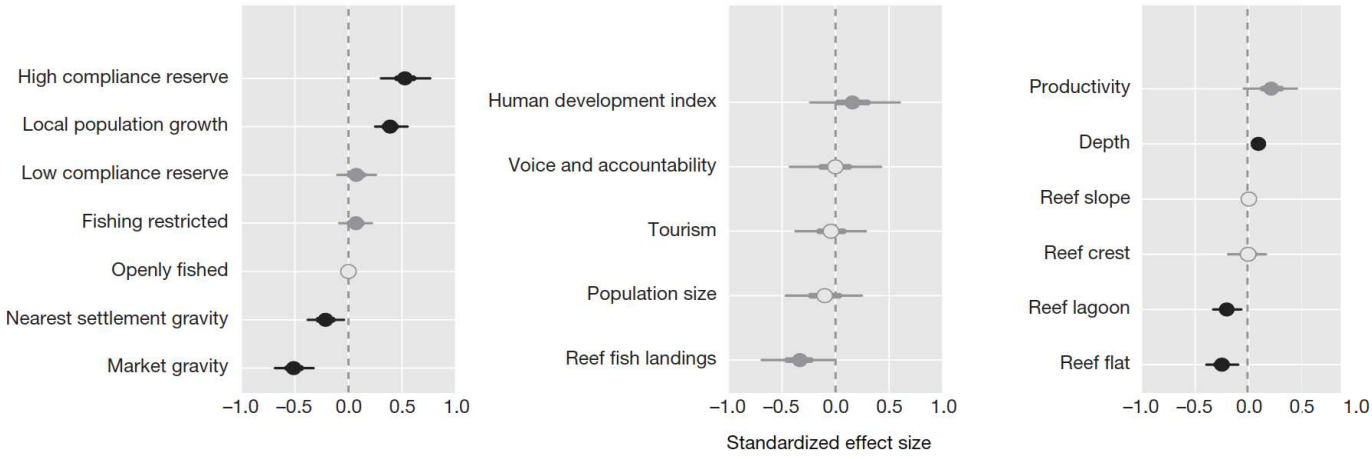


Figure 3.8 | Drivers of reef fish biomass*. Standardized effect size of local scale social drivers, nation/state-scale social drivers, and environmental covariates, respectively. Parameter estimates are Bayesian posterior median values, 95% uncertainty intervals (UI; thin lines), and 50% UI (thick lines). Black dots indicate that the 95% UI does not overlap 0; grey closed circles indicates that 75% of the posterior distribution lies to one side of 0; and grey open circles indicate that the 50% UI overlaps 0.* (Cinner *et al.* 2016)

The study also provided a sensitivity analysis to help justify the assumption that capital and landmark cities were a reasonable proxy for reef fish markets. This analysis consisted on a comparison of a series of candidate models that predicted biomass including different human variables such as (1) cumulative gravity of all cities within 500 km; (2) gravity of the nearest city; (3) travel time to the nearest city; (4) population of the nearest city; (5) gravity to the nearest human population above 40 people km^{-2} (assumed to be a small peri-urban area and potential local market); (6) the travel time between the reef and a small peri-urban area; (7) the population size of the small peri-urban population; (8) gravity to the nearest human population above 75 people km^{-2} (assumed to be a large peri-urban area and potential market); (9) the travel time between the reef and this large peri-urban population; (10) the population size of this large peri-urban population; and (11) the total population size within a 500 km radius.

AIC criterion revealed that two models were the best (delta AIC <3), those that included gravity of the nearest city and gravity of all cities within 500 km (Table 3.2).

Table 3.2 | Model selection of potential gravity and components (Cinner *et al.* 2016)

Model	Covariates	AIC	Delta AIC
M2	Gravity of nearest city	2666.4	0
M1	Gravity of all cities in 500km	2669.5	3.1
M3	Travel time to nearest city	2700.0	33.6
M5	Gravity of nearest small peri-urban area (40 people/km2)	2703.9	37.5
M11	Total Population in 500km radius	2712.0	45.6
M9	Travel time to the nearest large peri-urban area (75 people/km2)	2712.1	45.7
M6	Travel time to nearest small peri-urban area (40 people/km2)	2713.8	47.4
M8	Gravity to the nearest large peri-urban area (75 people/km2)	2722.9	56.5
M7	Population of nearest small peri-urban area (40 people/km2)	2792.7	126.3
M4	Population of the nearest city	2812.8	146.5
M10	Population of the nearest large peri-urban area (75 people/km2)	2822.2	155.8
M0	Intercept only	2827.7	161.27

Moreover, the best models are those including travel time components since all had a much lower AIC value than those including the population components, which is broadly consistent with previous systematic review studies highlighting importance of market access (Cinner *et al.* 2013). Similarly, travel time to the nearest city had a lower AIC score than any aspect of either the peri-urban or urban measures. This suggests that accessibility from capital and landmark cities (market) is likely to better capture exploitation drivers from markets rather than metrics simply based on population pressures related to human density. This may be because market dynamics are difficult to capture by population threshold estimates; for example, some small provincial capitals where fish markets are located have very low population densities, while some larger population centers may not have a market. At a global scale, the gravity of the nearest market was the best proxy to integrate market dynamics on fish biomass but downscaled regional or local analyses could attempt to use more detailed knowledge about fish markets.

3.2.3. The global distribution of human gravity on coral reefs

Beyond the case of sampled coral reefs, I calculated the gravity of humans (nearest market, nearest human population, cumulative gravity of every populated pixel within 500km) for every coral reef cell globally using a 10- × 10-km grid across the world. The global map of gravity of the nearest market is presented in Figure 3.9.

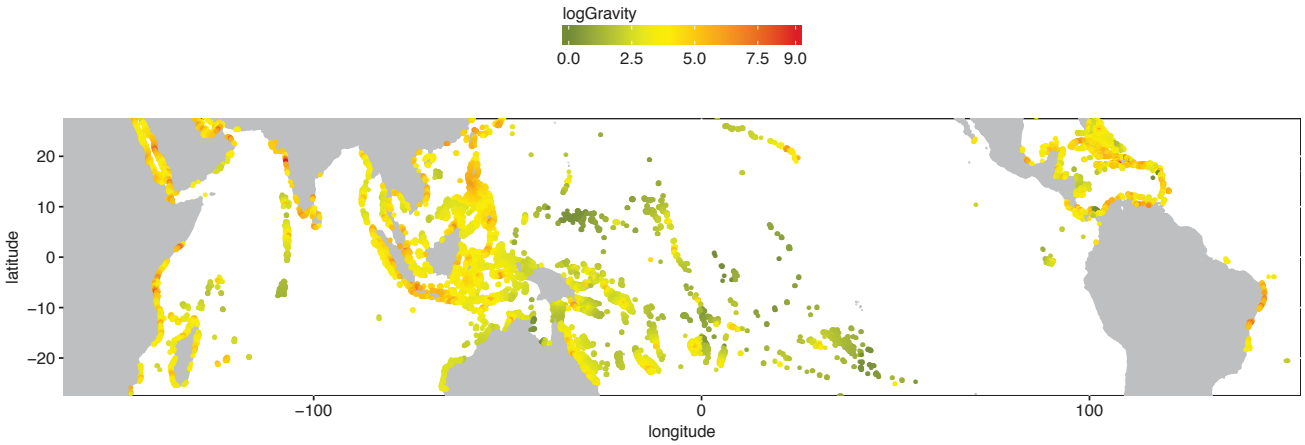


Figure 3.9 | Distribution of gravity of market on the world's coral reefs.

The distribution of gravity varies substantially among regions, with the central Indo-Pacific demonstrating lower gravity values (green points in Figure 3.9). Even within a region, there can be substantial variability in gravity values. For example, the Central Indo-Pacific has highly contrasting gravity patterns, with Southeast Asian reefs generally showing extremely high gravity values while Australian and Melanesian reefs are dominated by relatively low-gravity values (Figure 3.9). Among the French overseas territories, coral reefs in the Scattered Islands, the Chesterfield Islands and the French Polynesia show experience relatively low-gravity values (Figure 3.9).

3.3. Conclusion

The severity of human impacts on reef systems has been widely acknowledged while the causes and solutions of these impacts are still debated (Hughes *et al.* 2010; Rogers *et al.* 2015). It is clear that human population size and density are major drivers of change on reefs (Mora *et al.* 2006; Mora *et al.* 2011; Bellwood *et al.* 2012; Williams *et al.* 2015b), but in addition to these demographic pressures, drivers such as market integration and poverty also shape the

ways that people use and govern coral reefs (Cinner *et al.* 2009a; Cinner *et al.* 2013). However, these drivers of unsustainable exploitation are often poorly considered by both scientists and policy makers, leading to insufficient governance and diminished outcomes (Berkes *et al.* 2006). If the gravity of human populations seems to be the strongest predictor of fish biomass at the global scale, it remains unclear if *(i)* management can be affected by the gravity of human impacts, and *(ii)* if gravity will also be a key predictor of fish biomass at local scale given the socioeconomic context.

These two specific points will be addressed in Chapters 4 and 5 respectively.

4. Gravity of human impacts mediates coral reef conservation gains[2]

"I am glad I will not be young in a future without wilderness" - Aldo Leopold (1887-1948), American author and ecologist.

[2] *Published as Cinner, J. E., Maire, E., Huchery, C., MacNeil, M. A., Graham, N. A. J., Mora, C., McClanahan, T. R., Barnes, M. L., Kittinger, J. N., Hicks, C. C., et al. The gravity of human impacts mediates coral reef conservation gains. 2018. Proceedings of the National Academy of Sciences, 115 (27) E6116-E6125; doi:10.1073/pnas.1708001115.*

4.1. Introduction

The world's coral reefs are rapidly degrading (Hughes *et al.* 2003; Pandolfi *et al.* 2003; Hughes *et al.* 2017a), which is diminishing ecological functioning and potentially affecting the wellbeing of the millions of people with reef-dependent livelihoods (Teh *et al.* 2013). Global climate change and local human impacts (such as fishing) are pervasive drivers of reef degradation (Mora *et al.* 2011; Hughes *et al.* 2017a). In response to this "coral reef crisis", governments around the world have developed a number of reef conservation initiatives (Mora *et al.* 2003; Bellwood *et al.* 2004; Hughes *et al.* 2017a). Our focus here is on the efficacy of management tools that limit or prohibit fishing. Management efforts that reduce fishing mortality should help to sustain reef ecosystems by increasing the abundance, mean body size, and diversity of fishes that perform critical ecological functions (MacNeil *et al.* 2015; Hopf *et al.* 2016; Krueck *et al.* 2017). In practice, however, outcomes from these reef management tools have been mixed (McClanahan *et al.* 2006; Mora *et al.* 2011; Edgar *et al.* 2014; Gill *et al.* 2017).

A number of studies have examined the social, institutional, and environmental conditions that enable reef management to achieve key ecological outcomes, such as sustaining fish biomass (Mora *et al.* 2011; Williams *et al.* 2015b; Cinner *et al.* 2016), coral cover (Bozec *et al.* 2016), or the presence of top predators (Dulvy *et al.* 2004). These studies often emphasize the role of: 1) types of key management strategies in use such as marine reserves, where fishing is prohibited, or areas where fishing gears and/or effort are restricted to reduce fishing mortality (McClanahan *et al.* 2011; MacNeil *et al.* 2015); 2) levels of compliance with management (McClanahan *et al.* 2006; Pollnac *et al.* 2010; Bergseth *et al.* 2015); 3) the design characteristics of these management initiatives for example the size and age of reserves, and whether they are placed in remote versus populated areas (Graham & McClanahan 2013; Edgar *et al.* 2014); and 4) the role of social drivers such as markets, socioeconomic development, and human demography that shape people's relationship with nature (Cinner *et al.* 2009a; Cinner *et al.* 2016).

In addition to examining when key ecological conditions are sustained, it is also crucial to understand the context under which conservation gains can be maximized (Devillers *et al.*

2015; Pressey *et al.* 2015). By conservation gains, we are referring to the difference in a conservation outcome (e.g. fish biomass) when some form of management (i.e. a marine reserve or fishery restriction) is implemented relative to unmanaged areas. These conservation gains can be beneficial for both people and ecosystems. For example, increased fish biomass inside marine reserves is not only related to a range of ecosystem states and processes (McClanahan *et al.* 2011), but can also result in spillover of adults and larvae to surrounding areas, which can benefit fishers (Harrison *et al.* 2012; Januchowski-Hartley *et al.* 2012; Andrello *et al.* 2017). The potential to achieve conservation gains may depend on the intensity of human impacts in the surrounding seascape (Devillers *et al.* 2015; Pressey *et al.* 2015), yet, these effects have never been quantified.

4.2. Material and methods

Here, we use data from 1798 tropical coral reef sites in 44 nations, states, or territories (hereafter 'nation/states') in every major coral reef region of the world to quantify how expected conservation gains in two key ecological outcomes are mediated by the intensity of human impact (Chapter 2), namely: i) targeted reef fish biomass (i.e. species generally caught in fisheries); and ii) the presence of top predators (see details in Chapter 2, Table I). To quantify human impact at each site, we draw from a long history of social science theory and practice to develop a metric referred to as 'gravity' (Chapter 3). The concept of gravity (also called interactance) has been used in economics and geography to measure economic interactions, migration patterns, and trade flows since the late 1800s (Ravenstein 1889; Dodd 1950; Bergstrand 1985). We adapt this approach to examine potential interactions with reefs as a function of how large and far away the surrounding human population is (Chapter 3). At each site, we also determined the status of reef management, grouped into either: i) openly fished, where sites are largely unmanaged and national or local regulations tend to be poorly complied with; ii) restricted fishing, where there are actively enforced restrictions on the types of gears that can be used (e.g. bans on spear guns) or on access (e.g. marine tenure systems that restrict fishing by 'outsiders'); or iii) high-compliance marine reserves, where fishing is effectively prohibited (see details in Chapter 2). We also calculated size (median= 113.6km^2, mean = 217516 km^2, SD= 304417) and age (median= 9, mean = 15.5 years, SD= 14.5) of the no-take portion of each reserve.

We hypothesized that our ecological indicators (targeted fish biomass and presence of top predators) would decline with increasing gravity in fished areas, but that marine reserves areas would be less sensitive to gravity.

To quantify the relationships between gravity and target fish biomass, we developed a general linear mixed model in R, using a log-normal distribution for biomass. To quantify the relationships between gravity and presence/absence of top predators, we developed a generalized linear mixed model with a binomial family and a logit link function. For both models, we set reef cluster nested within nation/state as a random effect to account for the hierarchical nature of the data (i.e. reef sites nested in reef clusters, reef clusters nested in nations/states). We included an interaction between gravity and reserve age, as well as all the other social and environmental drivers and the sampling method and total sampling area as covariates.

We also tested interactions between gravity and management and used AIC to select the most parsimonious model. For fish biomass, the interaction between gravity and reserve age had AIC values >2 lower than the interaction between gravity and management (and a combination of both interactions). For the top predator models, both interactions were within 2 AIC values, so we chose the interaction with reserve age for consistency. All continuous covariates were standardized for the analysis, and reserve age was then normalized such that non-reserves were 0 and the oldest reserves were 1.

In summary, our models predicted target fish biomass or probability of top predators being observed at the reef site scale with an interaction between gravity and reserve age, while accounting within the random factors for two bigger scales at which the data were collected (reef cluster, and nation/state- see supplementary material), and key social and environmental characteristics expected to influence the biomass of reef fish (Cinner *et al.* 2016) which are: local population growth, Human Development Index (HDI), population size, depth, habitat, ocean productivity, climate stress and the sampling method and total sampling area as covariates (see details in Chapter 2).

To examine the expected conservation gains of different management strategies, we calculated: *(i)* the difference between the response of openly fished areas (our counterfactual) and high-compliance marine reserves to gravity; and *(ii)* the difference between the response of openly fished areas and fisheries restricted areas to gravity. For ease of interpretation, we plotted conservation gains in kilograms per hectare (kg/ha; as opposed to log[kg/ha]). A log-normal (linear) model was used to develop the slopes of the biomass *(i)* fished, *(ii)* marine reserve, and *(iii)* fisheries restricted areas, which results in the differences between *(i)* and *(ii)* and between *(i)* and *(iii)* being non-linear on an arithmetic scale.

4.3. Results

4.3.1. Gravity impacts on targeted fish biomass

Our analysis reveals that human gravity was the strongest predictor of fish biomass (Figure 4.1B, VI). Fish biomass consistently declined along a human gravity gradient, a trend particularly evident at the nation/state scale (Figure 4.1 C-E). However, this relationship can vary by management type (Figure 4.1, Figure VI). Specifically, we found that biomass in reserves demonstrated a flatter (but still negative) relationship with gravity compared with openly fished and restricted areas (Figure 1B). Interestingly, this differential slope between reserves and fished areas (Figure 1B) was due to a strong interaction between gravity and reserve age such that older reserves contributed more to biomass in high gravity situations than in low-gravity ones (Figure VI).

Thus, given average reserve age in our sample (15.5 years), biomass in reserves did not decline as rapidly with gravity compared with fished and restricted areas (Figure 4.1B). In the highest-gravity locations, modelled fish biomass in marine reserves was approximately five times higher than in fished areas (270 kg/ha compared with 56 kg/ha) (Figure 4.1B). At the reef site scale, there was considerable variability in reef fish biomass, particularly at low gravity (Figure 4.1 F-H). Critically, high-compliance marine reserves in the lowest gravity locations tended to support more than four times more fish biomass than the highest gravity reserves (1150 versus 270 kg/ha, respectively; Figure 4.1 F-H). Importantly, there was never extremely high biomass encountered in high gravity locations. Our estimate of fish biomass included key target species, including top-predators. As a supplemental analysis, we also examined target

fish biomass with the biomass of top predators excluded, which displays a similar trend, but with lower fish biomass in reserves at low gravity compared to when top predators are included (Figure VII).

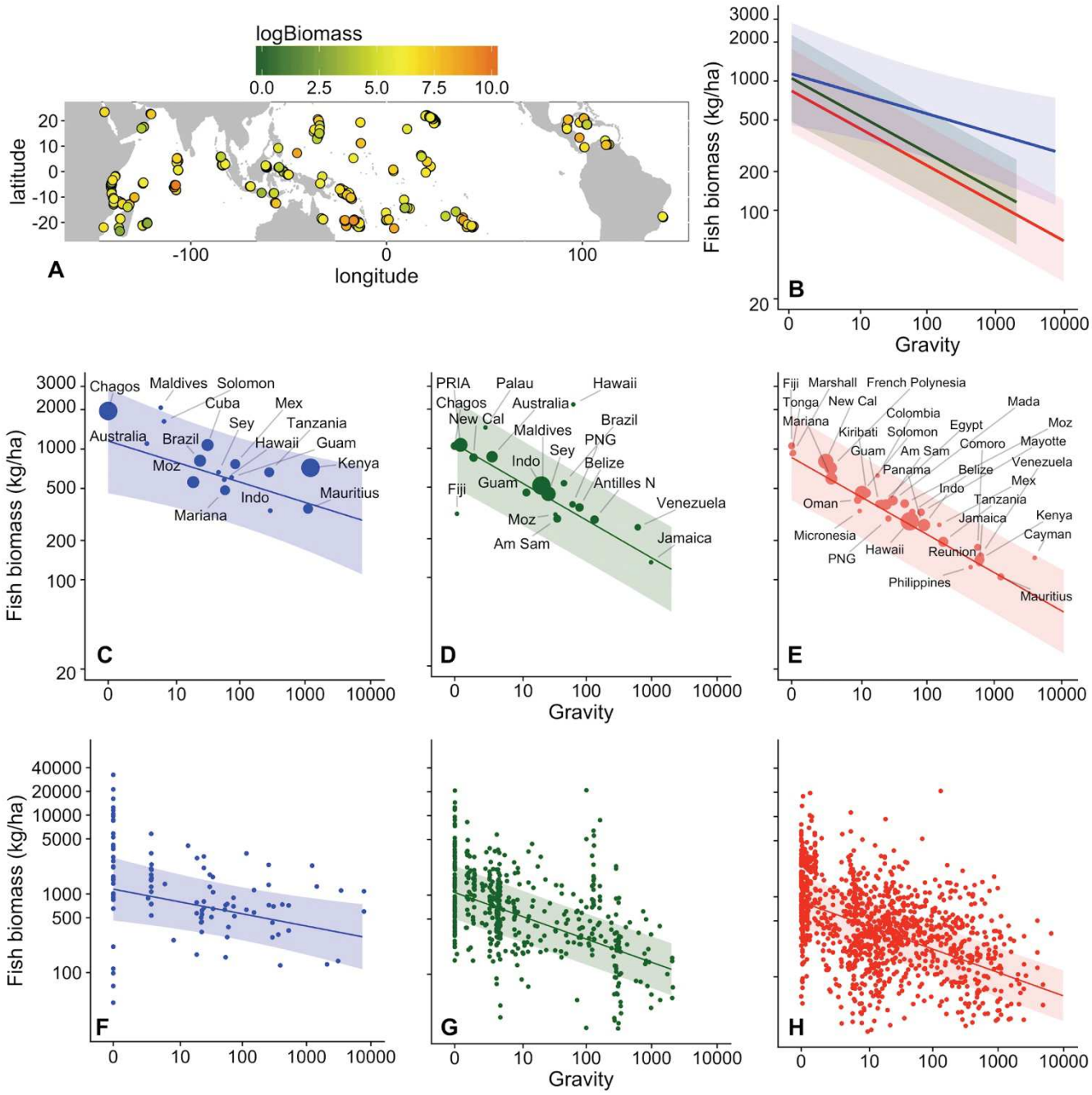


Figure 4.1 | Model-predicted relationships between human gravity and reef fish biomass under different types of fisheries management. *(A) Map of our study sites with color indicating the amount of fish biomass at each site. (B) Model-predicted relationships of how reef fish biomass declines as gravity increases by management type. Partial plots of the relationship between biomass and gravity under different types of management at the*

nation/state (C–E), and reef site (F–H) scale; openly fished (red), restricted (green), and high-compliance marine reserves (blue). Shaded areas represent 95% confidence intervals. Bubble size in C–E reflect the number of reef sites in each nation/state, scaled for each management type (such that the largest bubble in each panel represent the highest number of sites per nation/state for that type of management) (Table IV). Nation/state name abbreviations for F-H are in Table IV.

4.3.2. Gravity impacts on top predators

A key finding from our study is that top predators were encountered on only 28% of our reef sites, but as gravity increases, the probability of encountering top predator on tropical coral reefs dropped to almost zero (<0.005), regardless of management (Figure 4.2). The probability of encountering top predators was strongly related to gravity and the type of management in place, as well as sampling methodology and area surveyed (Figure 4.2, Figure VI). At low gravity, the probability of encountering a top predator was highest in marine reserves (0.59) and lowest in fished areas (0.14), when controlling for sampling and other environmental and social drivers (Figure 4.2, Figure VI).

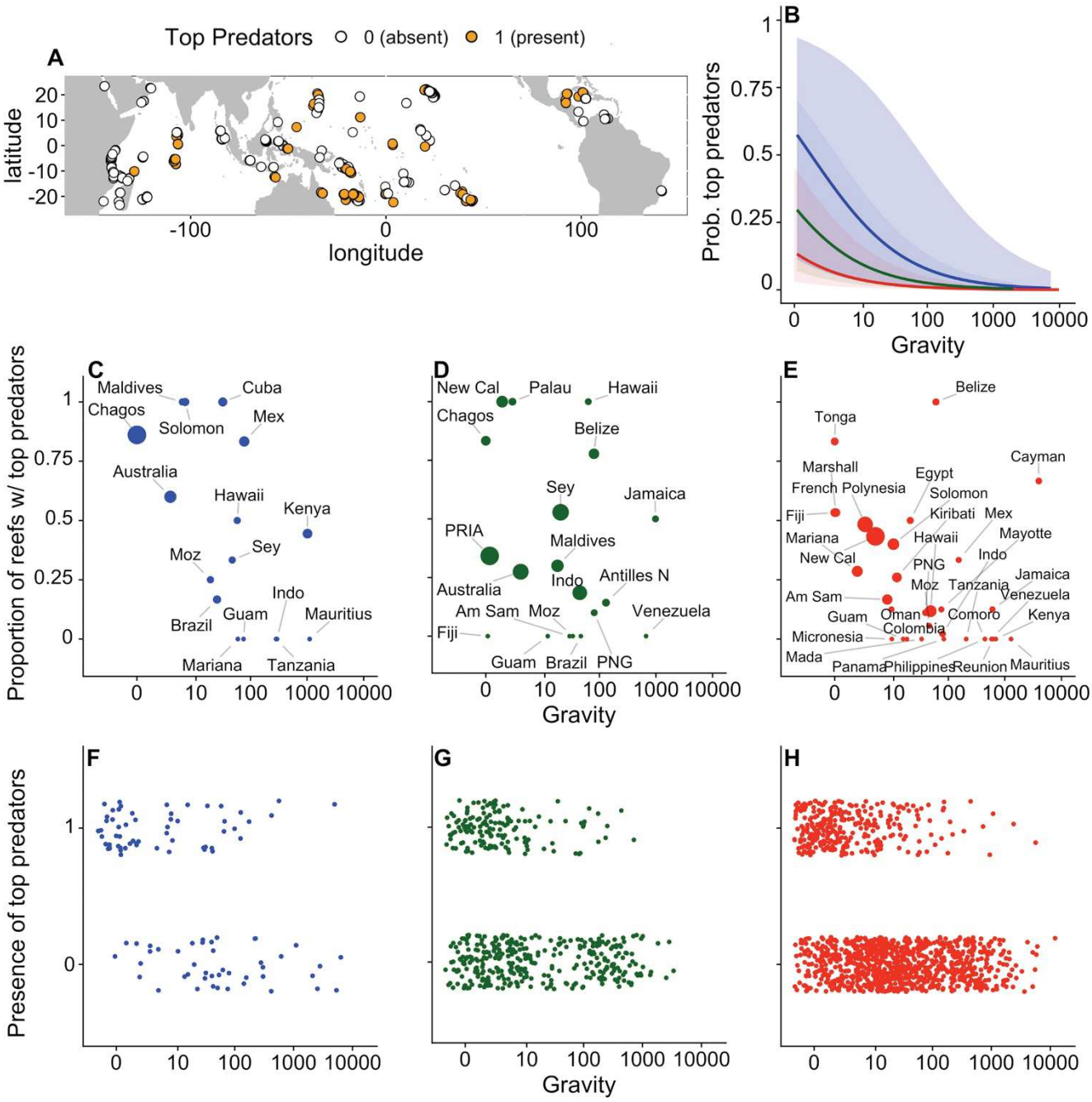


Figure 4.2 | Model-predicted relationships between human gravity and the probability of encountering top predators under different types of fisheries management. *(A) Map of our study sites indicating the presence of top predators. (B) Model-predicted relationships of how the probability of encountering predators declines as gravity increases. Shaded areas represent 95% confidence intervals. The presence of top predators along a gravity gradient under different types of management at the nation/state (C–E) and site (F–H) scale; openly fished (red), restricted (green), and high-compliance marine reserves (blue). Bubble size in C–*

E reflect the number of reef sites in each nation/state, scaled for each management type (such that the largest bubble in each panel represent the highest number of sites per nation/state for that type of management) (Table IV). Nation/state name abbreviations for F–H in Table IV.

4.3.3. Conservation benefits

Our results highlight how the expected differences between managed fished areas and marine reserves change along a gravity gradient, given a range of other social and environmental conditions that are controlled for within our model (Figure VI). Although absolute fish biomass and probability of top predators under all management categories declined with increasing gravity (Figure 4.1B & 4.2B), the maximum expected conservation gains (i.e. the difference between openly fished and managed) differed by management type along the gravity gradient (Figure 4.3).

We found that for non-top predator reef fishes, substantial conservation gains can occur at even the highest gravity locations but that optimal gain are obtained at moderate gravity (Figure 4.3A). For marine reserves, biomass conservation gains demonstrated a hump-shaped pattern that peaked at very low gravity when predators were included in the biomass estimates (solid blue line; Figure 4.3A). When top predators were excluded from biomass estimates, conservation gains peaked at intermediate gravity levels, and were higher in high gravity compared to low gravity (dotted blue line; Figure 4.3A). Interestingly, the conservation gains for restricted fishing is highest in low gravity situations, but rapidly declines as human gravity increase (solid green line; Figure 4.3A).

Our results also show that low gravity marine reserves (and to a lesser extent low gravity fisheries restrictions) are critical to support the presence of top predators (Figure 4.2). Yet, the expected conservation gains for top predators declines rapidly with gravity in both marine reserves and restricted areas (Figure 4.3B).

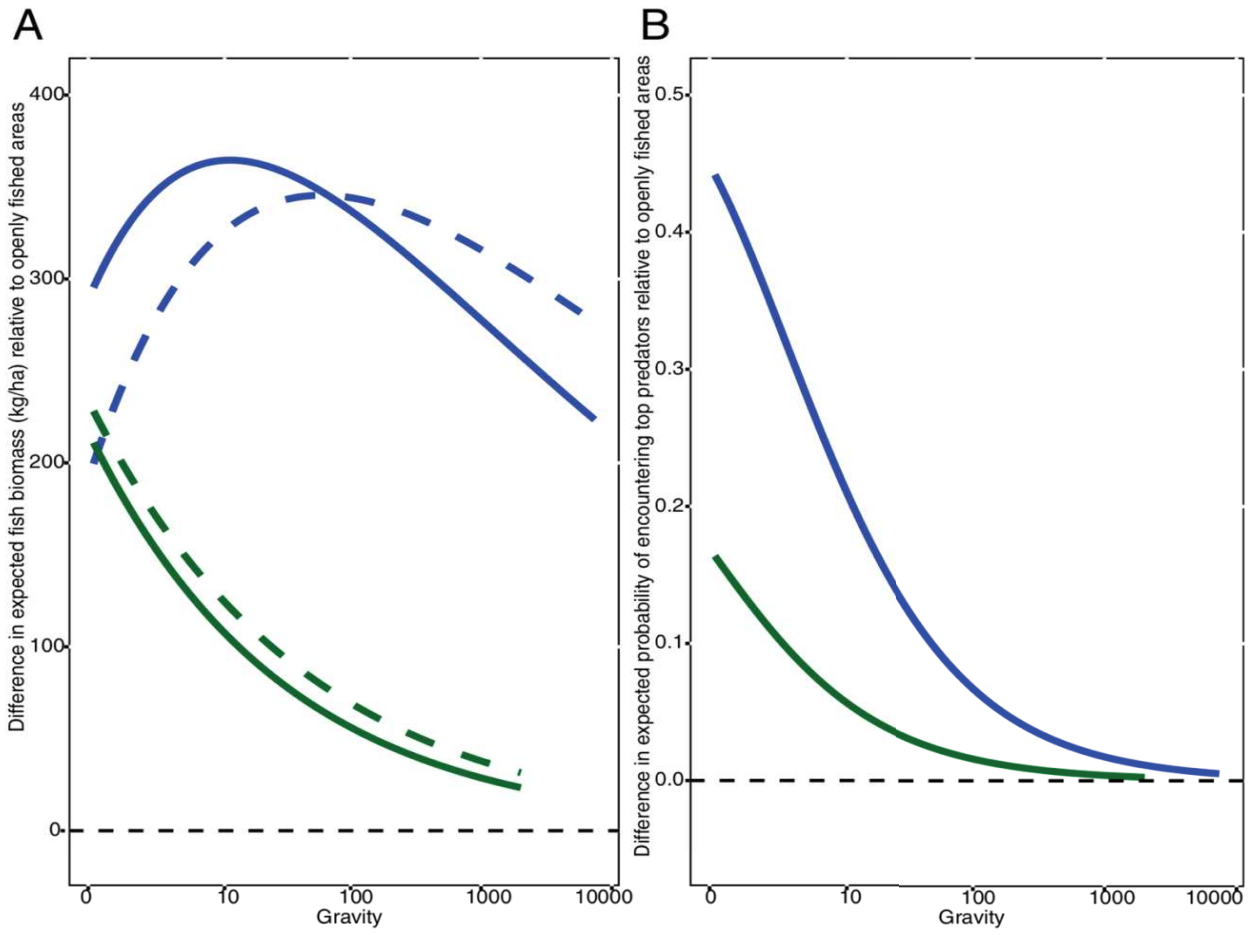


Figure 4.3 | The conservation gains (i.e. the difference between openly fished sites and managed areas) for high-compliance marine reserves (blue line) and restricted fishing (green line) *for (A) target fish biomass, and (B) the probability of encountering top predators change along a gradient of gravity.*

4.4. Discussion

4.4.1. Why do we observe decline of ecological conditions indicators within marine reserves along a gravity gradient?

Our study demonstrates the degree to which fish communities inside marine reserves can be affected by human impacts in the broader seascape (Figures 4.1 & 4.2). Critically, high-compliance marine reserves in the lowest gravity locations tended to support more than four times more fish biomass than the highest gravity reserves (1150 versus 270 kg/ha, respectively; Figure 4.1). Likewise, the modelled probability of encountering a top predator decreased by more than 100-fold from 0.59 in low gravity reserves to 0.0046 in the highest

gravity reserves (Figure 4.2B). Our study design meant that it was not possible to uncover the mechanisms responsible for this decline of ecological conditions indicators within marine reserves along a gravity gradient, but this pattern of depletion is likely related to: *(i)* human impacts in the surrounding seascape (fishing, pollution, etc.) affecting ecological processes (recruitment, feeding behavior, etc.) within reserves (Januchowski-Hartley *et al.* 2015; Gil & Hein 2017); *(ii)* almost every marine reserve is likely to have some degree of poaching, even where compliance is considered high (Bergseth *et al.* 2015; Bergseth *et al.* 2017) and the cumulative impacts from occasional poaching events is probably higher in high gravity situations; *(iii)* the life history of top predators, such as old age of reproduction and small clutch size which makes then particularly susceptible to even mild levels of exploitation (Ward-Paige *et al.* 2010); and/or *(iv)* high-gravity marine reserves in our sample possibly being too young, or too small to provide substantial conservation gains (Edgar *et al.* 2014; Krueck Nils *et al.* 2017).

We conducted a supplementary analysis to further examine this latter potential explanation. Because of collinearity, we could not directly account for reserve size in our model, but conducted a supplemental analysis where we separated reserves into small (<28km2) and large (Figure VIII). We found that the biomass and probability of encountering top predators was higher in large compared to small reserves, but surprisingly, we found a flatter slope for small compared to large reserves (Figure VIII). However, there were no large high compliance reserves in high gravity areas in our sample, likely due to the social and political difficulties in establishing large reserves near people (Christie *et al.* 2017). Since there is little overlap between large and small reserves along the gravity gradient in our sample, we are unable to distinguish the effects of reserve size from those of gravity, but this is an important area for future research.

Additionally, we modelled how the relationship between gravity and our ecological outcomes changed with reserve age, comparing outcomes using the average reserve age (15.5 years) to those from reserves nearly twice as old (29 years, which was our third quartile of our global distribution in reserve age). Older reserves were predicted to sustain an additional 180 kg/ha (+66%) of fish biomass at the highest levels of gravity compared to average age reserves. However, the effects of reserve age on the probability of encountering a top predator was less marked: the modelled probability of encountering a top predator in older reserves (29 years) was only 0.01, compared to 0.005 for average age (~15 years) reserves, suggesting that small

reserves common in high gravity situations can support high levels of biomass, but are unlikely to sustain top predators, even when they are mature.

4.4.2. Successful conservation strategies

Although absolute fish biomass under all management categories declined with increasing gravity (Figure 4.1B), the maximum expected conservation gains (i.e. the difference between openly fished and managed) differed by management type along the gravity gradient (Figure 4.3A). Interestingly, the conservation gains for restricted fishing is highest in low gravity situations, but rapidly declines as human impacts increase (Campbell Stuart *et al.* 2017).

For marine reserves, biomass conservation gains demonstrated a hump-shaped pattern that peaked at very low gravity when predators were included in the biomass estimates (solid blue line; Figure 4.3A). When top predators were excluded from biomass estimates, conservation gains peaked at intermediate gravity levels, and were higher in high gravity compared to low gravity (dotted blue line; Figure 4.3A). Our results highlight how the expected differences between openly fished and marine reserves change along a gravity gradient, given a range of other social and environmental conditions that are controlled for within our model (Figure VI, Table V). Thus, differences in these trends are relative to average conditions, and individual reserves may demonstrate larger or smaller biomass build-up over time depending on fish groups and/or families (e.g. McClanahan *et al.* 2007).

In an effort to minimize costs to users, many marine reserves, particularly the large ones, tend to be placed in remote locations that experience low human pressure (Devillers *et al.* 2015; O'Leary *et al.* 2018). However, critics of marine reserves in remote locations suggest that limited resources could be better-spent protecting areas under higher threat that could potentially yield greater conservation gains (Devillers *et al.* 2015; Ferraro & Pressey 2015; Pressey *et al.* 2015). Our results make explicit the types of benefits – and the limitations- to placing reserves in high versus low human impact locations. Our results illustrate a critical ecological tradeoff inherent in the placement of marine reserves: high gravity reserves can have the substantial conservation gains for fish biomass (Figure 4.3A), yet they are unlikely to support key ecosystem functions like predation, even with high levels of compliance (Figure 4.3B). This highlights the importance of having clear objectives for conservation initiatives and recognizing the tradeoffs involved (Beger *et al.* 2015; Boon & Beger 2016).

Our analysis does not allow us to uncover the mechanisms behind why we might observe the greatest differences in top predators between marine reserves and fished areas in low gravity locations. A plausible explanation is that top predators such as sharks are particularly vulnerable to fishing (Dulvy *et al.* 2004) and are exposed to some fishing even in the most remote fished areas because of the extremely high price for shark fins (shark fins can fetch US$960/kg in wholesale markets, (Clark 2014); compared to only $43/kg for parrotfish, (Thyresson *et al.* 2011)). Thus, even small amounts of fishing in remote openly fished areas may be depleting top predators, which creates a large difference between fished areas and marine reserves. This difference may diminish along the gravity because top predators tend to have large home range (Krueck Nils *et al.* 2017), and there were only small reserves in high gravity locations (Figure VIII), which may mean that existing high gravity reserves are not likely big enough to support the large home ranges of many predators (Green *et al.* 2014; Krueck Nils *et al.* 2017).

Successful conservation also depends on a range of social considerations (Bennett *et al.* 2017). For example, gear restrictions often have greater support from local fishers (McClanahan & Abunge 2016) and are usually implemented over greater reef areas than marine reserves. We show here that there are conservation gains produced by gear restrictions, though they are low relative to marine reserves (Figure 4.3). Thus, in locations where a lack of support makes establishing marine reserves untenable, gear restrictions may still provide incremental gains towards achieving some conservation goals (MacNeil *et al.* 2015) particularly for specific fish groups and/or families (Campbell Stuart *et al.* 2017).

As a supplemental analysis, we examined the conservation gains for biomass of non-target species (Figure VI D). This supplemental analysis addresses whether the effects of gravity on reef fish communities are from fishing or other impacts, such as sedimentation or pollution. We found very different patterns for non-target species compared to target species, suggesting the relationship between target fish biomass and gravity (Figure VI) is primarily driven by fishing pressure.

4.4.3. Securing the future of coral reefs

Overall, our results demonstrate that the capacity to not only sustain reef fish biomass and the presence of top predators, but also the potential to achieve conservation gains, may be highly dependent on the level of human impact in the surrounding seascape. It is therefore

essential to consider the global context of present and future human gravity in coral reef governance.

The ways in which gravity will increase over time, and how the impacts of gravity on reef systems can be reduced is of substantial concern for coral reef governance. The potential benefits of protecting locations that are currently remote could increase over time as human populations and the accessibility of reefs change (Watson *et al.* 2015). Demographic projections of high migration and fertility rates in some countries suggest substantial increases in coastal human populations in developing countries, where the majority of coral reefs are located (Mora *et al.* 2011; Gerland *et al.* 2014; Mora 2014, 2015). Development projects that address high rates of fertility through improvements in women's education, empowerment, and the expansion of family planning opportunities have successfully reduced fertility rates (Cottingham *et al.* 2012; Sen 2013). Such initiatives, when partnered with resource management, have the potential to be beneficial to both people and reefs. Demographic changes such as increased migration in coastal areas are also expected to be coupled with coastal development and road building that will increase the accessibility of reefs. For example, previously uninhabited areas have become more accessible, as evidenced by China's recent Belt and Roads Initiative (BRI) and island building enterprise in the South China Sea (Mora *et al.* 2016; Alamgir *et al.* 2017; Laurance & Arrea 2017). Investments in sustainable planning of coastal development and road building could help to minimize unnecessary increases in reef accessibility. Importantly, stemming increases in gravity is only part of the potential solution space- it will also be important to dampen the mechanisms through which gravity operates, such that a given level of gravity can have a lesser impact on reef systems (Hughes *et al.* 2017a). People's environmental behavior is fundamentally driven by their social norms, tastes, values, practices, and preferences (Hicks *et al.* 2016), all of which can be altered by policies, media, and other campaigns in ways that could change the local relationship between gravity and reef degradation.

4.5. Gravity future directions

Our gravity index (Chapter 3) makes several key assumptions that could potentially be refined in further applications. First, our application of gravity held friction constant across each

specific type of surface (i.e. all paved roads had the same friction value). Future applications of more localized studies could vary travel time to reflect the quality of road networks, topographic barriers to access (such as cliffs), and the availability of technology. Likewise, future applications could also aim to incorporate local information about fishing fleet efficiency. Secondly, our adaptation of the gravity model (Anderson 2011) is unidirectional, assuming a constant level of attraction from any reef (i.e. gravity varies based on human population size, but not on the quality or quantity of fish on a specific reef). Reefs with more fish, or higher fish value, could be more attractive and exert a higher pull for exploitation (Berkes *et al.* 2006). Likewise, societal values and preferences can also make certain fish more or less attractive. Our adaptation of gravity was designed to examine the observed conditions of reefs as a function of potential interactions with markets and local settlements, so our modification of the concept for this application was appropriate. However, future applications wishing to predict where reefs may be most vulnerable might wish to consider incorporating fish biomass or composition (i.e. potential market price of reef fish) in the gravity equation. Third, our database was not designed to look at ecological changes in a single location over time. However, future applications could examine whether ecological recovery in reserves (MacNeil *et al.* 2015) depends on the level of gravity present. To this end, we provide a global dataset of gravity for every reef pixel globally.

4.6. Conclusion

We demonstrate that human impacts deplete reef fish stocks and how certain types of management can mediate, but not eliminate these pressures. In an era of increasing change, the global network of marine reserves may not safeguard reef fish communities from human impacts adequately enough to ensure key ecological functions such as predation are sustained. Efforts must be made to both reduce and dampen key drivers of change (Cinner & Kittinger 2015; Hughes *et al.* 2017a), while maintaining or improving the wellbeing of reef dependent people. Importantly, we find evidence that both remote and human-surrounded reserves can produce different types of conservation gains. Ultimately, multiple forms of management are needed across the seascape to sustain coral reef fishes and the people that depend on them.

5. Influence of market in shaping practices of coastal communities in small-scale reef fisheries in Northwest Madagascar[3]

"Like the chameleon, one eye on the future, one eye on the past" - Malagasy proverb

[3] *Submitted as Maire, E., Cinner, J., Dagata, S., Aliaume, C. & Mouillot, D. in Ecology and Society*

5.1. Introduction

Earth's ecosystems have come under increasing pressure as globalization connects the world (Liu *et al.* 2013). Expanding trade, transportation, migration, and technology are altering intertwined dynamics between human and natural ecosystems across space and time (Rockström *et al.* 2009; Liu *et al.* 2015). Global trade through interconnected markets or new access to markets can increase accessibility through road networks and infrastructure expansion, which in turn, profoundly shape the exploitation of both terrestrial and marine natural resources (Laurance *et al.* 2009; Dobson *et al.* 2010; Mora *et al.* 2011; Ahmed *et al.* 2014; Barber *et al.* 2014; Alamgir *et al.* 2017). There are growing concerns about the risk of unsustainable resources use do to unregulated trade in those previously isolated areas, with obvious ecological and management implications for those key ecosystems. (Berkes *et al.* 2006, Rockström *et al.* 2009; Steffen *et al.* 2011; McCauley *et al.* 2013; Mora *et al.* 2016).

However, the mechanisms through which increasing accessibility influences social and ecological conditions are not straightforward. A parallel literature on the role of economic development and the environment impacts highlights three main mechanisms, which may be relevant to changing market accessibility: *(i)* a scale effect, whereby societies are able to displace their local environmental footprint by harnessing resources from further afield (typically in poorer or less regulated areas); *(ii)* a technique effect, whereby technologies used by human societies change as societies become more developed, leading to differing levels of impact on the environment; and *(iii)* a composition effect, which suggests that structure of the local economy changes with economic development to transition, for example from a natural-resource based economy to a service-based economy (Grossman & Krueger 1995). To date, research on market accessibility has mainly examined how increased market access affects resources users through trade and price changes (Delgado 2003; Schmitt & Kramer 2009; Thyresson *et al.* 2011; Thyresson *et al.* 2013), and changes in livelihoods diversification (Cinner & Bodin 2010; Chaves *et al.* 2017; Kramer *et al.* 2017) (composition effect) and technology introductions or changes (Brewer 2013; Stevens *et al.* 2014) (technique effect). Knowledge on how market access shapes local human communities remains overlooked and could hide important social and economic dynamics at very local scale, with significant consequences on ecosystem states.

Indeed, understanding how accessibility from human societies affects natural resources is a critical step toward a long-term management of the ecosystems where actions are needed to enhance their ecological and economic sustainability. This study aims to unravel the respective influences of the local fish market (hereafter "market") and coastal communities in the exploitation of natural resources and investigate how communities' socioeconomic and resource use characteristics change with increasing proximity to markets.

To address this problem, we focused on small-scale fisheries which remain an important source of food, employment and revenue for people around the world (Béné *et al.* 2007; Bell *et al.* 2009; Teh *et al.* 2013). Specifically, we focus on small-scale artisanal coral reef fisheries in Northwest Madagascar. We hypothesize that coral reefs resource conditions improve with decreasing accessibility to both markets and coastal communities, but the rate of increase will be different for fished and unfished reefs. We also expect that the socioeconomic and resource use characteristics of coastal communities change with access to markets. Here, we investigated: *(i)* the relative effects of management, market access, and key environmental variables on reef fish biomass in the northwest of Madagascar; and *(ii)* The influence of market proximity on coastal communities through the scale, the composition, and the technique effects. We address these questions using ecological data collected in 31 reefs and social drivers collected at household-level in 10 coastal communities in Northwest Madagascar.

5.2. Context and study area

Despite its biological and cultural richness, Madagascar is one of the world's poorest developing countries and its people depend heavily on the exploitation of natural resources for subsistence (World Bank 2010; Conservation International 2015). The artisanal fishery is a significant economic sector where adult males are engaged in multi-gear and multi-species fishing from the shore or using wooden pirogue canoes (McKenna & Allen 2003; Doukakis *et al.* 2007; Davies *et al.* 2009; Bernier *et al.* 2011). Artisanal fisheries in Madagascar are vital to food security and livelihoods for coastal communities and support the majority of the Malagasy coastal population (Barnes-Mauthe *et al.* 2013). This is particularly true along the west coast where agricultural production is mostly infeasible, and employment options are limited (Laroche & Ramananarivo 1995; Le Manach *et al.* 2012).

Reefs in this area have been recognized for their exceptional biodiversity and their resilience to climate change in the Western Indian Ocean (WIO) (McKenna & Allen 2003, McClanahan *et al.* 2011; Obura, 2012) and are now considered as a high priority for increased management efforts. Management actions implemented in Madagascar have mainly focused on empowering local communities to take greater responsibility for marine natural resources management while securing local populations' interests (Jadot *et al.* 2015). These local fisheries management, also called Locally Managed Marine Areas (LMMAs), aimed at increasing fish stocks and biodiversity, protecting cultural heritage, and promoting sustainable socio-economic development to contribute to poverty reduction (Govan *et al.* 2009; Jupiter *et al.* 2014; Rocliffe *et al.* 2014). Management actions are regulated by two main legal instruments at a local level in Madagascar: *(i)* the establishment of a 'dina' (traditional village laws) (Harris, 2011); and *(ii)* community managed Marine Protected Areas (MPAs) (IUCN categories V or VI). Most of the LMMAs contain temporary fishing closure and permanent reserves (no-take zones where fishing activities are prohibited) and implement gear and species restrictions. More specifically in the Northwest, beach seining, considered as a destructive fishing practice, is now prohibited, shark fishing and sea cucumber harvesting are regulated while some pelagic fish are under seasonal closures (such as *Rastrelliger kanagurta* or "mahaloky"). However, gear and species restrictions implemented in the two MPAs do not include the targeted fish species we considered in our study thus, reefs under these restrictions still experience fishing activities.

In April 2015, Ankarea and Ankivonjy MPAs, the two first community-led national Marine Protected Areas (MPAs) were officially established and have been trialing an access restriction strategy in which local fishermen (fishermen from the nearby village in the MPA boundaries) have exclusive access rights to fishing areas inside the MPA. Management of fishing areas is attributed to communities which should lead to direct benefits for them.

Our study covers an approximate linear distance of 150 km along the coast from Nosy Iranja at the south (Ankivonjy MPA) to Nosy Mitsio (Ankarea MPA) at the north and encompasses open-access reefs between those two MPAs (Figure 5.1). The area is characterised by many islands off the coast where coastal human settlements are relatively sparse, consisting of widely scattered small villages. Most of the fishing vessels are sailing wooden pirogue canoes

and the most commonly employed gears are the spear guns, gillnets, lines, and beach seines (Doukakis *et al.* 2007; Jonahson, 2002, Tiambahoaka, 2011, Randriambolona, 2007).

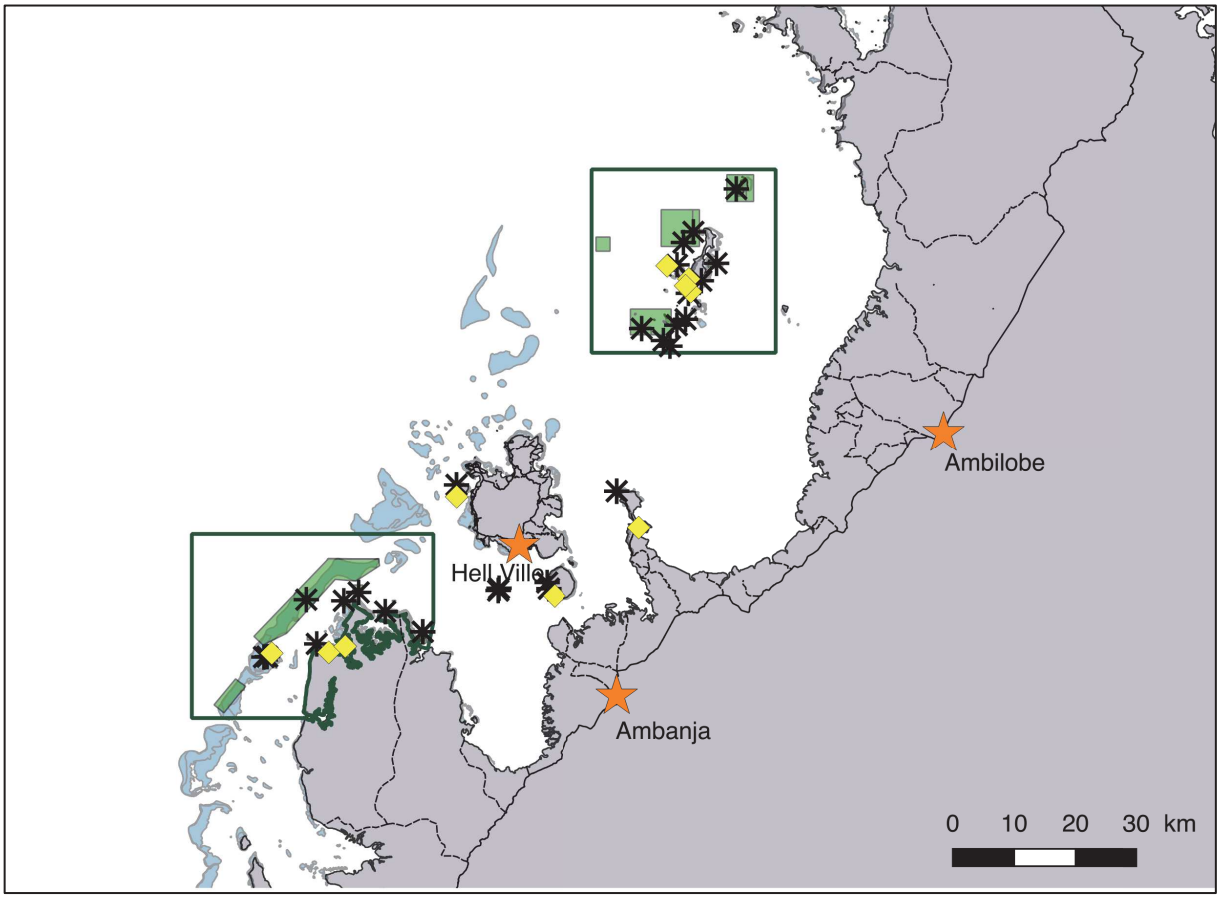


Figure 5.1 | Map of the Northwest Madagascar reefs. *Surveyed reefs (black asterisks) and coastal communities (yellow diamonds), local markets (orange stars), MPAs boundaries (green lines) with no-take zones (green polygons) and cartography of reefs (blue polygons) are represented.*

5.3. Methods

5.3.1. Ecological and social study sites

Data used in our analysis were collected on social and ecological study sites. Social sites consisted of 10 Malagasy coastal communities (Figure 5.1) where questionnaires were performed to collect information on socioeconomics, fishing and farming activities, resource use, and management. Coral reefs surrounding these 10 coastal communities were sampled while covering all the management types (open access, restricted and no-take reefs) to collect

ecological data. In total, 31 ecological sites (hereafter “reefs”) were surveyed with 16 fished reefs and 15 located in low to high compliance reserves where fishing activities were prohibited (Figure 5.1).

5.3.2. Reef surveys methodology

Distance-sampling underwater visual census (D-UVC) technique was used to survey finfishes along 50-m-long transects. Briefly, this method involved two divers, where each diver recorded the species, abundance, body length and distance perpendicular to the transect line of each fish or group of fish, while swimming slowly down the line (Labrosse *et al.* 2002).
The main reef types (biotope) in the area were included, mainly *(i)* fringing reefs of continental islands and *(ii)* complex patch reefs. For each reef, transects were performed on the slope. Transects were oriented parallel to the depth contour between 3 and 14 m.

Species density and biomass

We included only fish families (25 families e.g. *Acanthuridae, Balistidae, Caesionidae, Carangidae, Chaetodontidae, Ephippidae, Fistularidae, Haemulidae, Holocentridae, Kyphosidae, Labridae, Lethrinidae, Lutjanidae, Mullidae, Nemipteridae, Pempheridae, Pomacanthidae, Pomacentridae, Scaridae, Scombridae, Scorpaenidae, Serranidae, Siganidae, Sphyraenidae* and *Zanclidae*) which represent the main trophic groups of reef fish occurring in the study region and the main fish families targeted by fishermen. Transects width were truncated at 5 meters on each side allowing for species density estimation on a 500m2 transect (50x10m).
The biomass of individual fishes was estimated using the allometric length-weight conversion: $W=aTL^b$, where parameters a and b are species-specific constants, TL is the individual total fork length in centimeters and W is the weight in grams (Kulbicki *et al.* 2005). Biomass of each transect (hereafter ‘reef’) was further converted to kilograms per hectare of reef area.

Coral habitat and environmental variables

Point Intercept Transect 25cm (PIT25) (Hill &Wilkinson 2004) were performed at each reef to assess benthic conditions. This method consists of recording the benthic substrate at 25cm interval along a 50m transect among the list of substrate categories. Coral was identified at the genus level when possible. The percent cover of each genus was then obtained by dividing

the number of points for which the category of interest is recorded (n) by the total number of points (N, here 200 for 50 meters transect). In our study, we considered only the percent cover of live hard coral and macroalgae.

Structural complexity was estimated multiple times (e.g., every 5 to 10 meters) along each transect to provide an average structural complexity score per transect. Scores ranged from 0 (no vertical relief, flat or rubbly areas) to 5 (exceptionally complex relief with numerous caves and over hangs) along the 50 meters transect (method adapted from Wilson *et al.* 2007). Depth was also recorded during habitat characterization.

Weekly average Sea Surface Temperature (SST) and chlorophyll-a concentration which provides proxy information on the amount of primary production occurring in the ocean (Huot *et al.* 2007) were extracted during a 5-years period (2012-2016) at a 4km resolution from the GOES-POES dataset (Geostationary Operational Environmental Satellites and the Polar-orbiting Operational Environmental Satellites) and the MODIS (Moderate Resolution Imaging Spectro-radiometer; http://oceanwatch.pifsc.noaa.gov/). For each reef, we calculated the average of monthly temperature and ocean primary productivity over the 5-years period.

Because these environmental and habitat conditions may have confounding effects, we performed a Principal Coordinates Analysis (PCoA using Gower's distance) using the common environmental predictors which describe our ecological sites including: depth, weekly average SST and primary productivity, reef complexity, percent cover of macroalgae and live hard coral (Cinner *et al.* 2013; Maire *et al.* 2016; McClanahan *et al.* 2016), and kept only the two first principal components as environmental covariates for further analysis representing 74% of the total variance.

5.3.3. Socioeconomic variables

We considered two human settlements for each reef: *(i)* the nearest coastal community; and *(ii)* the nearest market.

Travel time was estimated as the shortest time of travelling between each reef and its nearest market, community respectively considering:

• Sea travel using wooden pirogues canoes: speed of 7 $km.h^{-1}$

• Primary roads using motorized vehicles: speed of 50 $km.h^{-1}$

• Track/secondary roads using motorized vehicles: speed of 20 $km.h^{-1}$

Road network data was extracted from the OpenStreetMap (OSM) project and was completed by GPS tracks obtained during the field campaigns in March-April 2016.

We also assessed the human population occurring within a 4km radius of each reef using the *WorldPop* dataset version 2.0 (WorldPop 2017) which estimates human population with national adjustments at a 100m resolution for the year 2015 (the year closest to 2016, year in which the ecological and social surveys were conducted). We set the cut-off at 4 km to reduce spatial overlap between reefs.

We split surveyed reefs into two different management categories as following: fished reefs or low to high compliance reserves (unfished). In fact, as gear and species restrictions implemented in the two MPAs do not include the targeted fish species we considered in our study, reefs under these restrictions still experience fishing activities.

5.3.4. Socioeconomic surveys methodology

To identify potential social drivers related to market proximity, we conducted social surveys in 10 Malagasy coastal communities across 3 districts in Northwest Madagascar from November to December 2016 by trained and experienced Malagasy interviewers in local language (Figure 5.1, Table VI). For villages with less than 50 households, we invited all households to be surveyed. In larger villages, we surveyed a random sample of 50 households when possible (Table VI). We conducted a total of 353 household surveys. All survey activities were approved by the Wildlife Conservation Society Institutional Review Board (IRB). Surveys were conducted with heads of households, which were defined as those who made household decisions. A household was defined as a group of people who regularly shared meals. Household surveys lasted from 45 to 60 minutes. Additionally, we conducted key informant interviews with community leaders or particularly knowledgeable fishermen to better understand village level characteristics of resource management and market connections.

Social characteristics of local communities

For each community, we estimated the mean value of 9 social indicators:

1. the proportion of households who ranked fishing as primary activity,
2. the proportion of households who ranked farming as primary activity,
3. the livelihoods diversity: the mean number of livelihood activities that households are involved in,
4. the mean number of community groups people are involved in,
5. the proportion of households consuming fish at least once a day,
6. the proportion of selective gears (hand line, hand spear and spear gun),
7. the proportion of nets (mosquito and gill nets),
8. the proportion of fish sold,
9. when fish sold, the preferred buyer: own community, middlemen from other community, local market.

A full description of those indicators is provided in Table 5.1. Fishers represented households who participated in some fishing activity and targeted mainly coral reef fishes (excluding households who targeted only sharks). Finally, we also described for each indicator whether coastal communities might be affected by market proximity through the technique, the composition or the scale effect (Table 5.1).

Table 5.1 | Description of the 9 social indicators estimated from household surveys for each community.

Indicator	Description	Survey method	Sample size	Expected effect on communities	Type of data	Mean	Range
Fishing activity	the proportion of households who ranked fishing as primary activity	All households surveys	354	Composition effect	Quantitative	46	25 - 67
Farming activity	the proportion of households who ranked farming as primary activity	All households surveys	354	Composition effect	Quantitative	14	3 - 44
Livelihood diversity	the mean number of livelihood activities that households are involved in	All households surveys	354	Composition effect	Quantitative	2	1 - 4
Social connection	the mean number of community groups people are involved in	All households surveys	354	Composition effect	Quantitative	1	0 - 4
Fish consumption	the proportion of households consuming fish at least once a day	All households surveys	354	Composition effect	Quantitative	51	38 - 65
Selective gears	the proportion of selective gears (hand line, hand spear and spear gun)	Fishers only	162	Technique effect	Quantitative	61	10 - 93
Nets	the proportion of nets (mosquito and gill nets)	Fishers only	162	Technique effect	Quantitative	28	0 - 87
Fish sold	the proportion of fish sold	Fishers only	162	Composition effect	Quantitative	86	71 - 93
Selling strategy	The preferred buyer when fish sold: own community, middlemen from other community, local market	Key informants	20	Composition effect	Qualitative	/	/

We performed two Principal Component Analysis (PCA) to explore correlations of *(i)* social characteristics of all households with travel time from the nearest market and *(ii)* social characteristics of fishers only with travel time from the nearest market. As remoteness of coastal communities from markets presented confounding effect with management actions in the study area (the most remote communities had marine reserves), we also included in each PCA a variable which accounted for this effect.

5.3.5. Fish biomass model

All the human and environmental variables considered in the model are described in Table 5.2.

Table 5.2 | Description and references for each human, environmental and habitat variable considered in the fish biomass model.

	Name	Description	References
HUMAN	Human population size	Number of inhabitants in a 4km buffer around the reef extracted from WorldPop 100m resolution dataset version 2.0	Mora et al. (2011), Brewer et al. (2012)
	Travel time from the nearest market	Travelling time between each reef and the nearest market	Brewer et al. (2012); Cinner et al. (2013); D'Agata et al. (2016); Maire et al. (2016).
	Travel time from the nearest community	Travelling time between each reef and the nearest coastal community	
	Management type	Whether reefs are fished or unfished	McClanahan et al. 2016, Cinner et al. (2018)
ENVIRONMENT	Sea Surface Temperature (SST)	Weekly average SST over 2012-2016 extracted from GOES-POES 4km resolution dataset	Williams et al. 2015
	Primary productivity	Weekly average chlorophyll-a concentration over 2012-2016 extracted from MODIS-Aqua 4km resolution dataset	Williams et al. 2015
HABITAT	Depth	Mean depth along the 50m transect	Srinivasan (2003); Brokovich et al. (2008)
	% Live hard coral	Sum of the percentage of the corresponding category within the 200 points along the 50m transect. Estimated during ecological surveys and following the Point Intercept Transect 25cm (PIT25) procedure described by Hill & Wilkinson (2004).	Luckhurst & Luckhurst (1978), Roberts & Ormond (1987), Bellwood et al. (2004), Norstrom et al. (2009), Stella et al. (2011),
	% Macro algae		
	Reef complexity	Score from 0 (no vertical relief, flat or rubbly areas) to 5 (exceptionally complex relief with numerous caves and over hangs) along the 50 meters transect. Estimated during ecological surveys and adapted from Wislon et al. (2007)	McCormick (1994); Nash et al. (2013); Ferrari et al. (2016)

To explore how proximity to markets and communities affects the reef conditions beyond ecological and human population size effects, we built generalized additive models (GAM) considering the two environmental covariates provided by PCA (see *Coral habitat and environmental variables* section), human population size, accessibility from human settlements and management. GAMs have the property of exploring non-linear relationships using smooth functions thus, there is no need to make any priori assumption on the shape of the relationship (Hastie & Tibshirani 1990). All terms used a reasonable spline smoothed function (k = 3) given the number of data. We considered all the possible sub-models (i.e. all the possible combination of variables) including travel time from the nearest market and the nearest community, and management type (fished or unfished). We also considered interactions between management and market or community. As all these models are nested, we performed a Likelihood Ratio Test (LRT) to determine which human variables significantly improved model fit (Wood 2006). We also assessed model fitting and parsimony by using AICc, Akaike Information Criterion corrected for small data samples (Hurvich & Tsai, 1989).

We first checked for collinearity among our covariates using bivariate correlations (all coefficients were < 0.7) and variance inflation factor (VIF) estimates (VIF < 5) indicating that multicollinearity is non-significant. We then performed control procedure to check whether smoothness selection criterion (k = 3) were adequately defined and detect outliers (penalization procedure described by Wood 2006). We lastly examined homoscedasticity by confronting residuals against fitted values and controlled that residuals were normally distributed.

5.4. Results

5.4.1. Travel time from human settlements: key predictors interacting with management to explain fish biomass at local scale

Among all the models tested, the best-fit model (LRT's p-value = 0.03 and lowest AICc = 18.6) explained up to 80% (adjusted R^2) of the variability observed in fish biomass (Tables 5.3 & 5.4).

Table 5.3 | Comparison of all the nested models to determine the best combination of human variables to explain fish biomass. *The two first components (Env1 and Env2) of the Principal Coordinates Analysis (PCoA) performed with habitat and environmental variables, human population size provided initial model M0. AICc and Likelihood Ratio (LR) test performed against nested reference (ref) model determined the best combination of human variables. The best-fit model (M3B) combined management, travel time from market and travel time from community in interaction with management.*

MODEL	COVARIATES	INTERACTION	AICc	LR test
M0 (ref)	Env1 + Env2 + Population	/	26.8	
M1	Env1 + Env2 + Population + Management	/	22.2	0.008 **
M1 (ref)	Env1 + Env2 + Population + Management	/	22.2	
M2	Env1 + Env2 + Population + Management + Market + Village	/	19.2	0.01 **
M2 (ref)	Env1 + Env2 + Population + Management + Market + Village	/	19.2	
M3A	Env1 + Env2 + Population + Management + Market + Village	Management * Market	24.0	0.4
M3B	Env1 + Env2 + Population + Management + Market + Village	Management * Village	**18.6**	0.028 *

This best-fit model integrated travel time from community in interaction with management, besides the effect of travel time from the nearest market (Table 5.4). Accessibility from human settlements (nearest market pvalue < 0.001 and community pvalue < 0.06), local human population size (pvalue < 0.007 and management (pvalue < 0.006) were the most important predictors (Table 4). We found that population had a significant negative influence on fish biomass meaning that fish biomass decreases non-linearly as human population size increases (Figure 5.2c) while biomass increases further away from market until reaching a plateau at approximately 6-7h from a market (Figure 5.2b, Table 5.4). Fished and unfished reefs presented the same relationship with human population size and travel time from market while unfished reefs had higher levels of biomass (Figure 5.2 b-d). Reciprocally, fish biomass increased non-linearly with increasing travel time from the nearest community, with a sharp increase at approximately 1.5 hours (Figure 5.2a). Conversely, fish biomass in unfished reefs showed no relationship with travel time from community (Figure 5.2a, Table 5.4).

Table 5.4 | Significance table for all covariates included in the best-fit model of fish biomass (R^2_{adj} = 0.8). *The two first components (Env1 and Env2) of the Principal Coordinates Analysis (PCoA) performed with habitat and environmental variables, human population size, travel time from the nearest market and travel time from village in interaction with management (fished vs unfished reefs) provided the best-fit model. Estimates and standard errors (SE) of estimates of fixed terms while estimated degree of freedom (edf) of smooth terms are provided with corresponding significance test.*

	Variable	Estimate	SE	t	Pr(>|t|)
R-sq.(adj) = 0.80	**Fixed terms**				
	Intercept	2.60	0.081	31.9	<2e-16
	Management (Unfished)	0.39	0.13	3.05	**0.006**
	Smoothed terms (k = 3)	**edf**		**F**	**p-value**
	Env1	1.00		1.70	0.21
	Env2	1.00		2.45	0.13
	Population	1.00		8.85	**0.007**
	Travel time market	1.80		9.50	**0.001**
	Travel time village	0.67		5.69	0.064
	Travel time village : Management (Fished)	1.47		1.73	0.12
	Travel time village : Management (Unfished)	0.69		7.58	**0.030**

Unfished reefs presented higher levels of biomass that fished reefs despite the recent implementation (2015) of the two MPAs in Northwest Madagascar and reached levels of reef fish biomass considered as resident biomass in the absence of fishing (median 1235 kg.ha^{-1}). Fished reefs were more exploited (median 345 kg.ha^{-1}) in less than 1 hour of travelling from village (Figure 5.2a,d). Fish biomass increased beyond 1 hour to reach comparable level of biomass than unfished reefs from 2.5 hours and outreached those same levels beyond 3 hours from the village (Figure 5.2a).

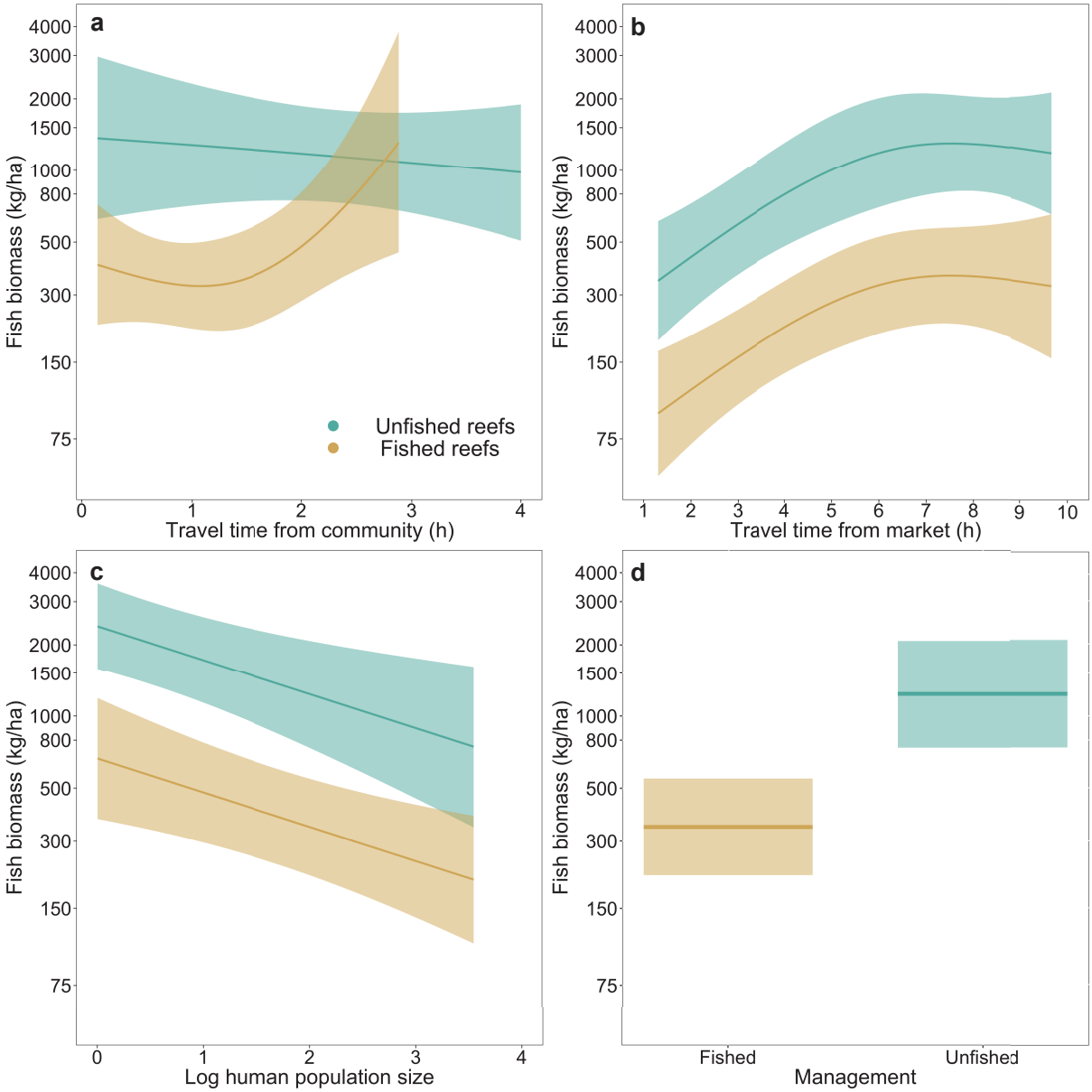


Figure 5.2 | Marginal effects of travel time from the nearest community (a), travel time from the nearest market (b), human population size (c) and management (d) for fished (green) and unfished reefs (orange).

5.4.2. Effect of market proximity on local communities

We found that on average 46% (range: 24 - 67%) of households ranked fishing as their first activity while only 14% (range: 3 - 44%) ranked farming as first activity in the 10 coastal communities (Table 5.5). The number of livelihoods of these communities was rather steady with a mean value of 2 (range at community level: 1.6 - 2.3; range of household responses: 1 - 4) demonstrating that many households had at least 2 activities. On average 51% (range at

community level: 38 - 65%) of households consumed fish at least once a day (Table 5.5). Outside their own related, households were involved on average in only 1 community group (range at community level: 0.2 - 1.1; range of household responses: 0 - 4) (Table 5.5).

Table 5.5 | Description of the four social characteristics measured for the 10 coastal communities. *Travel time from the nearest market and the presence of management actions are also provided.*

Coastal community	% of hh who ranked fishing as primary activity	% of hh who ranked farming as primary activity	Mean number of livelihoods	Mean social connection	% of hh consuming fish daily	Travel time from market (h)	Management
Amparamilay	67	7	2.3	0.17	60	7.8	Ankarea MPA
Andravorogna	61	28	1.9	1.1	50	6.4	Ankarea MPA
Marimbe	40	8	1.9	0.45	64	8.5	Ankarea MPA
Ratapenjke	53	6	2.0	1.1	38	6.4	Ankarea MPA
Amporaha	42	18	1.8	0.56	49	6.7	Ankivonjy MPA
Marotogny	50	5	1.8	0.90	65	6.7	Ankivonjy MPA
Nosy Iranja	26	3	1.6	0.80	51	7.9	Ankivonjy MPA
Anjiabe	34	44	2.0	1.0	42	1.9	*open-access*
Antafiambotry	62	4	1.6	0.84	50	1.9	*open-access*
Sakatia	25	14	2.1	1.0	43	0.8	*open-access*

We investigated whether proximity to market is related to communities' socioeconomic and resource use characteristics. We observed that communities further away from market tended to be more dependent on marine resources since more households were engaged in fishing as primary activity and presented higher consumption of fish while having fewer number of livelihoods (Nosy Iranja, Marimbe and Marotogny for example) (Figure 5.3, Table 5.5). Remoteness from market tended to limit social interactions within communities since more developed social network were mostly found in communities close to market (Sakatia and Anjiabe for example) (Figure 5.3, Table 5.5).

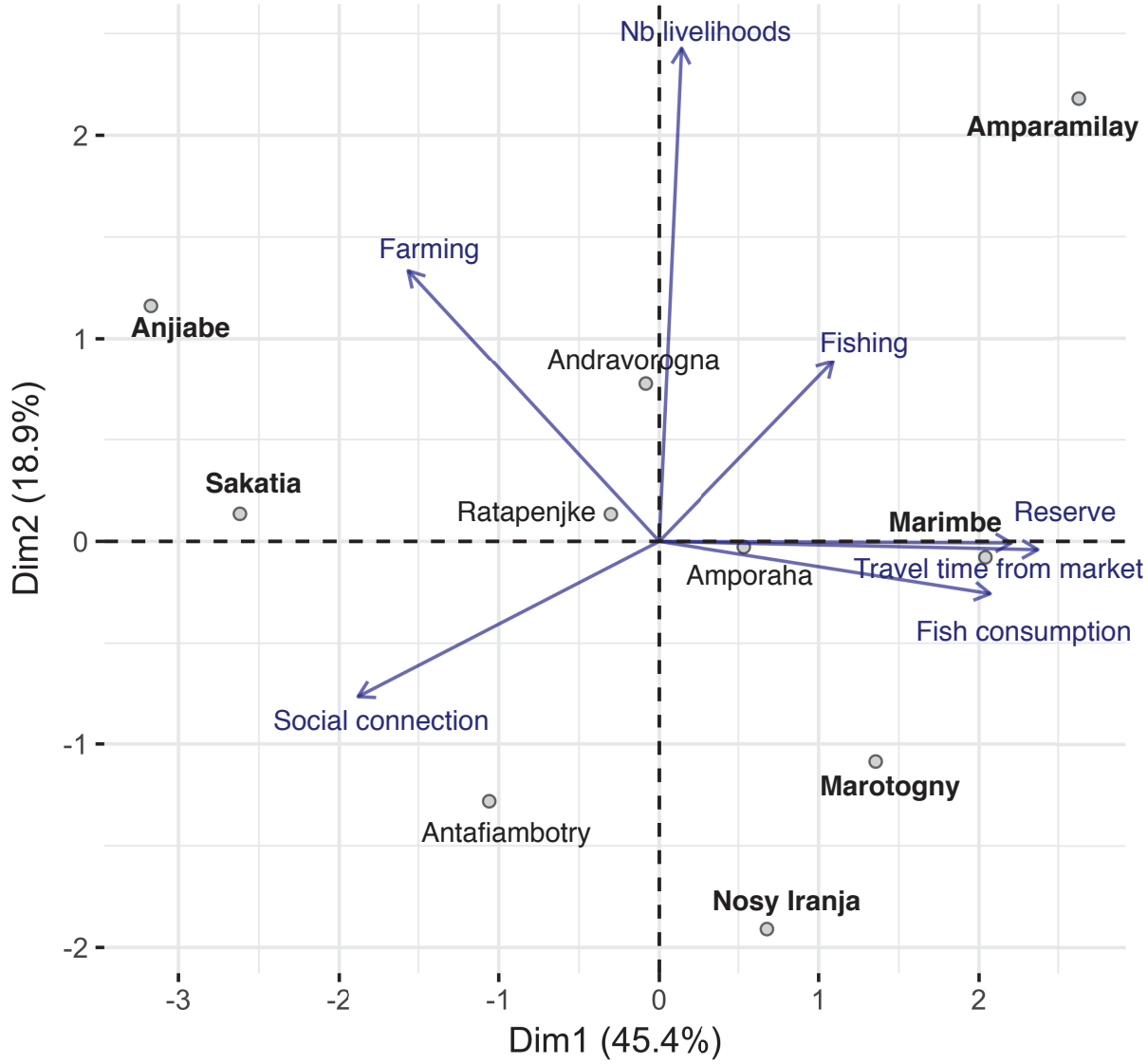


Figure 5.3 | Correlations between social characteristics of local communities and market access. *Five social indicators were assessed for each of the 10 coastal communities: the proportion of households who ranked fishing as primary activity, the proportion of households who ranked farming as primary activity, the livelihoods diversity: the mean number of livelihood activities that households are involved in, the mean number of community groups people are involved in, the proportion of households consuming fish at least once a day that were related to market access. As market accessibility and management actions had confounding effects in the study area (marine reserves are disproportionally located far from markets) we included one variable (Reserve) to take into account this effect. The 10 coastal communities are represented as grey dots and are in bold when the community is well represented by the first two components (Cos2 > 0.4).*

5.4.3. Effect of market on fishing and selling practices

We highlighted a high heterogeneity in fishing practices since on average 61% of households used selective gears (range: 10 - 93%) and 28% (range: 0 - 87%) used nets as the main gear. Communities sold the majority of fish catches (mean: 85%; range: 71 – 93%) with half of the communities (5 out of 10) which sold more than 90% of catches (Table 5.6).

Table 5.6 | Description of four social characteristics assessed from households engaged in fishing activities within the 10 coastal communities. *Travel time from the nearest market, the presence of management actions and the preferred sale to middlemen are also provided.*

Coastal community	% using selective gears as main gear	% using nets as main gear	% of fish catches sold	Travel time from market (h)	Management	Middlemen: (I) if first buyer, (II) if second buyer and (0) if absent
Amparamilay	88	0	92	7.8	Ankarea MPA	II
Andravorogna	73	9.0	93	6.4	Ankarea MPA	II
Marimbe	42	42	81	8.5	Ankarea MPA	I
Ratapenjke	93	0	90	6.4	Ankarea MPA	II
Amporaha	65	35	89	6.7	Ankivonjy MPA	II
Marotogny	53	12	90	6.7	Ankivonjy MPA	II
Nosy Iranja	67	22	71	7.9	Ankivonjy MPA	0
Anjiabe	33	63	79	1.9	*open-access*	II
Antafiambotry	10	87	92	1.9	*open-access*	I
Sakatia	83	13	78	0.8	*open-access*	II

Communities far from market tended to use more selective gears while nets are more common in villages closer to markets (Figure 5.4, Table 5.6). Finally, distant communities tended to sell a higher proportion of fish with no distinction between the destination (market, their own community, neighboring or inland community) (Figure 5.4).

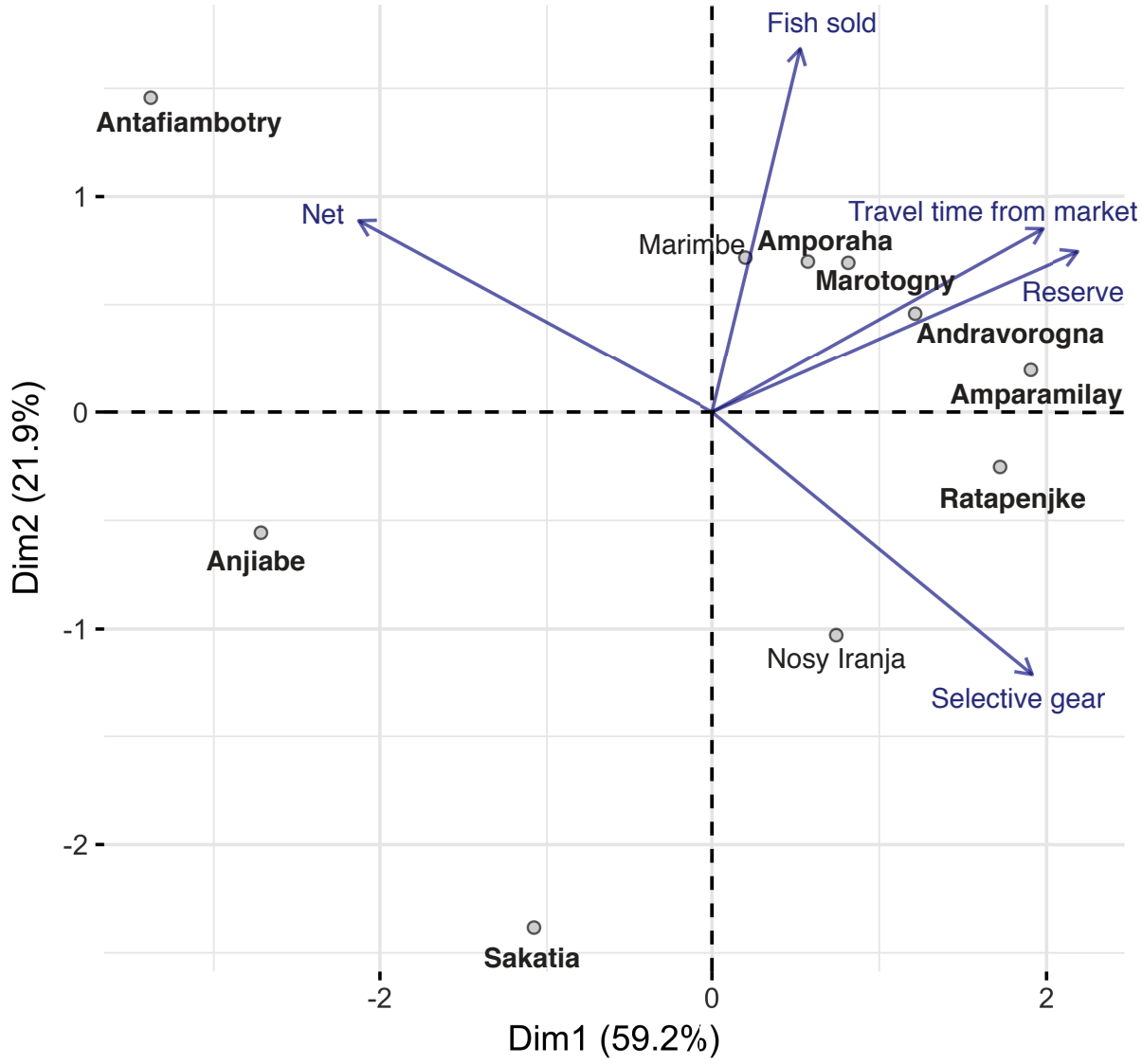


Figure 5.4 | Correlations between social characteristics of fishermen and market access. *We considered only households engaged in fishing activities and we assessed for each community: the proportion of fishermen who used as main gear nets or selective gears respectively and the proportion of fish catches sold that were related to market access. We also included one variable (Reserve) to take into account this confounding effect between market remoteness and the presence of marine reserves. The 10 coastal communities are represented as grey dots and are in bold when the community is well represented by the first two components (Cos2 > 0.4).*

Nonetheless, selling strategies tended to be affected by market proximity (Figure 5.5). We found that fishermen from distant communities (>2 hours) did not go to the nearby market to sell fish catches, sold preferentially to their own community or to middlemen who occasionally collected sea food products in those remote communities (Figure 5.5). Similarly, fishermen sold their own fish to market only if their community is located at less than 2 hours (Figure 5.5). Middlemen are widespread in the region since seemed to collect and buy seafood products from very close (< 2 hours) to more distant communities from markets (up to 8 hours) (Figure 5.5, Table 5.6).

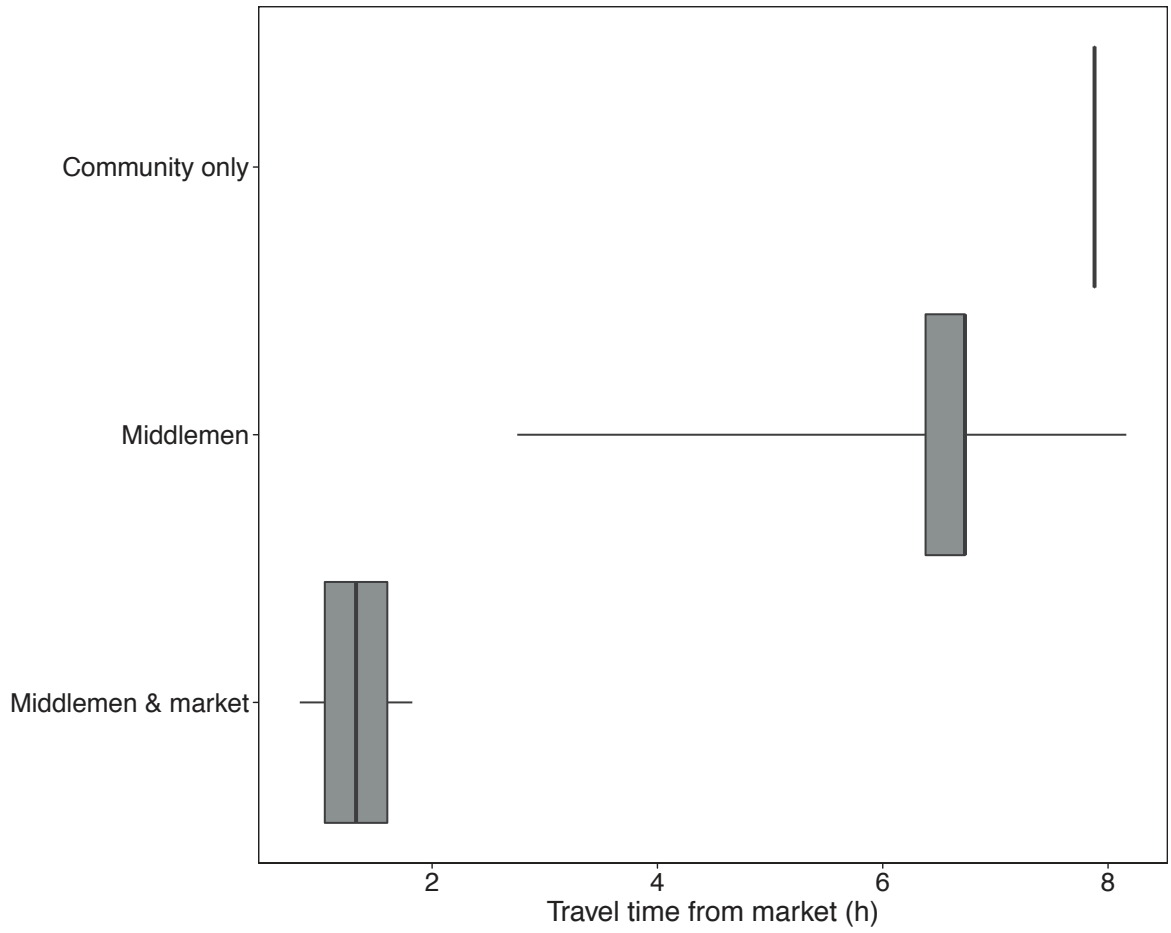


Figure 5.5 | Sea food selling strategy preferred by local communities in Northwest Madagascar. *When fish sold, we assessed for the 10 coastal communities surveyed the preferred buyer: own community, middlemen from other community or local market. At least part of fish catches was sold directly within the community, but fish was also sold to middlemen or at the local market. Middlemen were widespread in the region and seemed to buy seafood*

products from very close (< 2 hours) to more distant communities from markets (up to 8 hours). Distributions are represented using 95% confidence intervals when possible.

5.5. Discussion

Our fine-scale assessment showed how the accessibility of both markets and local communities are related to reef fish biomass. To examine potential explanations for these relationships, we investigated how the socioeconomic and resource use characteristics of coastal communities change with proximity to markets through three strategies: *(i)* the change in techniques people used to harvest fish (called the technique effect); *(ii)* the composition of the economy (called the composition effect); and *(iii)* the scale at which people act (called the scale effect). Despite a large amount of variation between communities, we highlighted that market proximity in Northwest Madagascar mainly affect coastal communities through the composition and the technique effects while we were not able to measure any change through the scale effect. We suggest that better quantifying effect of local market on households behaviors and practices could help our understanding of changes in natural resources exploitation, and ultimately support effective management of small-scale coral reef fisheries.

5.5.1. Unravelling human influence on fish biomass at local scale

Accessibility to markets can shape the composition and resource use techniques of local communities and, ultimately, trigger changes in natural resources exploitation. First, communities further from market tended to present a higher proportion of households engaged in fishing activities as primary occupation, a lower livelihoods diversity and a higher consumption of fish (composition effect) (Figure 5.3 and Table 5.5). Given that agricultural production is largely infeasible (especially on small islands distant from market, Figure 5.3) and employment options are limited far away from markets (Laroche & Ramananarivo 1995; Le Manach *et al.* 2012), it results higher levels of dependence on seafood and exploitation of marine resources further away from markets.

Moreover, it has also been shown that communities with lowest levels of development such as Malagasy communities tended to be more vulnerable to current climate impacts on fisheries, given their heavy dependence on fish for food and economy and the limits to societal

capacity for adaptation (Allison *et al.* 2009; Barnes-Mauthe *et al.* 2013). More specifically, lower livelihood diversity may reduce resilience of coastal communities to disturbances (natural disasters or economic shocks) because they are unable to spread risk across each of their livelihood sources (Allison & Ellis 2001; Badjeck *et al.* 2010; Forster *et al.* 2014).

Second, markets can also influence the fishing techniques used by households. Traditional coral reef fisheries in Northwest Madagascar is a multi-gear and multi-species fishery where few fishes are considered inedible (Doukakis *et al.* 2008; Davies *et al.* 2009; Brenier *et al.* 2011). Fishing practices are highly variable between households but we observed that gear selectivity increased as communities were located further away from markets (Figure 5.4). There is large amount of variation in how fishing gears differentially targeted the proportion and number of species (Cinner *et al.* 2009b). Thus, there is an urgent need to identify gears in Madagascar that preferentially target fishes such as grazers and scrapers/excavators, identified as critical to the resilience of coral reefs (Bellwood *et al.* 2004; Mumby 2006). Gear restrictions are already implemented in MPAs and it has been found that perceived benefits of such restrictions by fishing communities were generally high and widespread in Madagascar (McClanahan *et al.* 2014). Nevertheless, selectively banning or restricting fishing gears can be an effective tool to manage coral reefs experiencing climate change disturbances (Cinner *et al.* 2009b) given that permanent reserves are not practical in Madagascar. In our study area, there is a strong confounding effect between management actions and market accessibility since the two MPAs are located away from markets, which is consistent with previous studies showing that protected coral reefs around the world are disproportionally farther from people (Maire *et al.* 2016; Cinner *et al.* 2018). However, it doesn't negate the importance of markets in shaping practices of local communities given management.

Finally, middlemen are important intermediaries in coral reef fisheries who collect sea products directly from fishermen and provide links to markets (Crona *et al.* 2010; Brewer 2011). We found that middlemen are widespread in the region as in other countries (Dacks *et al.* 2018) and could explain why households further from markets sold more fish despite remoteness from markets (Figure 5.4 & 5.5). Even if we observed that in some cases, fishers preferentially sold their catches to middlemen, we still lack to better identify the drivers which encourage their decision-making. Moreover, we were not able to measure whether demand from middlemen can change fishing practices or fish species that are targeted by fishers. Indeed, right-based management actions are supposed to control harvesting pressure but this

does not prevent right holders from higher fishing pressure. A better investigation of the role of middlemen involved in small-scale fisheries in Madagascar could improve the governance of fish stocks and coastal social-ecological systems (Crona *et al.* 2010; Thyresson *et al.* 2013; Wamukota *et al.* 2014).

Beyond market proximity, we also found that travel time from community is a key driver of fish biomass interacting with management (Figure 5.2, Table 5.2). Accessibility from the nearest community is thus a relevant human indicator in reef exploitation since coral reef management is here implemented at the local scale (community-scale), as in many developing countries (Aswani *et al.* 2015). We found higher fish biomass in permanent reserves compared to fishing sites despite the recent (2015) LMMA implementation with no effect of local communities accessibility to those reefs. Previous studies in Madagascar have highlighted LMMA management effectiveness and positive impacts on fish stocks where higher fish density and biomass were found inside LMMAs compared to fishing sites outside (Komeno & Randriamanantsoa 2013). Here we show that MPAs in northwest Madagascar, through gear restrictions and higher compliance are effective tool to enhance fish biomass. Thus, community access in interaction with local management (temporary and permanent reserves vs open-access) could be an important driver of resource use in Madagascar which should be considered when monitoring coral reef fisheries.

5.5.2. Redefining market effect of fish stocks and fishing communities to sustain social-ecological systems

Given that communities further away from markets had more households engaged in fishing, higher dependence on marine resources and limited number of livelihoods, we would expect lower biomass far from markets. Surprisingly, we found that fish biomass increased as reefs were further away from market (Figure 5.2). Thus, market proximity in Northwest Madagascar heavily affect the way coastal communities use marine resources but have an even greater effect on reef fish biomass. This finding is consistent with previous studies conducted at larger-scale (i.e. national and global) highlighting that market integration is a major driver of fish biomass through scales (Brewer *et al.* 2012; Cinner *et al.* 2013; Cinner *et al.* 2016; Maire *et al.* 2016; McClanahan *et al.* 2016).

Community-based management with gear restrictions, limited access, marine protected areas, and rights-based fishing seem to be effective approaches to manage fisheries resources and the human communities that depend upon them. More specifically, LMMAs could succeed in engaging people in conservation towards conservation strategies. However, it is not clear how increased economic growth and new markets can result in improved environmental conditions especially in coral reef fisheries (Cinner *et al.* 2009a). More specifically, innovation and access to more efficient technology can generate inequality and poverty (Pauly 2006) and can lead to "social-ecological traps" where poorest fishers are spurred to use destructive technologies (Cinner 2011). Innovation and technology are both driven by resource demand and at the same time, regulated by governance and managers. We suggest that better quantifying links between markets and fishing communities through household-level surveys should be a priority. Factors that influence households behaviors and decision-making, especially in the sale of fish catches are not clearly identified. Such information is crucial to implement market-based actions that could help to regulate effect of markets on fish stocks and fishing communities.

5.6. Conclusion

Market proximity affects the composition and techniques of fishing communities and, ultimately, triggers changes in marine resources exploitation. Markets also shape reef fish biomass with an even greater effect than fishing communities even in managed reefs. Understanding the human-environmental interrelations relies on a scaling-down to highlight the drivers of resource use and governance by considering households behaviors and decision-making. A better assessment of accessibility from human societies (market and village) is thus a critical step toward a long-term management of the coral reef fisheries.

6. Community-wide scan flags fish species associated with coral reef services across the Indo-Pacific [4]

"We should preserve every scrap of biodiversity as priceless while we learn to use it and come to understand what it means to humanity" - Edward O. Wilson, American biologist, 'the father of sociobiology'

[4] *Published as Maire, E., Villéger, S., Graham, N., Hoey, A., Cinner, J., Ferse, S., Aliaume, C., Booth, D., Feary, D., Kulbicki, M., Sandin, S., Vigliola, L., Mouillot, D. (2018). Community-wide scan flags fish species associated to coral reef services globally. Proc. R. Soc. B. 20181167, doi: 10.1098/rspb.2018.1167*

6.1. Introduction

Within the context of global changes and biodiversity loss, effective ecosystem management relies on a better understanding of the causal pathways between ecological communities and the myriad of services they sustain (Cardinale *et al.* 2012; Cheung *et al.* 2016; Ricketts *et al.* 2016; Ratcliffe *et al.* 2017). Experiments that manipulate community compositions have unambiguously demonstrated the positive effect of species diversity on ecosystem functioning over short and long timescales (Cardinale *et al.* 2006; Isbell *et al.* 2011; Isbell *et al.* 2015; Isbell *et al.* 2018). Recent studies have also convincingly shown that natural species-rich communities are more productive and can deliver higher rates of ecosystem services than impoverished communities (Grace *et al.* 2016; Duffy *et al.* 2017). Beyond the mere number of species, the diversity of species traits and evolutionary histories have been shown to promote ecosystem functioning in both controlled experiments and natural communities (Cadotte *et al.* 2009; Flynn *et al.* 2011; Mora *et al.* 2014; Gross *et al.* 2017). In parallel, another line of evidence suggests that particular species are key to ecosystem functioning as they contribute disproportionally to certain processes when present (Bellwood *et al.* 2012; Reich 2012; Bozec *et al.* 2016; Tobner *et al.* 2016; Meyer *et al.* 2018). However, identifying these key species remains highly challenging in diverse ecosystems, such as tropical reefs or rainforests, where many species co-occur and can have multiple or unique contributions to ecosystem functions and services (Bozec *et al.* 2016; Pigot *et al.* 2016).

To tackle this challenge, ecologists can now use the increasing availability of extensive and standardized databases that have compiled environmental, social and ecological information across space and time (Cinner *et al.* 2016; Duffy *et al.* 2017). This emergence of large social-ecological databases parallels what happened 20 years ago in genetics with advances in genome sequencing generating millions of genetic variants for individual loci. To identify genetic variants among this myriad of sequences that are more frequent in people with a particular disease or traits of biomedical significance, genome-wide scans or genome-wide association studies (GWAS) were developed (Bush & Moore 2012). Such an approach is powerful to relate a given biological feature or trait to its underlying genetics, based on the simple idea that if a genetic variant increases the frequency of a given trait it should be more frequent in individuals with this trait than expected by chance (Visscher *et al.* 2017). Although this approach does not attribute causality, it can uncover previously unsuspected, yet

important, potential biological mechanisms and pathways (McCarthy & Hirschhorn 2008). Although similar approaches have not been used in ecology, they hold much promise in empirical community ecology where only a few, among dozens or even hundreds of species (the ecological equivalents of genetic variants) can disproportionally drive ecosystem functioning and the delivery of services (the equivalents of diseases, traits or phenotypes) (Bellwood *et al.* 2006; Straub & Snyder 2006; Bozec *et al.* 2016; Meyer *et al.* 2018). This approach could also reveal the unknown level of ecological pleiotropy in communities, i.e. the propensity that a single species can be key to many ecological functions and services (Hooper *et al.* 2005; Gascon *et al.* 2015). This term was initially coined by Strauss & Irwin (2004) [48] by analogy to genetic pleiotropy, where one gene can influence two or more seemingly unrelated phenotypic traits. Under ecological pleiotropy a few species, so only a small fraction of biodiversity, may underpin many different ecosystem functions or services and would deserve particular conservation actions.

Identifying functionally important or key species is particularly challenging in biodiverse ecosystems, due largely to the complexity of interactions between species and with their environment including human disturbances. For example, despite the large body of research on coral reefs, the identification of fish species that disproportionally drive ecosystem functioning is still in its infancy (Hoey & Bellwood 2009; Bellwood *et al.* 2012). The functional importance of most coral reef fishes is still poorly understood, and no study has scanned entire fish communities to detect potential links with ecosystem functioning and services at large scale. Here, we develop a new community-wide scan (CWS) approach, analogous to the GWAS approach, to identify key fish species that are linked to the delivery of services on coral reef ecosystems. Here 'key' has a different meaning than 'keystone' which corresponds to a "species whose effect is large, and disproportionately large relative to its abundance" (Paine 1966; Power *et al.* 1996). We define key species as those consistently and significantly associated, i.e. above a certain statistical threshold, to a certain level of ecosystem functioning or services.

More precisely, we propose a statistical framework and use empirical data from 1,824 Indo-Pacific coral reefs hosting ~400 fish species to determine species whose presence is disproportionately related to fish biomass and live coral cover which insure, for instance, fisheries yield (McClanahan Timothy 2018) and coastal protection (Harris *et al.* 2018), respectively. We then place those key species on a reef fish phylogeny, and in a functional

trait space (Villeger *et al.* 2008) to show the extent of species traits and evolutionary lineages that are necessary to sustain these two services on coral reefs. Identifying key species can provide new research priorities to elucidate ecological processes by which such candidate species positively affect coral reefs and to motivate a diversification of management options to maintain fish communities and their associated services in the face of a highly uncertain future.

6.2. Material and methods

6.2.1. General framework

The Community-Wide Scan (CWS) framework to identify species that are associated with higher levels of ecosystem services involves three steps (Figure 6.1): i) collecting environmental, socioeconomic, species presence and/or abundance, and indicators of ecosystem services data across many sites; ii) modelling a given (or several) ecosystem service as a function of this large set of predictor variables (socioeconomic, environmental conditions, and species richness). The accuracy and parsimony of this comprehensive initial, or reference, model (M_0) is validated according to its R^2 and its Akaike Information Criterion (AIC_{M0}), respectively; iii) testing the effect of each species separately on each ecosystem service beyond the effect of previous variables including species richness. For this, the presence of a given candidate species in a community (coded as a binary variable) is added as an explanatory variable to M_0. The resulting model M_1, so the importance of the candidate species to explain variations of a given ecosystem service, is evaluated according to its AIC (AIC_{M1K}). A species is declared as a potential key contributor to the ecosystem service if ΔAIC (AIC_{M0}-AIC_{M1k}) > 4 and if its partial effect is positive (Figure 6.1).

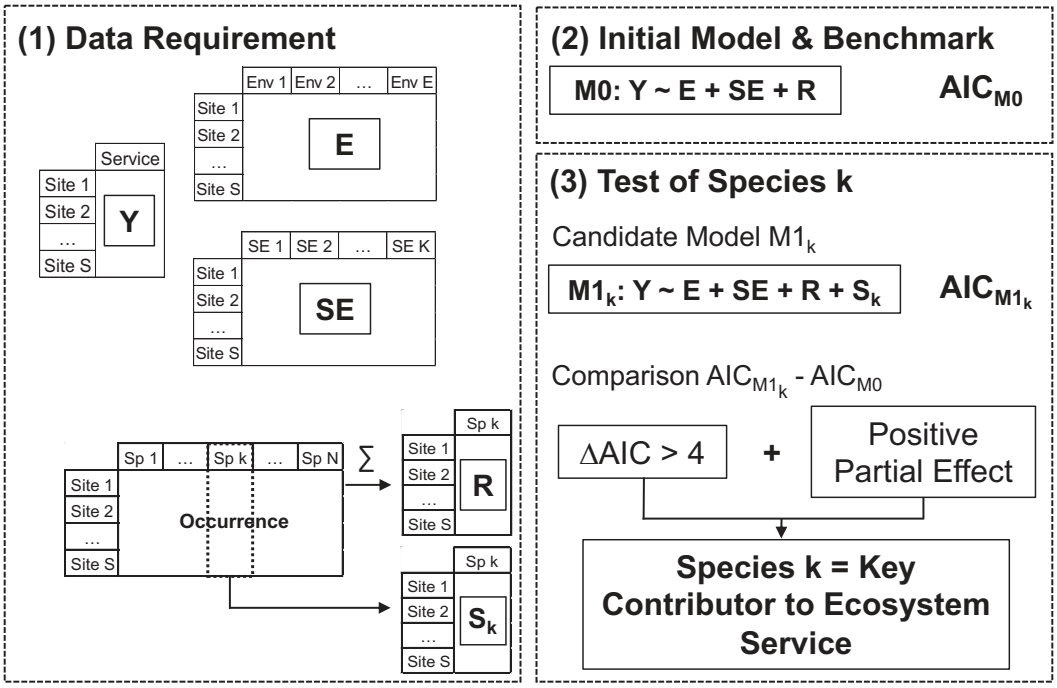


Figure 6.1 | Statistical framework to assess the significant potential contribution of species to ecosystem services beyond the effects of environmental and socioeconomic conditions and species richness.

<u>Step 1:</u> Collecting datasets: for a (large) set of sites, variables describing a given ecosystem service (Y), Environmental (E) and Socio-Economic conditions (SE), and the occurrence of species. Species richness (R) is computed for each site from the Sites-Species matrix as well as the vector (S_k) with presence-absence of each species in sites.

<u>Step 2:</u> The goal is to model a given ecosystem service (Y) according to Environmental (E) and Socio-Economic conditions (SE) and species richness (R); to check its relevance according to its explanatory power and to save its Akaike Information Criterion (AIC_{M0}) as a reference for the next step.

<u>Step 3:</u> The goal is to identify species key for the studied ecosystem service (Y) adding each candidate species (presence-absence, S_k) as an additional explanatory variable to M0 to compute model M1 and its associated AIC (AIC_{M1k}). Finally, a species is declared as a key potential contributor to the ecosystem service if ΔAIC (AIC_{M0}-AIC_{M1k}) > 4 and if its partial effect is positive (positive coefficient in the model).

6.2.2. Coral reef data

Coral reef services. The proxies for coral reef services we considered are fish biomass and live coral cover which support, among many others, food security, shoreline protection and recreational value (Burke *et al.* 2011; Kittinger *et al.* 2012; Harris *et al.* 2018; McClanahan Timothy 2018). Fish biomass and coral cover are already monitored at the global scale using visual censuses as well as underwater video surveys (e.g. Reef Life Survey, Catlin Sea Survey) and are highly sensitive to local human activities (e.g. fishing, habitat destruction, pollution) and global climate change (Hughes *et al.* 2018) and thus, can be considered as key variables for the health and productivity of coral reefs (Bozec *et al.* 2016; Cinner *et al.* 2016; Hughes *et al.* 2017b). We used data from 1,824 coral reefs in 26 nations/states located across the Indo-Pacific which include fish biomass (Figure S1) and live coral cover (Figure S2) estimates (details are provided in the Supplementary Material).

Initial models and species candidates. For each of the 1,824 reefs located in the Indo-Pacific we collected and used 12 relevant social and environmental variables (listed below), together with the occurrence, abundance and size of 739 reef fish species (Cinner *et al.* 2016). To build the initial model (M_0) and estimate the reference Akaike Information Criterion (AIC_{M0}) we modelled fish biomass and live coral cover using linear mixed models (LMM) with the complete set of socioeconomic and environmental conditions plus species richness as predictor variables. For each of the 739-fish species present in this dataset, we estimated the number of reefs where a given fish species was present. To avoid results only influenced by a few reefs we chose to remove rare species. Rarity can be seen as a relative (compared to other species) or absolute (compared to the number of sampled reefs) concept while cut-offs are always subjective (Gaston 1994; Leroy *et al.* 2012). Here we excluded species present on less than 1% of the reefs (i.e. 18 and 7 reefs for fish biomass and coral cover dataset, respectively), so we retained 381 species which corresponds to roughly half (51%) of the species pool, a conservative threshold to define rarity (Gaston 1994). These 381 fish species belonged to 116 genera and 30 families were considered as potential candidate species.

6.2.3. Identifying potential key contributors to ecosystem services.

Each of the 381 species was tested as candidate for improving prediction of reef fish biomass and live coral cover given the socioeconomic and environmental conditions at each study site.

More precisely, we tested presence of each candidate species as an additional explanatory binary variable to M_0 to compute model M_1 and its associated AIC (AIC_{M1K}). Finally, a species was identified as a potential key contributor to a given ecosystem service if, when included, $\Delta AIC > 4$ and if its partial effect was positive (positive coefficient in the model). The binary variable describing the presence/absence of a species was strictly related to its occurrence in our study (i.e. presence of at least 1 individual) but could be also determined using any relative abundance threshold (Figure 6.1 and Supplementary Material).

6.2.4. Environmental and socioeconomic variables.

The variables included in the models were environmental: 1) oceanic productivity, 2) habitat type, 3) depth and socioeconomic: 4) management 5) local human population growth rate, 6) gravity of local population, 7) gravity of markets, 8) levels of human development (Human Development Index), 9) human population size, 10) levels of tourism, 11) degree of voice and accountability of citizens, and 12) reef fish landings (tons)/km^2 of reef (definitions and details are provided in Chapter 2 and in the Supplementary Material).

6.2.5. Statistical analyses.

We first built two linear mixed models (LMM), which predicted fish biomass and live coral cover respectively, while accounting for the different scales at which the data were collected as random effects (reef location, site, and nation/state, see Supplementary Material), with 12 key environmental and socioeconomic variables expected to influence reef conditions (Cinner *et al.* 2016; Cinner *et al.* 2018) and fish species richness as fixed effects (Supplementary Material). To evaluate the fit of the two linear mixed models, we checked the relationship between observed and predicted values. Model validation and quality control procedures are described in the Supplementary Material.

In order to quantify the potential net benefit of each identified key species, we extracted the net effect of each key species for biomass and live coral cover using a partial plot from linear mixed models while the other variables were held constant.

We next investigated whether reefs with several key species show high levels of fish biomass and live coral cover. To control for the effects of species richness we compared modelled estimates of fish biomass and live coral between reefs while increasing the number of key species. We estimated the number of key species present on each reef and chose the richest

quartile as a threshold (i.e. 4 and 6 key species for biomass and live coral cover respectively). We next created 3 categories of reefs: those with no key species, those with at least one key species but below the richness threshold (4 and 6 for biomass and live coral cover respectively) and those with more key species than the threshold.

6.2.6. Functional space and entities.

The 381 candidate fish species were functionally described using six traits: (1) size, (2) mobility, (3) period of activity, (4) schooling, (5) vertical position in the water column, and (6) diet. Values for these six traits were taken from the global trait database on tropical reef fishes from Mouillot *et al.* (2014) (Mouillot *et al.* 2014) (Supplementary Material). Since all traits were categorical, species with identical traits were grouped into functional entities. The 381 candidate species represented 240 functional entities and most functional entities comprise species from different genera (Mouillot *et al.* 2014).

We assessed functional richness (FRic), i.e. the functional space occupied by the key fish species for biomass and coral cover respectively, using the convex hull volume index proposed by Cornwell *et al.* (2006) (Cornwell *et al.* 2006). This volume corresponds to the amount of multidimensional (four in our case) functional space filled by key species, where axes are defined by species traits.

6.2.7. Fish phylogeny.

We used a time-calibrated phylogeny of Acanthomorph fishes (Near *et al.* 2013) which covers all 30 reef fish families of the present study (Table S1). Some fish genera (e.g. *Elagatis* and *Parupeneus* for example) recorded on reefs were missing in this phylogeny.

6.3. Results

6.3.1. Predictability of fish biomass and coral cover

The two initial (M0) models explained 79% and 61% of the variance in fish biomass and live coral cover, respectively (Figure S3; Supplementary Material). The residuals of the two models were normally distributed (Figure S3). In total, 8 and 6 variables had the highest importance (Akaike weight = 1) in predicting fish biomass and live coral cover, respectively (Tables S2 &

S3). Fish species richness, oceanic productivity, population size, tourism and census method were the main predictors of both fish biomass and coral cover. Depth, management, and sampling area were also important predictors of fish biomass while habitat type was important in predicting coral cover (Tables S2 & S3).

6.3.2. Key species associated with reef fish biomass

Among the 381 fish species considered as candidates, only 26 species (7%) were significantly related to fish biomass beyond the initial set of variables (ΔAIC > 4 and positive effect), after considering their presence (at least 1 individual) (Table S4). Those 26 key species covered a wide breadth of phylogenetic lineages (Figure 6.2), representing 16 out of 116 genera and 8 out of 30 families (i.e. Acanthuridae, Carangidae, Labridae, Lethrinidae, Lutjanidae, Mullidae, Scombridae, Serranidae).

When considering functional traits, we found that those 26 key species represented 24 different functional entities (Table S6) demonstrating a very low functional redundancy with 1.1 species per functional entity (median=1; range: 1-2). In addition, key species had contrasting functional traits with all body sizes (from 10cm to > 50cm) and all diets (7 trophic categories) represented (Table S6). Together these 26 key species filled 20% of the whole functional space defined by the 240 functional entities corresponding to the 381 candidate species (FRic = 0.20; Figure 6.3).

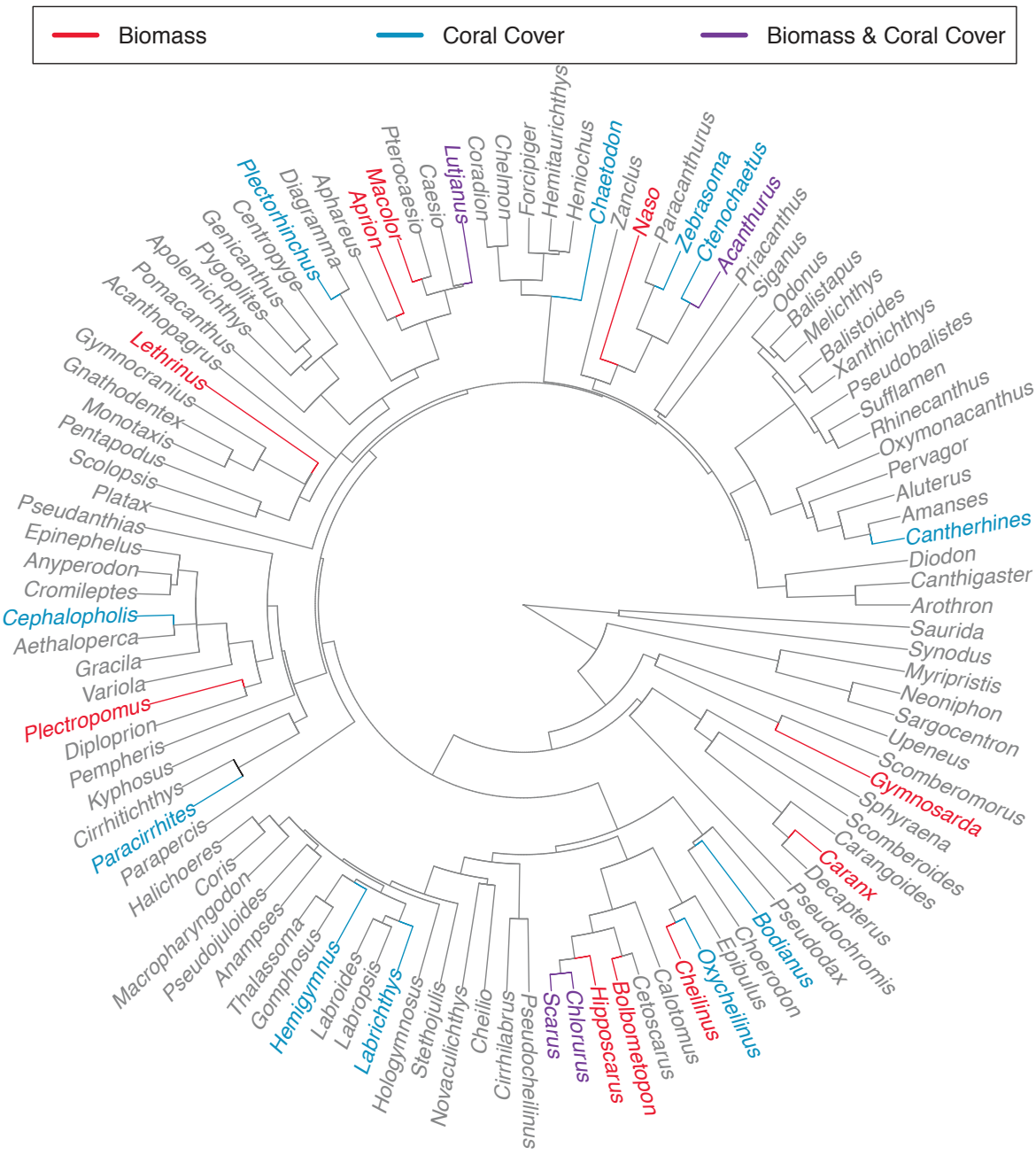


Figure 6.2 | Positions of key species for biomass (red), live coral cover (blue) or both of them (purple) represented as their corresponding fish genera in the Tree of Life of Coral Reef Fishes, adapted from Near et al. (2013). *The 26 key species for biomass represent 16 genera while the 28 key species for coral cover represent 15 genera with 4 common genera. Elagatis and Parupeneus genera are missing.*

6.3.3. Key species associated with live coral cover

We found that 28 reef fish species out of 381 (7%) were significantly and positively related to coral cover (ΔAIC > 4), after considering their presence (Table S5). Those 28 key species also encompassed a wide breadth of phylogenetic lineages (Figure 6.2), representing 15 out of 116 genera and 8 out of 30 families (i.e. Acanthuridae, Chaetodontidae, Cirrhitidae, Haemulidae, Labridae, Lutjanidae, Monacanthidae, Serranidae).

When considering functional traits, we found that the 28 key fish species were distributed among 17 different functional entities (Table S6). Key fish species with regard to coral cover showed some degree of functional redundancy with, on average, 1.6 key species per functional entity (median=1; range: 1-6 species). This higher functional redundancy translated into a more restricted functional space filled by these key species (only 5% with FRic = 0.05; Figure 6.3). Species of all sizes (from 10cm to > 50cm) and almost all diets (6 diet categories out of 7) were significantly associated with live coral cover. However, large mobile predators and large herbivorous fishes were not considered as key for live coral cover (Table S6).

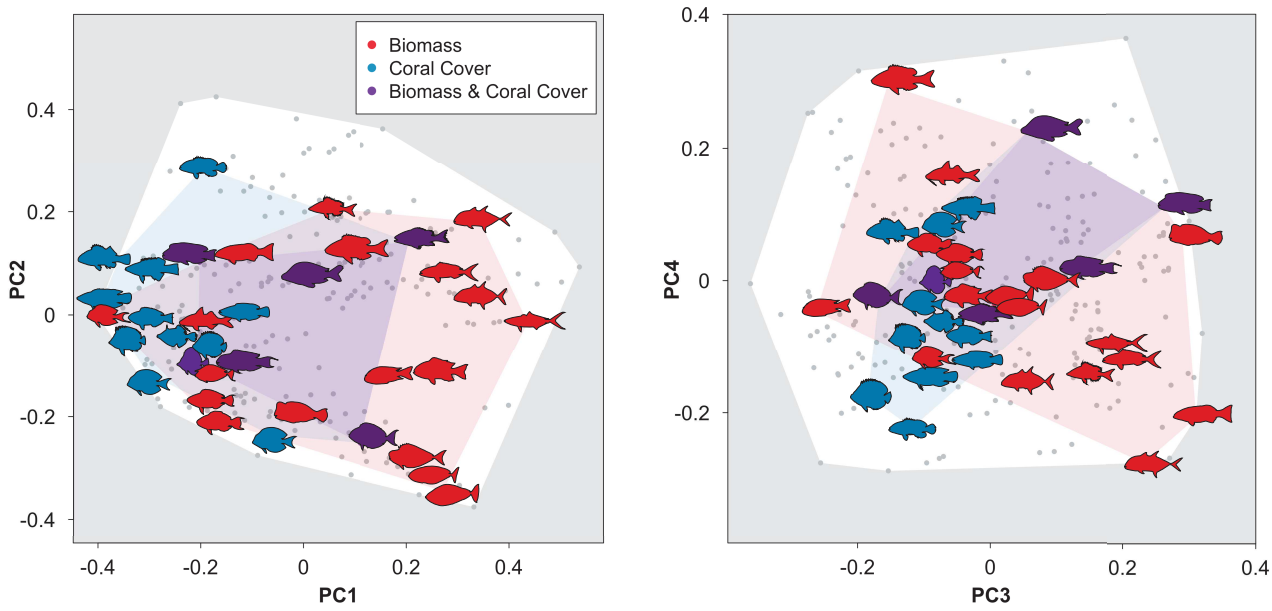


Figure 6.3 | Functional attributes of key fish species. *In total, 51 fish species which correspond to 35 out of 240 functional entities (15%) have been identified as strongly related to high biomass (18 red shapes), high live coral cover (11 blue shapes) or both of them (6 purple shapes). The positions of each of those 35 functional entities in the 4-dimensional functional space are defined according to species trait values. Fish shapes were chosen to illustrate the*

main genus of the species comprised in each functional entity. Other functional entities are represented with grey dots. Colored areas represent the functional volume filled by the functional entities that have been identified as strongly related to high biomass (red, FRic = 0.2), high live coral cover (blue, FRic = 0.05), both of them (purple, FRic = 0.01) or all functional entities (e.g. all species, white) present in the dataset.

6.3.4. Low overlap between species key with regard to fish biomass and coral cover

The two sets of key fish species associated with total fish biomass and live coral cover (26 and 28 key species, respectively) each represented less than 10% of the 381 fish species tested as candidates. Only three species (*Acanthurus albipectoralis, Lutjanus bohar, Lutjanus gibbus)* were common to both sets while four genera (*Acanthurus, Chlorurus, Lutjanus, and Scarus*) and four families (Acanthuridae, Labridae, Lutjanidae and Serranidae) presented key species significantly associated with the two reef services (Figure 6. 2, Table S6).

Only six functional entities were common and significantly associated with both biomass and live coral cover (Figure 6.3), namely small and medium herbivores, small planktivores, medium and large fishes targeting mobile invertebrates and meso-predators (Table S6).

6.3.5. The net benefit of key species for fish biomass and live coral cover

When present, each key species belonged to a community with a median level of fish biomass higher (560 $kg.ha^{-1}$, range: 439-773 $kg.ha^{-1}$) than the median biomass observed when absent (370 $kg.ha^{-1}$, range: 337-385 $kg.ha^{-1}$). Similarly, live coral cover was estimated at a median value of 50% (range: 36-82%) when each key species was present against 34% (range: 26-38%) when absent (Figure 6.4). For clarity, we only presented the net effect of the four most significant key species (lowest AIC, Tables S4 & S5) associated with biomass and live coral cover (Figure 6.4). It is important to note that these four most significant key species (lowest AIC) were not necessarily related to the highest level of biomass and coral cover (Figure S4).

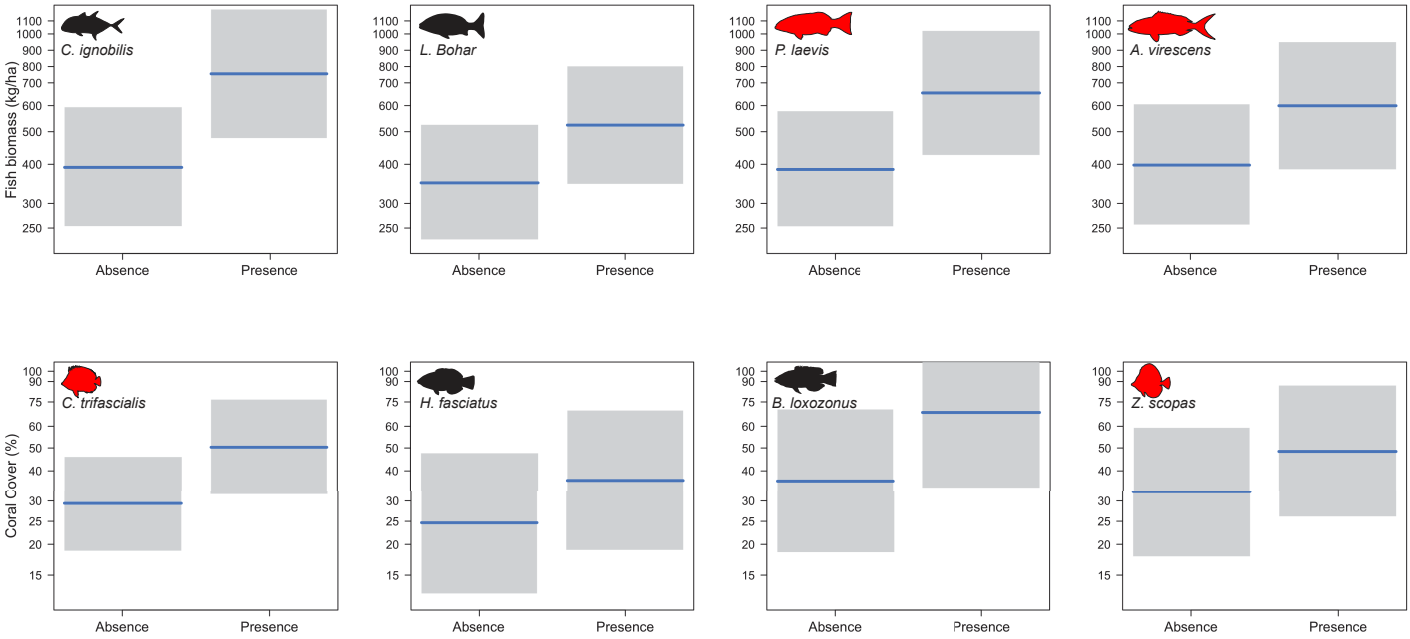


Figure 6.4 | Net effect of the 4 most significant (lowest AIC) key fish species when present for fish biomass (top) and live coral cover (bottom) *(among the 26 and 28 key species respectively) using a partial plot from the linear mixed models while the other variables are held constant. When present, each key species is linked to a median level of biomass and live coral cover significantly ($p<0.05$) higher than the level observed where absent.*

It is not only individual key species, but also the accumulation of key species that was linked to high levels of ecosystem services. For instance, reefs with more than four key species reached a median level of biomass of 1,150 kg.ha^{-1} (range: 362-3,715 kg.ha^{-1}), i.e. three times the median biomass observed (370 kg.ha^{-1}, range: 86-1,380 kg.ha^{-1}) in reefs with an intermediate number of key species (from 1 to 3 key species) and more than seven times higher than the median level of fish biomass reached in reefs having no key species (156 kg.ha^{-1}, range: 12-812 kg.ha^{-1}). Although less pronounced, reefs with at least 6 key fish species showed a median live coral cover of 40% (range: 20-68%) while reefs with no key species had a median level of 31% (range: 18-54%) live coral cover (Figure 6.5).

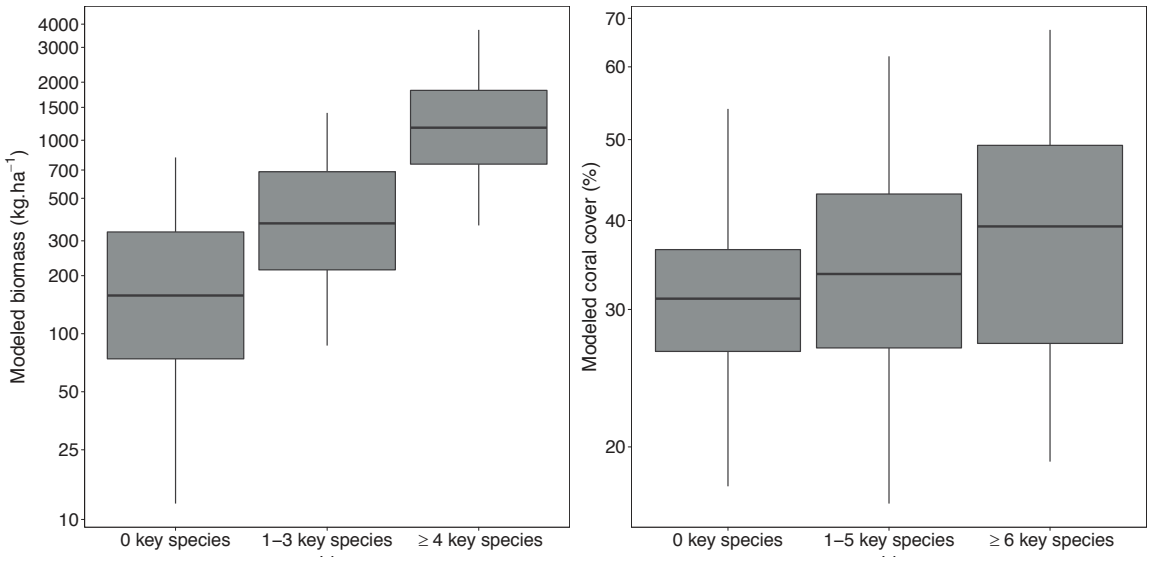


Figure 6.5 | The accumulation of key species co-occurring on coral reefs is positively related to fish biomass (left) and live coral cover (right). *To control for positive effect of species richness on ecosystem functioning, we compared modelled estimates of fish biomass and live coral between reefs while increasing the number of co-occurring key species. 3 categories of reefs were considered based on the 3rd-quartile of the number of key species as threshold (≥4 and ≥6 key species for biomass and coral cover, respectively). Reef with the highest number of co-occurring key species reached higher levels of biomass (1,150 kg.ha^{-1}) and coral cover (40%) than their counterparts having no key species (156 kg.ha^{-1}, 31% respectively). Distributions are represented using 95 percent confidence intervals.*

6.4. Discussion

6.4.1. Sustaining healthy and productive coral reefs

Even if the purpose of the present study was not to disentangle effects of anthropogenic, environmental and biodiversity drivers on fish biomass and coral cover, we found consistent results (Tables S2 & S3) with previous large-scale studies highlighting the primary importance of human density, species richness and ocean productivity on fish biomass and coral cover (Mora *et al.* 2011; Williams *et al.* 2015a; Duffy *et al.* 2016).

In the present study, many different fish species (~400 species candidates) were scanned and only 26 and 28 species were identified as significantly and positively related to fish biomass and live coral cover, respectively, with only three species being common to both. In total, these 51 species (i.e. ~13% of the species pool tested) represent 35 distinct functional entities (out of 240, i.e. 15%) that are widespread in the functional space. While large-bodied species may be expected to disproportionately contribute to fish biomass, our results indicate that only 25% (7 out of 26, Table S6) of key species for fish biomass were large-bodied (>50cm), which is directly comparable to the percentage of large-bodied species among the initial candidate species (24% or 91 fish species out of 381). In addition, 35% of key species for fish biomass were smaller than 30cm (9 out of 26, Table S6). The positive association with fish biomass is thus independent of body size.

It comes as no surprise that some key fish species identified in this study have already attracted considerable interest in coral reef ecology. Herbivorous fish support coral reef resilience by controlling algal growth, influencing competitive interactions between corals and macroalgae, and preventing coral-algal phase shifts (Bellwood *et al.* 2004; Mumby *et al.* 2006; Hughes *et al.* 2007; Rasher *et al.* 2013; Graham *et al.* 2015; Bozec *et al.* 2016), and therefore may contribute to the maintenance of high coral cover and fish biomass. In particular, scarine parrotfishes (i.e., *Bolbometopon, Chlorurus, Hipposcarus* and *Scarus,* Tables S4, S5 & S6) play critical roles as grazers and bioeroders of the reef substratum (Bellwood *et al.* 2003; Mumby 2006), and their abundances have strong positive effects on cover of corals and hence accretion rates of the reef (Cramer *et al.* 2017). Further, grazing and detritivorous acanthurids (i.e., *Acanthurus* and *Ctenochaetus*, Tables S4, S5 & S6) intensely graze epilithic algal turfs (Marshell & Mumby 2012; Rasher *et al.* 2013), while benthic-feeding unicornfishes (i.e., *Naso*, Tables S4 & S6) play a significant role in macroalgal removal (Fox & Bellwood 2008; Hoey & Bellwood 2009).

By contrast, some key species identified in the present study have not previously been identified as playing significant roles. While predation is a key process shaping prey behavior and populations (Rasher *et al.* 2017), structuring ecological communities (Boaden & Kingsford 2015), and promoting nutrient capacity (Allgeier *et al.* 2016; Allgeier *et al.* 2017), no individual predator species have been expressly identified as beneficial for total fish biomass and coral

cover. Here, we show that predatory species like *Aprion, Caranx, Cephalopholis, Elagatis, Gymnosarda, Lethrinus, Lutjanus, Oxycheilinus,* and *Plectropomus* (Figure 6.4, Tables S4 & S5, Figure S4) may play a critical role for fish biomass and live coral cover, although the exact pathways through which they act remain to be elucidated.

6.4.2. Low ecological pleiotropy on coral reefs

The finding that a limited number of functionally and evolutionary different species are positively related to high levels of fish biomass and coral cover (Figures 6.2, 6.3 & S4) supports the idea that sustaining ecosystem services may require a large breadth of particular attributes beyond the number of species (Soliveres *et al.* 2016; Gross *et al.* 2017). The limited overlap between the two sets of species significantly associated with two reef services (3 species, 4 genera and 6 functional entities) suggests a low level of ecological pleiotropy (Strauss & Irwin 2004), i.e. that a single species, genus or functional entity cannot be key to many independent ecosystem functions and services. Extended to the community level, we show that ecological pleiotropy, the opposite of functional redundancy, is not the norm on coral reefs. This finding may explain why the multi-functionality of ecosystems relies more strongly on biodiversity than do single functions (Isbell *et al.* 2011; Lefcheck *et al.* 2015; Soliveres *et al.* 2016; Gross *et al.* 2017), since some species play unique and thus irreplaceable roles in ecosystems (Bellwood *et al.* 2006; Petchey *et al.* 2008). However, it is important to keep in mind that the results may change depending on which traits and functions are considered in the analysis, and a number of yet unknown but relevant traits or functions not considered here could be included in future studies. We suggest that this ecological pleiotropy reconciles two opposing views in Biodiversity and Ecosystem Functioning **(**BEF) research since many complementary species groups and lineages, and hence a large amount of biodiversity, are necessary to sustain ecosystem multi-functionality and associated services. Rather than providing multiple functions individually, those key species appear to provide high benefits in terms of fish biomass and live coral cover once combined (Figure 6.5). Maintaining habitat heterogeneity and associated processes as well as high species diversity is thus a major component of management and conservation. Our results call for more species-focused management strategies such as the banning of fishing species considered as key for the ecosystem (Bozec *et al.* 2016). Additionally, sustaining multi-functionality also requires a

broader portfolio approach which may reduce local extinction risk by securing the biodiversity level in an increasingly uncertain future (Webster *et al.* 2017).

6.4.3. CWS as a flexible framework to link biodiversity to ecosystem functioning and services

The community-wide scan (CWS) approach can be adapted for a wide range of ecosystems, combinations of taxa or interactions and services. Here we only tested the presence of key species, while it would be possible to look for key species groups (pairs or more), key evolutionary lineages or even key biotic interactions. Since those interactions are potentially multiple in species-rich communities they cannot be experimentally tested but they can emerge from empirical data using the CWS approach. The way candidates are tested can be modified while respecting independence between predicted and explanatory variables. As positive effects of some species may only be revealed beyond particular thresholds, presence data can also be determined by any abundance threshold such as a minimum number of individuals, cover rate, biomass or level of interactions.

On coral reefs, defining species presence based on distribution of its biomass across study area (using upper percentiles or deciles) can promote the inclusion of small-bodied species but can also discriminate against species that are not commonly encountered or have skewed biomass distributions (Supplementary Material and Table S7-10). Rather, defining species presence according to its relative biomass in communities can be applied independently of the species biomass distribution. However, we found consistent results between these two procedures since the majority of species detected as key species using the intracommunity approach are also significant using the intraspecific approach, reinforcing the robustness of our findings.

The CWS framework thus offers a new and flexible way to analyze empirical data relating biodiversity to ecosystem functioning and services. CWS studies can also be considered as initial forays into a better understanding of the complex relationships between particular species, species groups or interactions and ecosystem functioning and associated services. A large number of false-positives, species being detected as key while they are not, may be revealed. Furthermore, no causality is determined in this approach; the main merit is to identify unsuspected and statistically significant positive associations. The logical progression

would be to conduct experiments focusing on potential key species or interactions with the ultimate aim of highlighting the underlying ecological or biological processes and pathways that potentially sustain healthy and productive ecosystems.

6.5. Conclusion

The community-wide scan (CWS) approach has the potential to reveal unsuspected contributions to ecosystem functioning and its associated services, especially in complex and biodiverse ecosystems where the detection of such contributions remains challenging. The CWS approach holds much promise in empirical BEF studies where only a few species, functional or phylogenetic groups, can disproportionally drive ecosystem functioning and the delivery of services. Ultimately, the key species identified form tractable conservation targets and encourage a diversification of management options to maintain fish species considered as key for the ecosystem. Given the growing interest in the assessment and consequences of the ongoing extinction crisis on ecosystem functioning, such a framework is extremely timely and widely applicable. Our framework offers a new and flexible way to analyze the ongoing massive empirical data relating biodiversity to ecosystem functioning and services with the potential to reconcile two opposing views: species identity vs. diversity.

7. General discussion and perspectives

7.1. Conclusion

There is a clear consensus that coral reefs are under threats. Securing a future for coral reefs under these multiple anthropogenic forcing factors (Hughes *et al.* 2017a) requires urgent alternatives to sustain coral reef socio-ecological systems. Like all ecosystems, coral reefs are facing increasing pressure as globalization connects the world (Liu *et al.* 2013). In particular, in both terrestrial and marine biomes, accessibility through road networks and infrastructure expansion are primarily driving the conditions of ecosystems, with the most accessible resources being most at risk of overexploitation and collapse (Laurance *et al.* 2009; Dobson *et al.* 2010; Mora *et al.* 2011; Ahmed *et al.* 2014; Barber *et al.* 2014; Alamgir *et al.* 2017). Accessibility is also important determinant of people's ability to use natural resources and ultimately, has raised serious ecological and management issues (Berkes *et al.* 2006; Rockström *et al.* 2009; Steffen *et al.* 2011). To date, measuring the extent to which global marine resources are accessible to humans was strictly limited to examining the linear distance between fishing grounds and markets or ports (Watson *et al.* 2015). However, for most coastal ecosystems and artisanal fisheries, this linear distance ignores ragged coastlines, road networks and other features that can affect the time required to reach fishing grounds and ultimately can produce biased conclusions.

In response to this urgent need, one major objective of the thesis was to develop new metrics of human accessibility on coral reefs taking into account the heterogeneity of the seascape and taking advantage of the most up-to-date spatial information and optimization algorithms (**Chapter 3**). Specifically, the thesis shows that travel time and ultimately human gravity, provide a better explanation of variations in reef fish biomass than linear distance at both local (**Chapter 5**) and large scale (Cinner *et al.* 2016). Most specifically, the thesis highlights the importance of market access to predict fish biomass conditions (**Chapter 5**) which is consistent with several studies that have shown proximity to market to be the strongest predictor of overfishing on coral reefs (McClanahan *et al.* 2006; Cinner *et al.* 2012; Cinner *et al.* 2013).

Coral reefs contain the most diverse fish assemblages worldwide and it is clear that biodiversity determines, at least partly, fish biomass in conjunction with sea surface

temperature, productivity and human impacts (Mora *et al.* 2011; Williams *et al.* 2015b; Duffy *et al.* 2016; Maire *et al.* 2018a). More broadly, biodiversity would promote high productivity, resistance and resilience of ecosystems in the face of climate change (Isbell *et al.* 2015; Duffy *et al.* 2016; Isbell *et al.* 2018). However, the processes by which this positive biodiversity effect is acting remains under scrutiny (McClain *et al.* 2016; Soliveres *et al.* 2016; Mori *et al.* 2018); and sometimes controversial (Mora *et al.* 2014).

To disentangle the imbricated relationships between biodiversity, ecosystem functioning and human impacts, the thesis contributed to improve the explanation of variations in fish biomass on coral reefs through *(i)* a more accurate quantification of human impacts and *(ii)* a community-wide scan approach to identify key species, functional groups and evolutionary lineages. I used the global dataset on coral reefs (**Chapter 2**) and modelled fish biomass using socio-economic and environmental covariates expected to influence reef conditions (Cinner *et al.* 2016; Cinner *et al.* 2018) . This analysis then consisted on a comparison of a series of models that predicted fish biomass including different variables such as (0) linear distance from the nearest market, (1) travel time from the nearest market, (2) total gravity, (3) total gravity and species richness and (4) total gravity, species richness and the number of fish species defined as "key" for biomass (Chapter 6).

At global scale, the model including travel time provides a better explanation of fish biomass than linear distance (4 units-lower AIC) and explains 58% of the variance observed (Figure 7.1), even if linear distance and travel time are highly correlated globally (**Chapter 3**). It means that locally or regionally (see Madagascar or New-Caledonia **Chapters 3 & 5**) this correlation is not so high owing to heterogenous seascape and accessibility patterns across land. Compared to travel time, total gravity provides the best predictive model (23 units-lower AIC) of fish biomass while the proportion of variance explained by the gravity model is slightly higher (60% see Figure 7.1). In short, new metrics of human impacts based on accessibility provide a better explanation of fish biomass compared to linear distance with a more likely model given the combination of covariates (lower AIC implies higher maximum likelihood as the number of parameters is hold constant).

When considering total gravity and species richness, the model still provides a better explanation of fish biomass (>1000 units-lower AIC) and explains 0.77% of the variance observed. There is no surprise as it has already been shown that species richness is a major driver of fish biomass (Duffy *et al.* 2016). However, some species can have more influence on ecosystem functioning than others and can considered as key for a given process function or service. So lastly, the best model is obtained when adding gravity, species richness and key species (50 units-lower AIC) and explains 78% of the variance explained (Figure 7.1). Once again, the best improvement is related to the maximization of log-likelihood and thus, optimal values of the estimated coefficients.

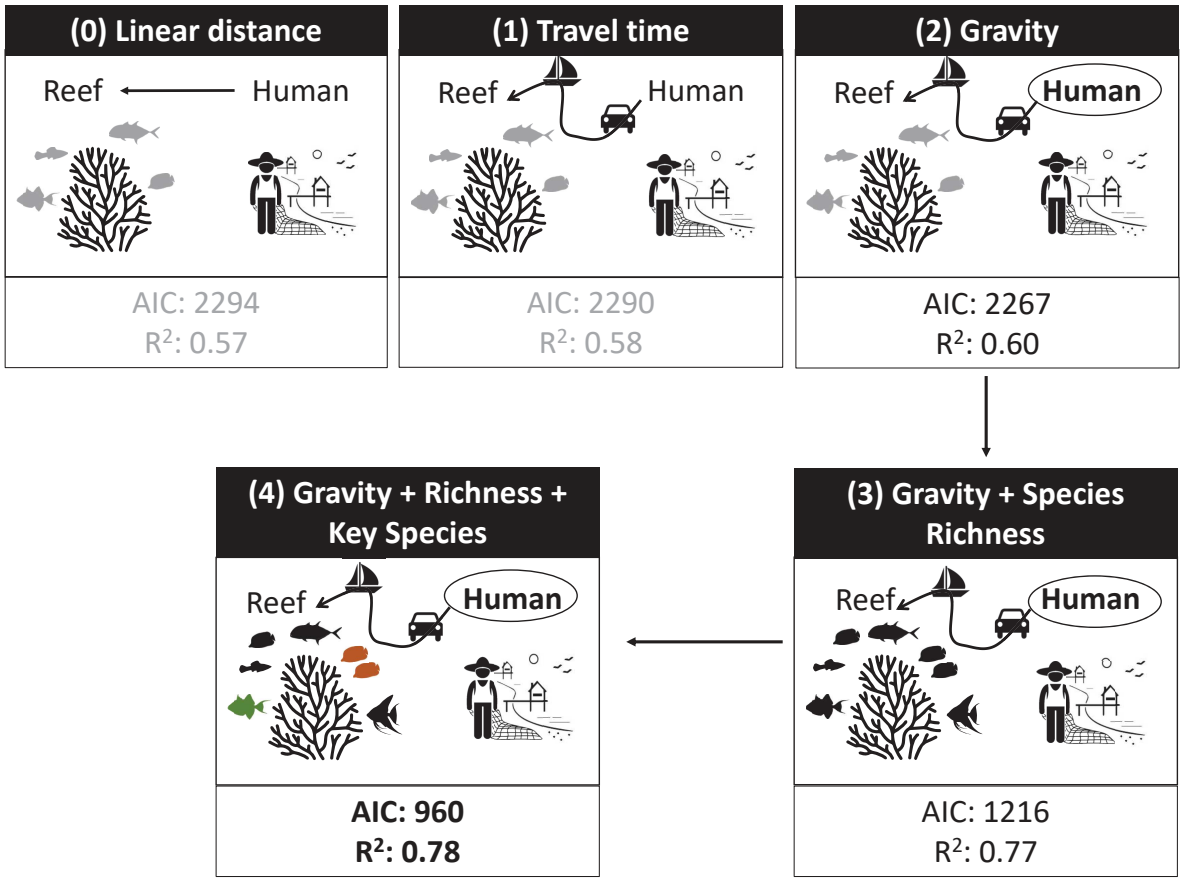


Figure 7.1 | Comparison of a series of models that predicted fish biomass *including different variables such as (0) linear distance from the nearest market, (1) travel time from the nearest market, (2) total gravity, (3) total gravity and species richness and (4) total gravity, species richness and the number of key fish species. The same pool of environmental and socio-economic covariates expected to influence fish biomass is included in every model.*

7.2. Contributions to the field

Beyond a better comprehension of the drivers of fish biomass, the thesis has contributed to the emergence of potential solutions to sustain coral reefs as social-ecological systems. Assessing the ability of management actions to be beneficial for both people and ecosystems first requires an accurate assessment of how human populations affect coral reefs and their resources. Thus, the implementation of travel time and gravity represents the first essential step and has been applied in three different case study.

7.2.1. Management implications

Effectiveness of tropical reefs MPAs. Effective solutions to the crisis facing coral reefs depend in part on our understanding of the context under which different types of conservation benefits can be maximized (Devillers *et al.* 2015; Pressey *et al.* 2015). **Chapter 4** uses a large-scale analysis of nearly 1,800 tropical reefs and reveals how the gravity of human impacts in the surrounding seascape, diminishes the effectiveness of marine reserves at sustaining reef fish biomass and the presence of top predators, even where compliance with reserve rules is high. Critically, fish biomass in high-compliance marine reserves located where human impacts were intensive tended to be less than a quarter that of reserves where human impacts were low. Similarly, the probability of encountering top predators on reefs with high human impacts was close to zero, even in high-compliance marine reserves.

However, the study also shows that conservation gains (the relative difference between openly fished sites and reserves) are highest for fish biomass where human impacts are moderate (nearly a surplus of 400 kg of fish per hectare so 900 kg/ha in reserves against 500 kg/ha in fished area) and for top predators where human impacts are low. These results illustrate critical ecological trade-offs in meeting key conservation objectives: reserves placed where there are moderate-to-high human impacts may provide substantial conservation gains for fish biomass, yet they are unlikely to support and secure key ecosystem functions like top predation, which is only prevalent in reserves with low human impacts in surrounding areas.

Market, fish and fisherman: the eternal triangle. Rapid degradation of the world's coral reefs (Hughes *et al.* 2003; Pandolfi *et al.* 2003; Bellwood *et al.* 2004; Hughes *et al.* 2017a) jeopardizes their ecological functioning and ultimately imperils the wellbeing of the millions

of people with reef-dependent livelihoods (Teh et al. 2013). Understanding how accessibility from human societies affects natural resources is a critical step toward a long-term management of the ecosystems where actions are needed to enhance their ecological and economic sustainability. **Chapter 5** highlights results from an archetypal study case in Northwest Madagascar where I modelled the respective influence of local communities and local market on the conditions of coral reefs, given management.

I show that communities further away from markets had more households engaged in fishing, higher dependence on marine resources and limited number of livelihoods. Therefore, we may expect a lower fish biomass in such areas far from markets where fisheries dependency is high. Surprisingly, the study reveals that fish biomass increases as reefs were further away from the market. Thus, market proximity constrains fish biomass with an even greater effect than fishing communities even in managed reefs.

Thus, a better assessment of accessibility from human societies (market and village) appears as a critical step toward a long-term management of the coral reef fisheries. In addition, market access is now one key indicator in the global monitoring framework used by some major non-governmental organizations operating in Madagascar like the Wildlife Conservation Society, Blue Ventures or Conservation International.

7.2.2. Biodiversity

Within the context of global changes and biodiversity loss, restoring reefs to past configurations is no longer an option in the Anthropocene. Instead, we need a clearer understanding of multiple drivers and ecosystem responses to better anticipate the potential futures of coral reefs under various scenarios. Effective ecosystem management relies on a better understanding of the causal pathways between ecological communities and the myriad of services they sustain (Cardinale *et al.* 2012; Cheung *et al.* 2016; Ricketts *et al.* 2016; Ratcliffe *et al.* 2017). Determining whether many functionally complementary species or only a subset of key species are necessary to maintain ecosystem functioning and services is a critical question in community ecology and biodiversity conservation. Identifying such key species remains challenging, especially in the tropics where many species co-occur and can potentially support the same or different processes. In **Chapter 6** I develop a new community-wide scan (CWS) approach, analogous to the genome-wide scan, to identify fish species that significantly

contribute, beyond the socio-environmental and species richness effects, to the biomass and coral cover on Indo-Pacific reefs.

The study reveals that only a limited set of fish species (51 out of ~400, approximately 13%), belonging to various functional groups and evolutionary lineages, are strongly and positively associated with fish biomass and live coral cover. Many of these species have not previously been identified as functionally important and thus, may be involved in unknown, yet important, biological mechanisms that help sustain healthy and productive coral reefs. The finding that a limited number of functionally and evolutionary different species are positively related to a high level of fish biomass and coral cover supports the idea that sustaining ecosystem services may require a large breadth of particular attributes beyond the number of species (Soliveres *et al.* 2016; Gross *et al.* 2017). These results call for more species-focused management strategies such as the banning of fishing species considered as key for the ecosystem (Bozec *et al.* 2016). Additionally, sustaining multi-functionality also requires a broader portfolio approach which may reduce local extinction risk by securing the biodiversity level under uncertain futures (Webster *et al.* 2017). CWS has the potential to reveal species that are key to ecosystem functioning and services and to guide management strategies as well as new experiments to decipher underlying ecological processes.

7.2.3. Open-source data

To facilitate applications related to coral reefs accessibility, potential travel time estimates (Chapter 3) and gravity of human impacts (Chapter 4), global spatial layers at 10 km-resolution are freely available (Cinner & Maire 2018).

CWS framework offers a new and flexible way to analyse the ongoing massive empirical data relating biodiversity to ecosystem functioning and services, thus codes and data supporting the analysis are freely available in a public repository (Maire *et al.* 2018b).

7.3. Limits

Refining travel time in accordance with local infrastructures and technology

In the first assessment of travel time (**Chapter 3**), speed values required to cross the different types of land cover were adapted from a global assessment of travel time between major cities (Nelson, 2008). These assume that road and maritime travels are made by motorized

vehicles while off road travel is foot based. This also supposes a single value or a single motorized vehicle for all the countries while many reefs are located in developing countries where wooden canoes are commonly used and motorized vehicles are not so common. Future applications should consider variable travel speeds according to per capita Gross Domestic Product or empirical values in order to reflect different levels of infrastructure and technology in developed versus developing countries.

Escaping the spatial resolution constraint to assess travel time

The least-cost distance algorithm used to assess travel time, requires a friction-surface grid where each cell contains a unique cost value according to land cover. As regular spatial grids, the friction-surface uses a specified resolution (a 1km-resolution was used for the global assessment of travel time in **Chapter 3**) which determines the size of every cell. Consequently, landscape heterogeneity would be smoothed and road networks would have a minimum width constrained by the resolution of the grid. A more relevant alternative would be to implement a network-based spatial analysis which is a spatial tool commonly used in GPS devices to define the fastest path between two locations. Adapting such tools is very promising as it may provide more realistic travel time estimates while modulating speed values according to local constraints (roadworks), facilities (infrastructures) or technology (engines). Nonetheless, its implementation has just begun and still needs more computing work. First trials were used in **Chapter 5**, where field campaigns in Madagascar have enabled to *(i)* validate spatial road networks available in OpenStreetMap©, *(ii)* complete missing roads using GPS tracks, and *(iii)* check road surface and associated speeds of the transport modes used by Malagasy people (bicycle, motorcycle, four-wheel drive etc.). These three steps are crucial for a more realistic implementation of network-based assessment of travel time.

Re-thinking travel time and gravity

Travel time computation assumes that each trip is unidirectional, so with a constant level of attraction from any reef. Reefs with more fish, or higher fish value (like trophy or particular commercial interest), could be more attractive and exert a higher pull for exploitation (Berkes et al. 2006). Indeed, gravity varies based on human population size, but not on the quality or quantity of fish on a specific reef, therefore incorporating fish biomass or composition through potential market price of reef fish could modulate the attraction from a given reef.

In the same vein, the spatial allocation of fishing effort is not a random process since fishermen could favor specific reefs which are not necessarily the most productive. Thus, the 'potential' travel can fail to capture the real fishing effort experienced by reefs.

7.4. Future research directions

Predicting the future human impacts on reefs.

The global network of roads is rapidly expanding under multiple needs of accessibility to resources, industries, and infrastructures. Most of the 25 million kilometers of new roads anticipated by 2050 will be built in developing countries to sustain their social and economic development, but this could have profound impacts on biodiversity (Laurance *et al.* 2014). The spread of this road network in the last terrestrial wilderness areas (e.g. Amazon) and its ecological consequences have been widely documented particularly the accentuated depletion of natural resources (Barber *et al.* 2014). Comparatively the impact of road construction on marine ecosystems remains largely overlooked (Schmitt & Kramer 2010). Firstly, travel time provides a framework to assess scenarios of future road development on reef systems, highlighting potential ecological consequences and trade-offs associated with specific plans. Development of new and faster roads along the coasts will increase the accessibility of some reefs to humans (**Chapter 3**), likely resulting in overfishing and potential impacts on corals (Mumby *et al.* 2006; Hughes *et al.* 2007). Travel time calculations using future scenarios of road building may help to identify reefs that are particularly at risk and develop potential alternatives that could still meet socioeconomic goals with less environmental impact.

Secondly, the ways in which gravity will increase over time may be crucial to sustaining coral reef social-ecological systems. Demographic projections of high migration and fertility rates in some countries suggest substantial increases in coastal human populations in developing countries, where the majority of coral reefs are located (Gerland *et al.* 2014; Mora 2014, 2015). More specifically, the highest population growth are expected in Africa (Gerland *et al.* 2014) where millions of people are food insecure (Black *et al.* 2013; FAO 2016). Moreover, demographic changes such as increased migration in coastal areas are also expected to be coupled with coastal development and road building that will increase the accessibility of reefs.

Predicting the future accessibility of reefs and ultimately the future gravity may become a matter of substantial concern for coral reef governance and still requires more consideration.

More broadly, scenario analysis has long been identified as a strategic management tool to explore future changes and associated impacts for supporting adaptation decision-making under uncertainty. Better anticipating biodiversity and ecosystem trajectories requires diverse information about the future including climate, socio-economic, and policy dimensions. A global scenario framework (RCP–SSP–SPA) including three components: *(i)* climate through Representative Concentration Pathways (RCP), *(ii)* society and economy through Shared Socio-economic Pathways (SSP), and *(iii)* adaptation and mitigation through Shared climate Policy Assumptions (SPA), has been developed by the Intergovernmental Panel on Climate Change Fifth Assessment Report (IPCC-AR5) to better predict the future world development and its impact on ecosystems. Diverse initiatives have emerged to apply and couple these three components (RCP, SSP, SPA) at smaller scale, which have proven to be more effective (Boke-Olén *et al.* 2017; Kebede *et al.* 2018; Kummu *et al.* 2018). In the same vein, some studies have already demonstrated how travel time from cities can be a robust predictive variable in diverse research domains including economy, education, health and food security (Bhatt *et al.* 2015; Frelat *et al.* 2016; Weiss *et al.* 2018). Thus, accessing the future accessibility of both ecosystems and human populations may be essential for many applications such as socio-economic assessments, environmental impact analyses and spatial planning.

Fishing effort

Sustainable fisheries management is key to restoring and maintaining ecological function and benefits to people, but it requires accurate information about patterns of resource use, particularly fishing pressure. In most coral reef fisheries and other data-poor contexts, obtaining such information is challenging, often locally or regionally assessed (Delaney *et al.* 2017) and remains an impediment to effective management.

For small-scale and artisanal fisheries, information on fishing effort is often difficult to study because of the number of fishing units and the spatial and temporal dispersal of landing points. The past 10 years have seen remarkable advances in our ability to monitor ecosystems from space. High-resolution satellite imagery is increasingly available at the global scale and

contains an abundance of information about landscape features that could be linked with fishing activity.

A recent study has trained a convolutional neural network using satellite data from African countries to explain the variation in local-level economic outcomes (Jean *et al.* 2016). Such tools could be used to track fishing units, identify landing points and determine reefs which experience high fishing pressure.

Another study has provided the first map of global fishing activity using the automatic identification system (AIS) originally designed to help prevent ship collisions (Kroodsma *et al.* 2018). Nonetheless, this tracking tool is mainly used by industrial fleets while small fishing units are not equipped by such devices. Information from GPS tracking system or high-resolution satellite imagery would be essential to better map how local fishermen exploit the surrounding reefs and to propose effective and sustainable management of the coral reef fisheries.

Recently, many initiatives such as *Vulcan Inc.* or *the Leonardo DiCaprio Foundation* have emerged and support projects around the world to help solve the most pressing environmental issues through grantmaking, public campaigns and media initiatives or by providing expertise in technology, aerospace, biodiversity, and maritime security. Both initiatives have, for example provided financial support and have contributed to deliver an unprecedented level of analysis and data that may help improve enforcement in the fight against illegal fishing. Current and future engagement of such initiatives could also be crucial for the future of coral reefs.

Human impact on fish communities

Reef fish biomass can reflect a broad selection of reef fish functioning and benthic condition (McClanahan *et al.* 2011; Mora *et al.* 2011; Edwards *et al.* 2014; MacNeil *et al.* 2015), and is a key metric of resource availability for reef fisheries. Nonetheless, coral reefs provide numerous ecosystems services and the delivery of these services relies on critical ecosystem functions performed by fishes (Bellwood *et al.* 2004; Bozec *et al.* 2016) which are not fully captured when considering only fish biomass. It remains unclear how human impacts affect the composition of fish communities and more precisely the trophic structure of fish communities.

Using the global dataset on coral reefs (Chapter 2), I first have investigated how similar are trophic structures in fish communities globally and our ability to predict them. Using clustering analysis, I have found that coral reefs show a limited number of distinct trophic structures. More precisely, fish communities are distributed in only six main trophic structures (e.g. trophic pyramids) that can be secondly reduced to three main trophic structure. Thus, fish communities have different composition (fish biomass and species) and experience various environmental and socio-economic conditions but present similar trophic structure at global scale. Secondly, I have modelled the probability of belonging to each of the three trophic structure given environmental and socio-economic conditions (using multinomial models). Based on the first results (Figure 7.2), I found that travel time from human populations would be a key driver in interaction with management to predict the trophic structure of fish communities. Travel time from the nearest human population would be a better driver compared to travel time from market or any gravity metric.

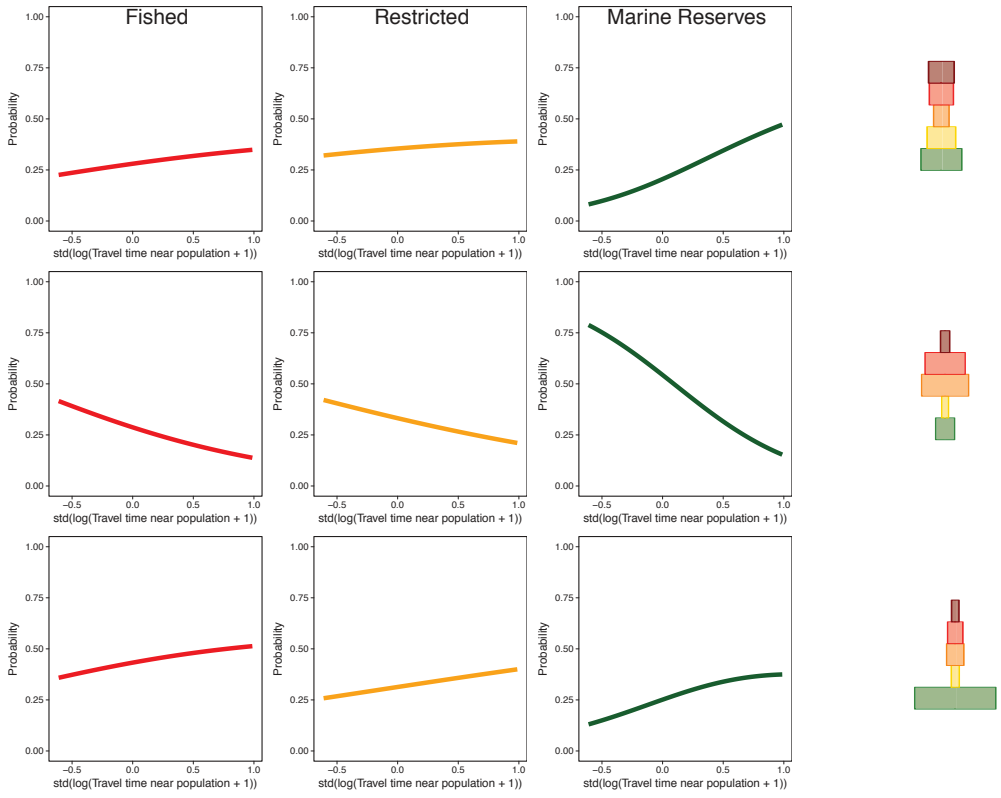


Figure 7.2 | Predictions of each main trophic structure along a travel time gradient and according to the three main types of management *(red: fished, orange: restricted reefs and green: marine reserves). The corresponding trophic pyramids are also represented.*

More specifically, the concave pyramid (upper line) is more likely to be encountered in marine reserves far from humans. This is in line with recent studies showing that top predators (top trophic level in dark red) are nearly absent on reefs close to humans (Cinner *et al.* 2018). The second trophic pyramid (second line) is commonly observed in (over)exploited reefs where the intensive fishing of top predators results in a dominance of intermediate trophic levels (Graham et al. 2017). Such trophic structures are commonly observed close to humans but become less likely further away from people as exploitation decrease especially in marine reserves. The third pyramid is less typical but can result from light fishing pressure (Sandin & Zgliczynski 2015) and tends to show no relationship with protection status (Figure 7.2).

These results are promising but the next step would be to implement Bayesian modelling to integrate the scale of the data into the multinomial models which is an essential step given the hierarchical structure of data. Nonetheless, this was not feasible with the modelling tools used during the PhD.

8. References

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9. Appendices

9.1. Appendices - Chapters 2-5 (Roman numbering)

Table I | List of fish families recorded in the global dataset (Chapter 2), their common name, and whether they are commonly targeted in artisanal coral reef fisheries or considered at top predators. Due to varying tastes, values, and preferences, not all families listed as target species will necessarily be targeted in ever coral reef fishery. X means not included in category.

Fish family	Common name	Fishery target	Top predator
Acanthuridae	Surgeonfishes	All	X
Balistidae	Triggerfishes	Non-Target<20cm Target >20cm	X
Carangidae	Jacks/Trevallies	<50cm	> 50cm
Carcharhinidae	Sharks	X	All
Diodontidae	Porcupinefish	Non-Target	X
Ephippidae	Spadefishes	All	X
Ginglymostomatidae	Sharks	X	All
Haemulidae	Grunts/Sweetlips	All	X
Heterodontidae	Sharks	X	All
Kyphosidae	Sea Chubs/Drummers	All	X
Labridae	Wrasses and Parrotfish	Non-Target<20cm Target >20cm	X
Lethrinidae	Emperors	All	X
Lutjanidae	Snappers	All	Selected species > 50cm
Monacanthidae	Filefish	Non-Target	X
Mullidae	Goatfishes	All	X
Nemipteridae	Coral Breams	All	X
Pinguipedidae	Sand perch	Non-Target	X
Pomacanthidae	Angelfishes	Non-Target<20cm Target >20cm	X
Serranidae	Groupers	All	Selected species > 50cm
Siganidae	Rabbitfishes	All	X
Sparidae	Porgies	All	X
Sphyraenidae	Barracuda	X	Selected species > 50cm
Sphyrnidae	Sharks	X	All
Synodontidae	Lizardfish	Non-Target	X
Tetraodontidae	Pufferfish	Non-Target	X
Zanclidae	Moorish Idol	Non-Target	X

Table II | Travel time estimates by land cover type. Adapted from Nelson (2008)

Global Land Cover Class	***Speed associated (km/h)***
Tree cover, broadleaved, deciduous & evergreen, closed; regularly flooded Tree Cover, Shrub, or Herbaceous Cover (fresh, saline, & brackish water)	1
Tree cover, broadleaved, deciduous, open *(open= 15-40% tree cover)*	1.25
Tree cover, needle-leaved, deciduous & evergreen, mixed leaf type; Shrub Cover, closed-open, deciduous & evergreen; Herbaceous Cover, closed-open; Cultivated and managed areas; Mosaic: Cropland / Tree Cover / Other natural vegetation, Cropland / Shrub or Grass Cover	1.6
Mosaic: Tree cover / Other natural vegetation; Tree Cover, burnt	1.25
Sparse Herbaceous or sparse Shrub Cover	2.5
Water	20
Roads	60
Track	30
Artificial surfaces and associated areas	30
Missing values	1.4

Table III | Human, Environment and habitat variables used to predict reef fish biomass in the New Caledonian study case (Chapter 3).

	Name	Description	Units	Mean	Range
HUMAN	People/20k buffer	Number of inhabitants in a 20km buffer around the site	Number of people	12 570	0 - 116 110
	Linear distance from the nearest market	Linear distance from Noumea	km	218	2.2 - 867
	Travel time from the nearest market	Travel time from Noumea	hours	7.3	0.13 - 50.4
ENVIRONMENT	Sea Surface Temperature (SST)	annual average of SST	Degrees Celsius	25.5	24.2 - 26.6
	Type of island	**High island, Low island, Atoll**	**High island** (large island with a fringing reef and a small lagoon),	**High island**: 24	
			Low island (small island surrounded by a large lagoon)	**Low island:** 1279	
			Atoll (no island)	**Atoll:** 54	
HABITAT	Zone	Flat or Slope	qualitative	-	-
	Mean Depth	Mean depth	Meter	3.8	0.6 - 17
	% Live coral	Sum of the percentage of coral components of the substrate: 1) encrusting live coral, 2) massive and sub-massive live coral, 3) digitate live coral, 4) branching live coral, 5) foliose live coral, 6) tabulate live coral and 7) Millepora sp.	%	0.18	0 - 1
	% Macro algae	% of macroalgae	%	0.08	0 - 1
	Reef type	The four geomorphological structures sampled: Coastal (fringing reef), Lagoon, Back (back of the barrier), Outer (external part of the barrier)	qualitative	-	-

Table IV | List of nation/states included in the study detailed in Chapter 4, and number of reef sites by management type.

COUNTRY	OPENLY FISHED	RESTRICTED	HIGH COMPLIANCE RESERVES
AMERICAN SAMOA	96	8	0
AUSTRALIA	0	91	15
BELIZE	3	9	0
BRAZIL	0	6	12
BRITISH INDIAN OCEAN TERRITORY	0	6	36
CAYMAN ISLANDS	3	0	0
COLOMBIA	3	0	0
COMMONWEALTH OF THE NORTHERN MARIANA ISLANDS	70	0	2
COMORO ISLANDS	7	0	0
CUBA	0	0	3
EGYPT	6	0	0
FEDERATED STATES OF MICRONESIA	1	0	0
FIJI	15	1	0
FRENCH POLYNESIA	122	0	0
GUAM	9	4	1
HAWAII	221	1	2
INDONESIA	90	108	2
JAMAICA	8	2	0
KENYA	23	0	9
KIRIBATI	50	0	0
MADAGASCAR	38	0	0
MALDIVES	0	40	1
MARSHALL ISLANDS	15	0	0
MAURITIUS	10	0	4
MAYOTTE	8	0	0
MEXICO	3	0	6
MOZAMBIQUE	18	2	4
NETHERLANDS ANTILLES	0	14	0
NEW CALEDONIA	224	10	0
OMAN	8	0	0
PALAU	0	2	0
PANAMA	13	0	0
PAPUA NEW GUINEA	18	10	0
PHILIPPINES	1	0	0
PRIA	0	111	0
REUNION	14	0	0
SEYCHELLES	0	53	3
SOLOMON ISLANDS	60	0	2
TANZANIA	37	0	4
TONGA	6	0	0
VENEZUELA	7	7	0

Table V | Model fit estimates for both targeted fish biomass and top predator are measured with the marginal R-squared, which describes the proportion of variance explained by the fixed factors alone, and conditional R-squared, which describes the proportion of variance explained by both the fixed and random factors. The relative importance of each variable is also presented for both targeted fish biomass and top predator models. To get those, all the possible models (i.e. all the possible combination of variables) are ranked using AICc, and all models within ΔAICc< 3 of the top ranked model are kept. The relative importance of each variable is based on the sum of Akaike weights of all the possible models (i.e. all the possible combination of variables) in which the variable is present.

Variables	Targeted biomass model	Top predator model
Model fit estimates		
marginal R-squared	0.18	0.47
conditional R-squared	0.58	0.63
Relative variable importance		
Management*Gravity	0.13	0.57
Management	0.14	1
Gravity	1	1
Local population growth	0.43	0.31
Reef fish landings	0.21	0.35
Population size	0.26	0.51
Tourism	0.50	0.51
Voice and accountability	0.21	0.31
Human Development Index	0.22	0.34
Census method	0.60	X
Total sampling area	1	1
Habitat	0.89	1
Depth	1	1
Productivity	0.16	0.32

Table VI | Description of households surveyed in Northwest Madagascar. Proportion of households surveyed and total estimated number of households in each community are provided.

Village	Estimated number of households	Number of households interviewed
Amparamilay	16	16
Amparoha	30	30
Andravorogna	23	23
Anjiabe	188	50
Antafiambotry	215	50
Marimbe	25	25
Marotogny	111	40
Nosy Iranja	105	40
Ratapenjke	33	30
Sakatia	290	50
Total	**1036**	354

Figure I | Potential travel time from the nearest human population to reach reefs A and B near Kimbe in Papua New Guinea. The populated pixels (grey pixels) were identified using the human density layer provided by the LandScan™ 2011 database. Travel time from the nearest populated pixel using land (road and land cover) and water (navigable river, lake and ocean) was calculated to reach coral reefs A and B.

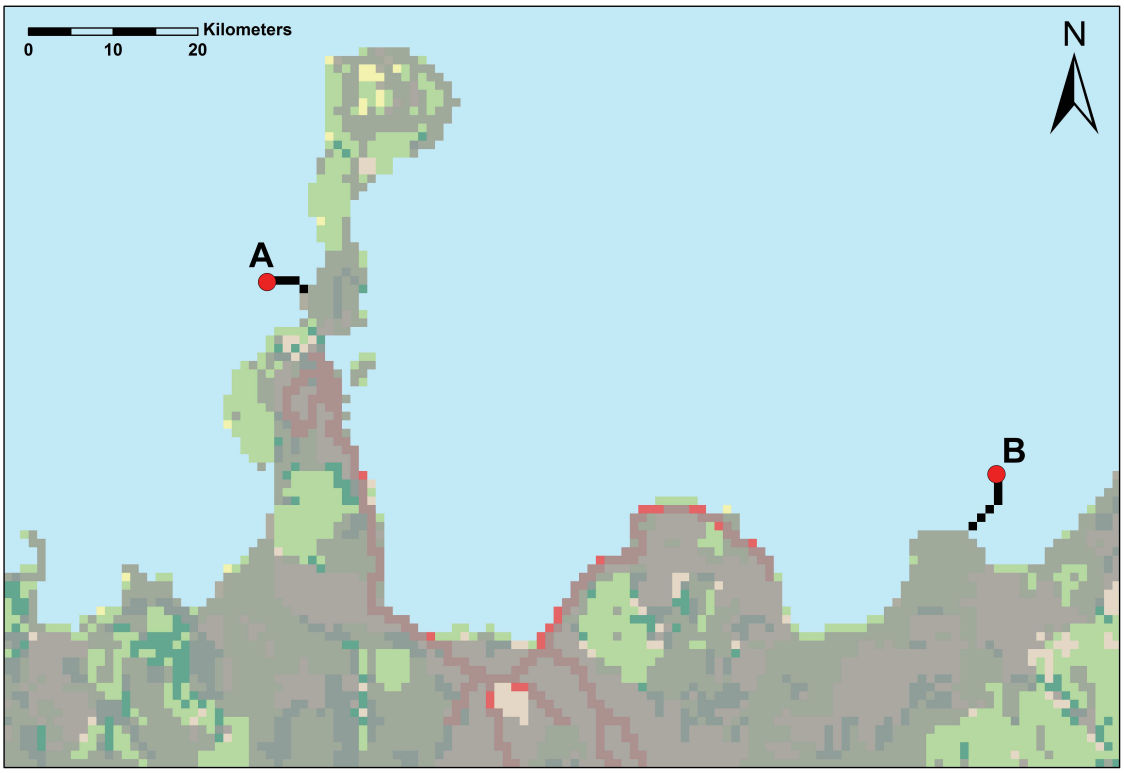


Figure II | Residuals between travel time from the nearest major market to reach 23,940 cells of coral reefs globally and values estimated using linear distance. A linear model linking travel time and linear distance from the nearest major market to reach any reef cell (Figure 3.4 B) is used to estimate travel time based on linear distance (estimated travel time) and the corresponding residual. Residual is calculated for each reef cell as follows: *Residual = (travel time - estimated travel time) / estimated travel time*.

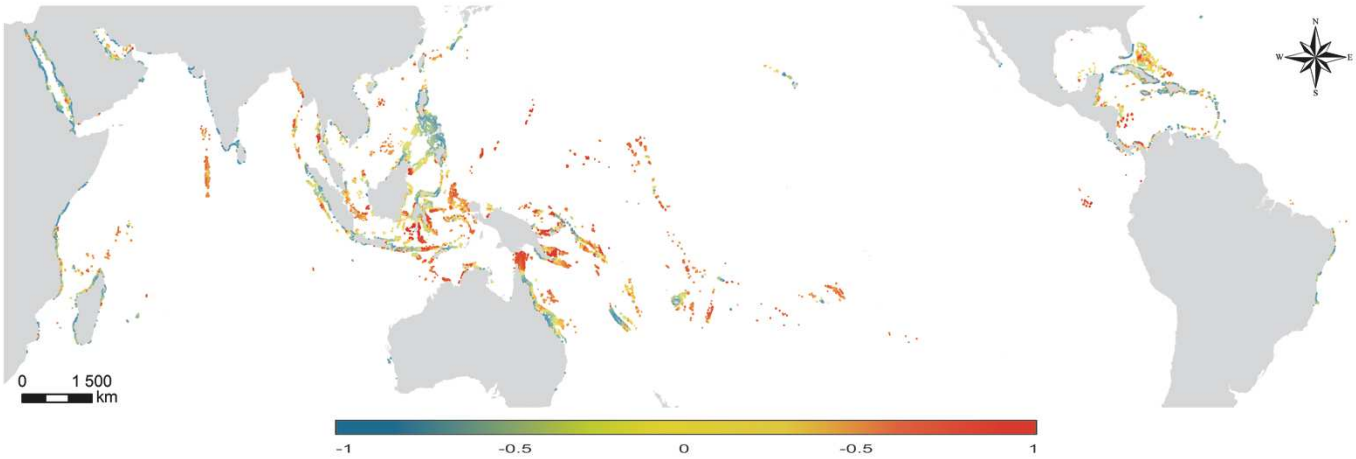


Figure III | Pairwise Pearson correlations between variables used to predict reef fish biomass in New Caledonia. Pearson coefficient of correlations and confidence intervals between all pairs of variables (total reef fish biomass, human, habitat and environmental variables) are presented into the lower panel. The colored upper panel presents positive (blue) and negative (red) correlations.

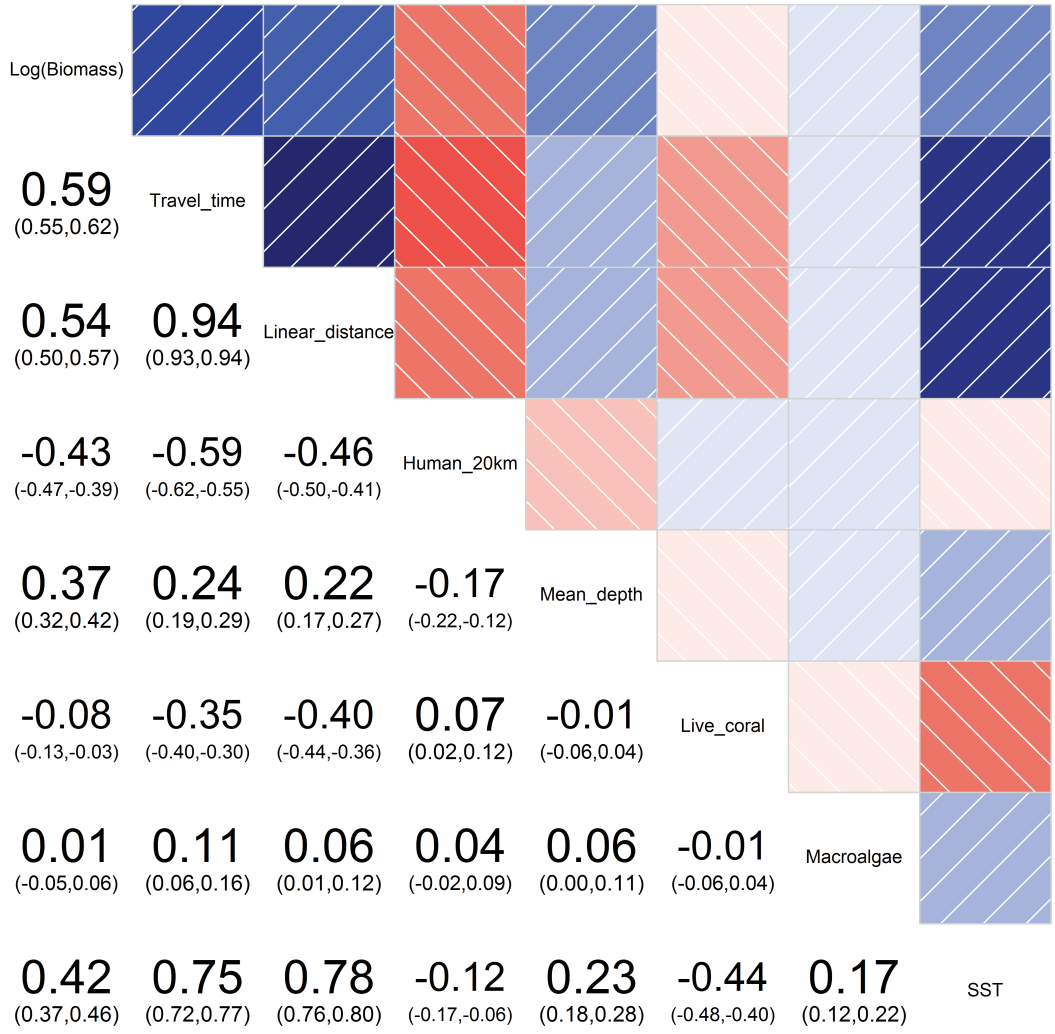


Figure IV | Accessibility of any coral reef from people (nearest market and nearest human settlement) around the world with slow boats. Coral reef accessibility was also calculated considering slower boats (10 $km.h^{-1}$) instead of 20 $km.h^{-1}$). Mean accessibility of coral reefs from people increased from 1h50 (SD = 4h15) to 3h40 (SD = 8h30) and from markets increased from 10h (SD = 9h) to 17h (SD = 17h30) using slower boats.

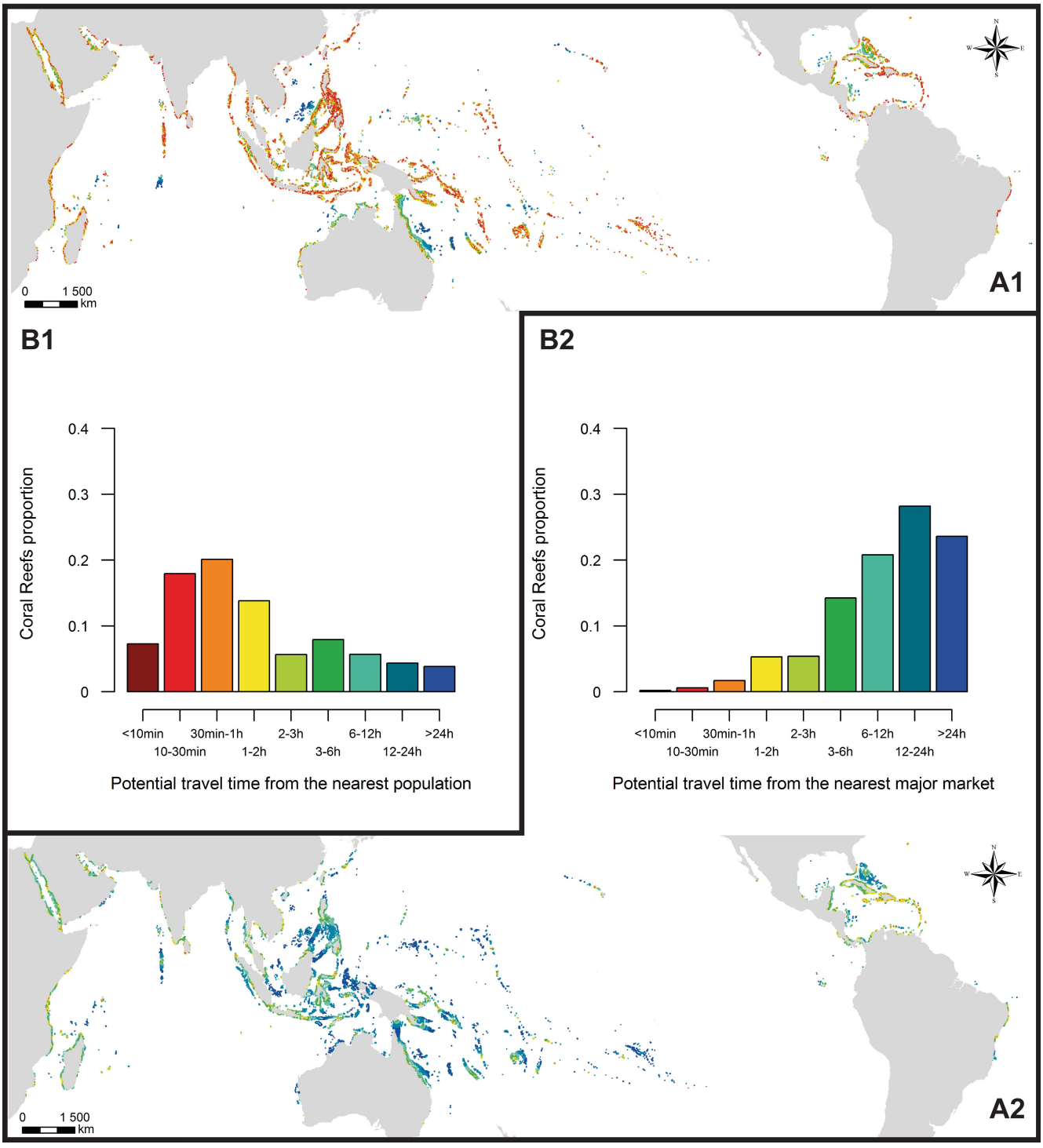


Figure V | Accessibility of any coral reef from people (nearest market and nearest human settlement) around the world with fast boats. Coral reef accessibility was also calculated considering faster boats (40 km.h^{-1} instead of 20 km.h^{-1}). Mean accessibility of coral reefs from people decreased from 1h50 (SD = 4h15) to 1h10 (SD = 3h) and from markets decreased from 10h (SD = 9h) to 6h10 (SD = 4h40) using faster boats.

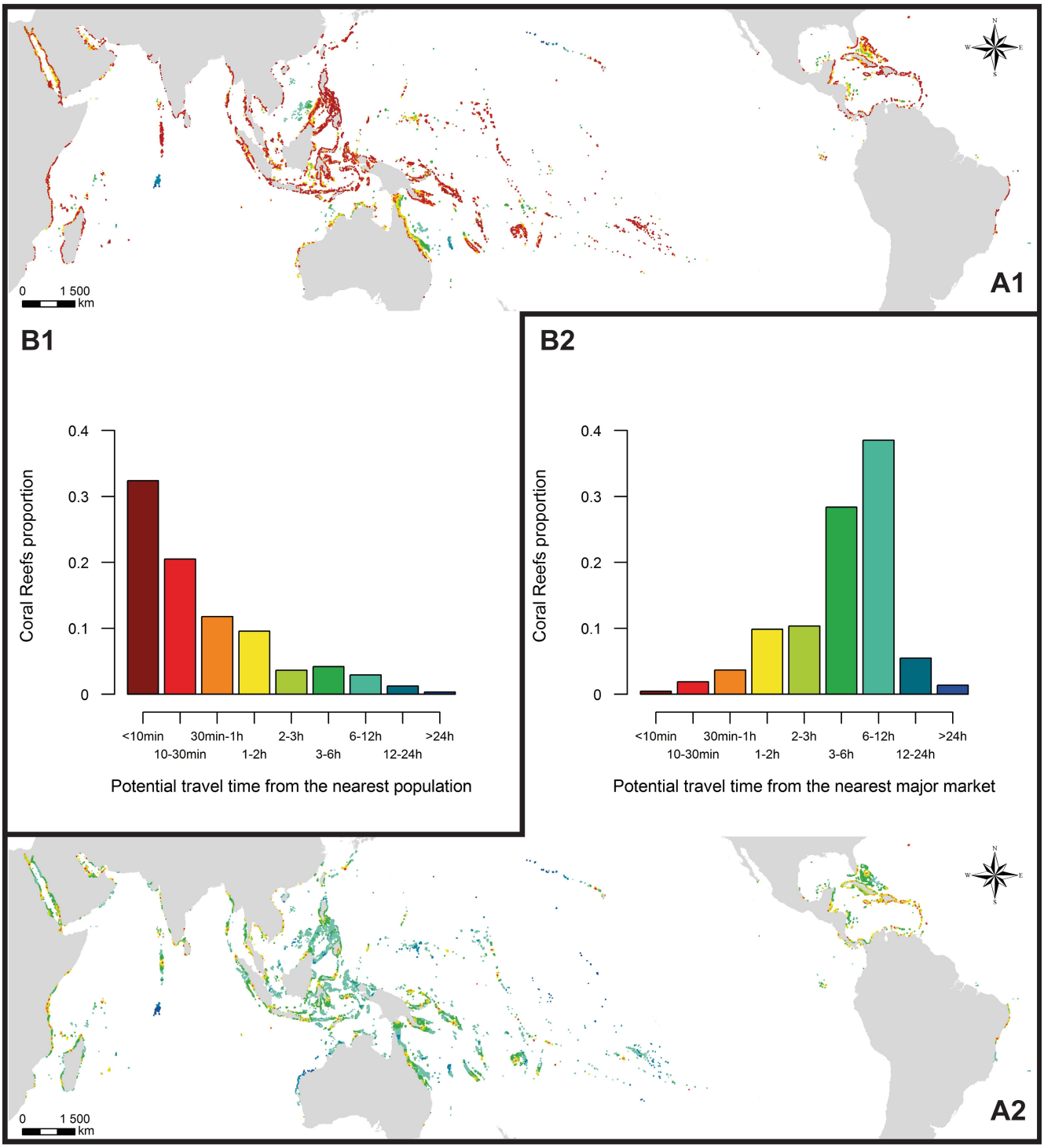


Figure VI | Standardized effect size of social drivers and environmental covariates, including 95% uncertainty intervals (thin lines), and 50% (thick lines) for (A) the full biomass model (including top predators); (B) targeted fish biomass model (excluding top predators); (C) the top predators presence/absence model; and D) untargeted Biomass model.

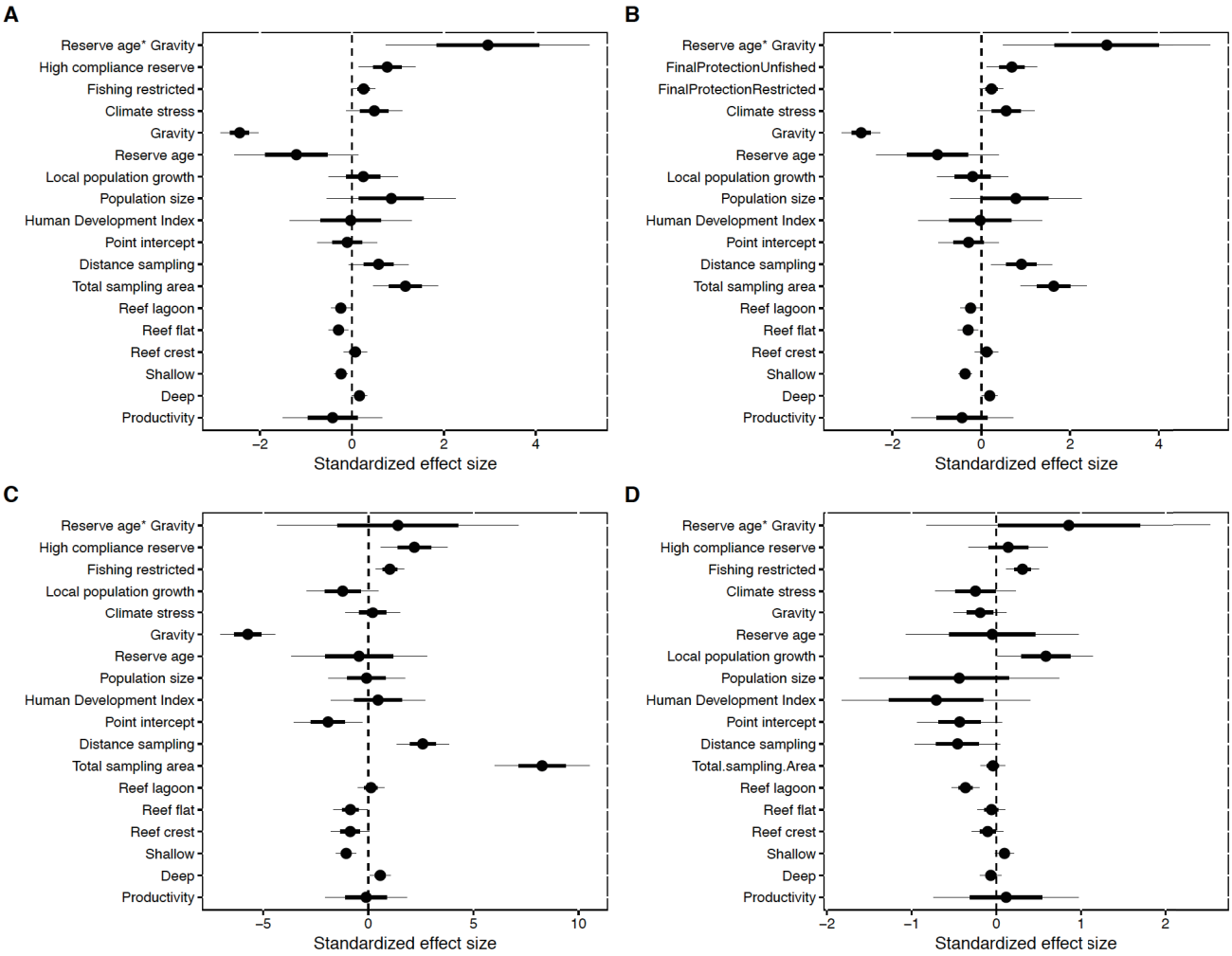


Figure VII | Model-predicted relationships for targeted-only fish biomass excluding top predators. Blue = marine reserves, red=openly fished, green= restricted fishing. Shaded areas represent 95% confidence intervals.

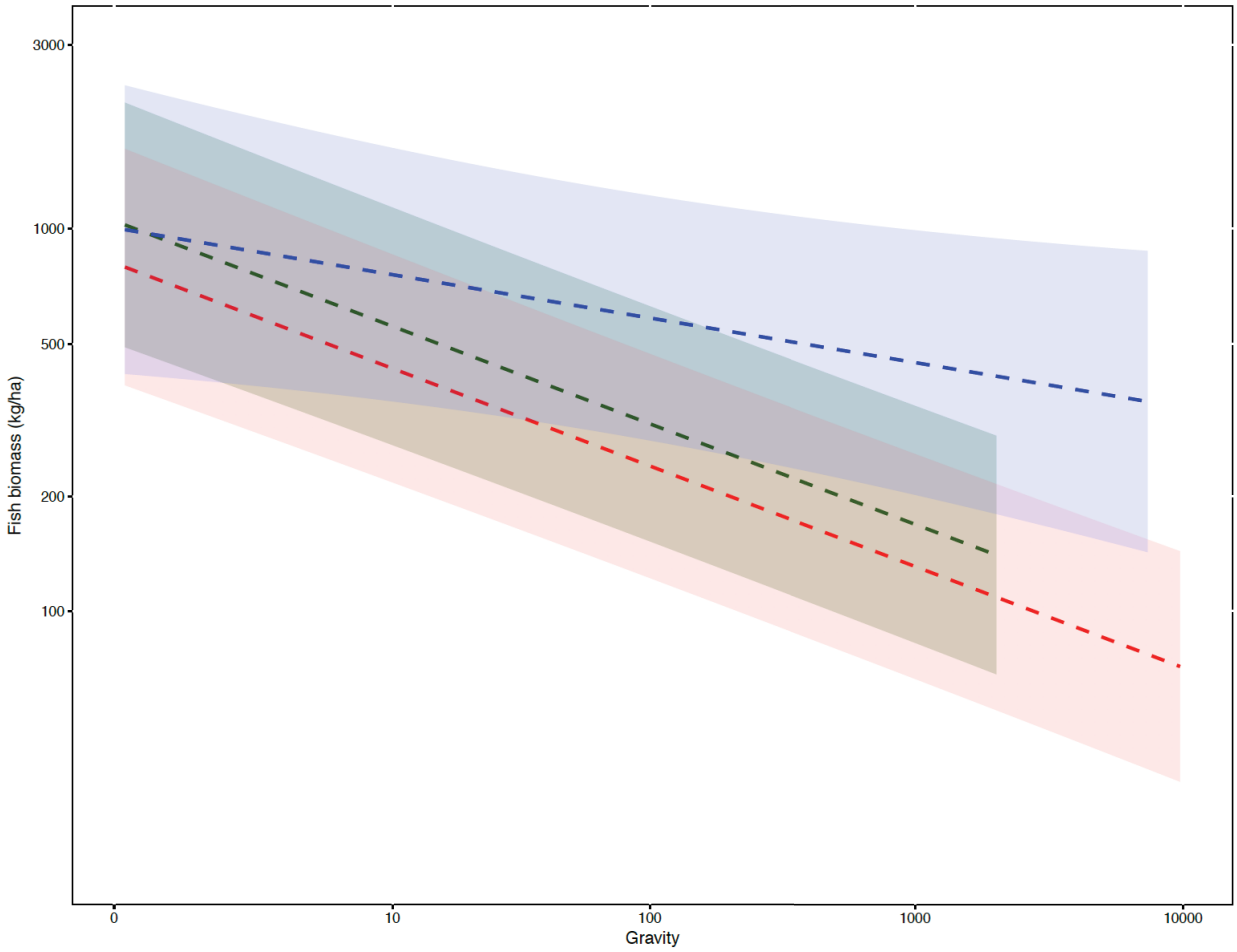
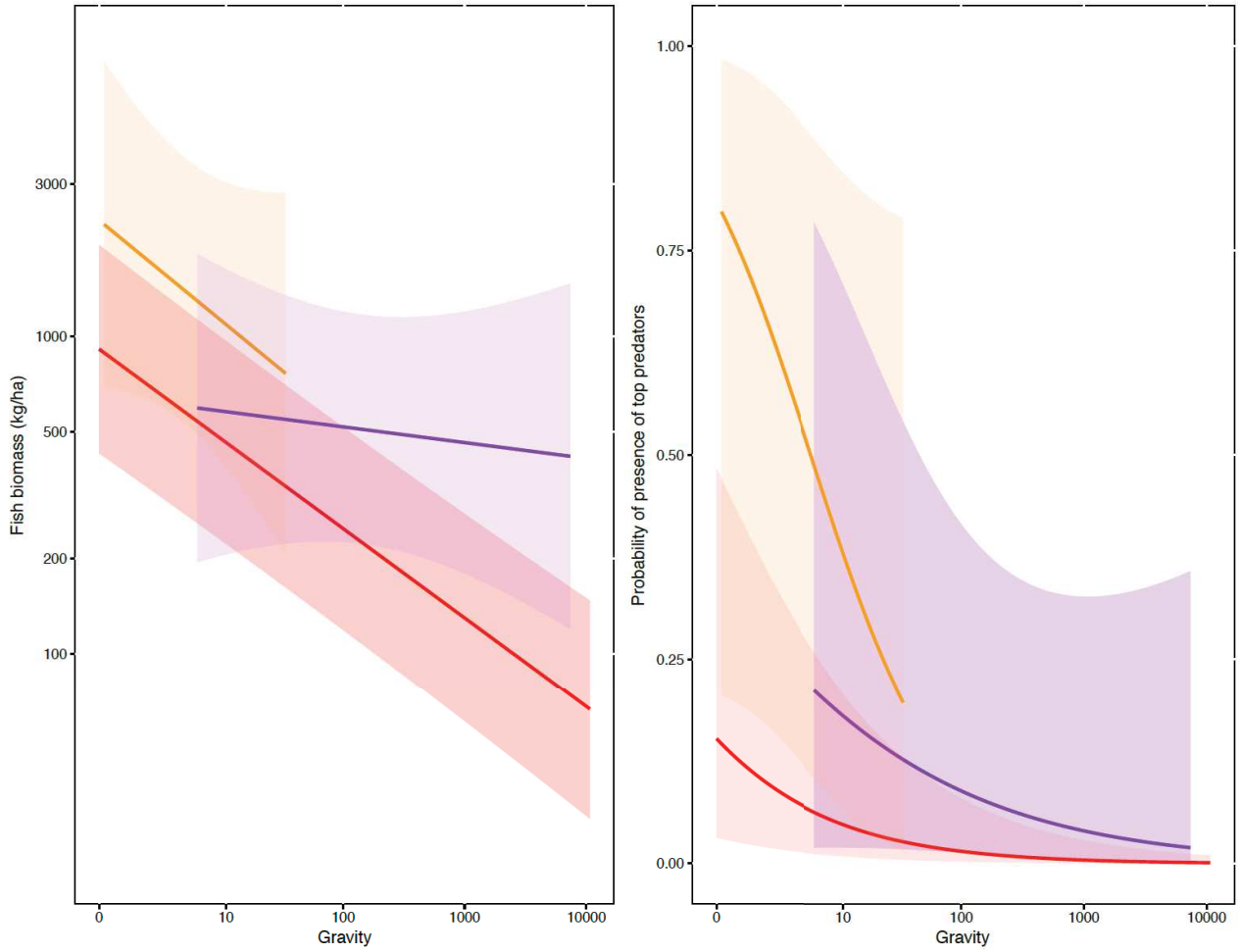


Figure VIII | Model-predicted trends in fish biomass (left) and probability in encountering top predators (right) with reserves broken into small (<28km^2, purple) and large (orange). Shaded areas represent 95% confidence intervals.



9.2. Supplementary Material – Chapter 6

Community-wide scan identifies fish species associated with coral reef services across the Indo-Pacific

Additional information

Coral reef services

We considered fish biomass and live coral cover as two proxies for coral reef services as support, among many others, food security, shoreline protection and recreational value (Burke *et al.* 2011; Kittinger *et al.* 2012; Harris *et al.* 2018; McClanahan Timothy 2018). Fish biomass and coral cover are already monitored at the global scale using visual censuses as well as underwater video surveys (e.g. Reef Life Survey, Catlin Sea Survey) and are highly sensitive to local human activities (e.g. fishing, habitat destruction, pollution) and global climate change (Hughes *et al.* 2018) and thus, can be considered as key variables for the health and productivity of coral reefs (Bozec *et al.* 2016; Cinner *et al.* 2016; Hughes *et al.* 2017b).

Fish Biomass

Reef fish biomass estimates were based on instantaneous visual counts from 4,694 surveys collected from 1,824 reefs (Fig. S1). Surveys were carried out using two census methods (belt-transects or distance sampling) and were conducted between 2004 and 2013. On average 2.4 transects (sd=1.32; range: 1-10) were performed on each reef. Within each surveyed area, reef associated fishes were identified to species level, abundance was counted, and total length (TL) estimated.

To make estimates of biomass from these transect-level data comparable among studies, we:

i) Considered only Indo-Pacific reefs and retained families that were consistently included in surveys and were above a minimum size cut-off. Thus, we only retained counts of non-cryptic reef fish species >10cm in total length, that are reef-associated (30 families, 748 species) (Table S1). We did not include sharks as they were often excluded from visual surveys. We calculated total biomass of fishes on each reef using published species-level length-weight relationship parameters or those available on FishBase [39]. When length-weight relationship parameters were not available for a species, we used the parameters for a closely related species or genus.

ii) Depth and habitat were included as environmental variables in the model.

iii) Reef fish biomass estimates were based on instantaneous visual counts using belt-transects or distance sampling. Because several biases were associated with these two methods (Usseglio 2015) and the total area of transects changed between locations, we included census method and sampling area as covariates in the model.

Biomass values were calculated at the reef scale and showed a high variability (mean=1,055 $kg.ha^{-1}$; range: 2-25,910 $kg.ha^{-1}$).

Live coral cover

Percent cover of live coral was based on 1,715 point-intercept transects or quadrats collected from 741 reefs (Fig. S2). All surveys were conducted between 2008 and 2013. On average 2.3 transects (sd=1.03; range: 1-4) were performed on each reef. To make estimates of coral cover from these transect-level data comparable among studies, we included depth, habitat and census method (which already different in the sampling area) as covariates in the model (see details in Supplementary Material).

Coral cover values were calculated at the reef scale and showed a high variability (mean=27%; range: 3-94%).

Socioeconomic and environmental variables

The variables included in the models were environmental: 1) oceanic productivity, 2) habitat type, 3) depth and socioeconomic: 4) management 5) local human population growth rate, 6) gravity of local population, 7) gravity of markets, 8) levels of human development (Human Development Index), 9) human population size, 10) levels of tourism, 11) degree of voice and accountability of citizens, and 12) reef fish landings (tons)/km^2 of reef. Full definitions and details are provided in Chapter 2.

Analyses

We used linear mixed models to analyze biomass and live coral cover after checking that both log-transformed variables were normally distributed. For both models, we set site, regional locations and nation/state as random effects to account for the hierarchical nature of the data (i.e. reefs nested in sites, sites nested in regional locations and in nations/states). All

continuous covariates were standardized for the analysis and their corresponding Akaike weights were computed to assess their importance (Table S2 & S3).

To check the fit of the linear mixed model, we checked for the representation of actual versus predicted values and we calculated the accuracy of the two models which came to 88% for biomass and 83% for coral cover. To examine homoscedasticity, we checked residuals against fitted values. We checked that the residuals were normally distributed. All analyses were undertaken using R (3.3) statistical packages.

Functional traits to describe fish species.

The 381 candidate fish species were functionally described using six traits extracted from (Mouillot *et al.* 2014): *(1)* size, coded using 3 ordered categories: 10-30cm, 30.1-50cm, >50cm; *(2)* mobility, coded using 3 ordered categories: sedentary, mobile within a reef and mobile between reefs; *(3)* period of activity, coded using 3 ordered categories: diurnal, both diurnal and nocturnal, and nocturnal; *(4)* schooling, coded using 5 ordered categories: solitary, pairing, or living in small (3-20 individuals), medium (20-50 individuals) or large groups (>50 groups); *(5)* vertical position in the water column, coded using 3 ordered categories: benthic, bentho-pelagic and pelagic; *(6)* diet, coded using 7 trophic categories: herbivorous-detritivorous, macro-algal browser, invertivorous targeting sessile invertebrates, invertivorous targeting mobile invertebrates, planktivorous, piscivorous, and omnivorous, i.e. fish for which both plant and animal material are important in their diet. Since all traits were categorical, species with identical traits were grouped into functional entities.

Defining presence of species based on abundance threshold.

The community-wide scan (CWS) approach can be adapted for a wide range of taxa from all the ecosystems. The way candidates are tested can be modulated while respecting independence between predicted and explanatory variables (binary variables are a convenient way to test the effect of candidates). More specifically, presence of terrestrial or marine taxa can be determined using any convenient abundance threshold such as a minimum number of individuals, cover rate or biomass.

As an application, we tested two procedures to define presence of reef fish species based on a biomass threshold and compared key species found with those two procedures:

(i) the relative intraspecific biomass which defines presence of a species in a community as soon as its biomass reaches upper percentiles of the distribution of biomass of this species over all studied communities. We used the 99^{th} and 95^{th} percentiles (the top 1 and 5%) of the biomass distribution over reef sites as thresholds. This approach is particularly relevant for species widely distributed with normal distribution of biomass while it may not be used for species infrequently encountered or with a skewed biomass distribution.

(ii) the relative community biomass which defines presence as soon as the focal species reach a defined minimum percentage of the total biomass of the fish community. Hence, this approach is not affected by biomass distribution among sites. As two thresholds, we tested a contribution of species to total biomass in excess of 1 and 5%, respectively.

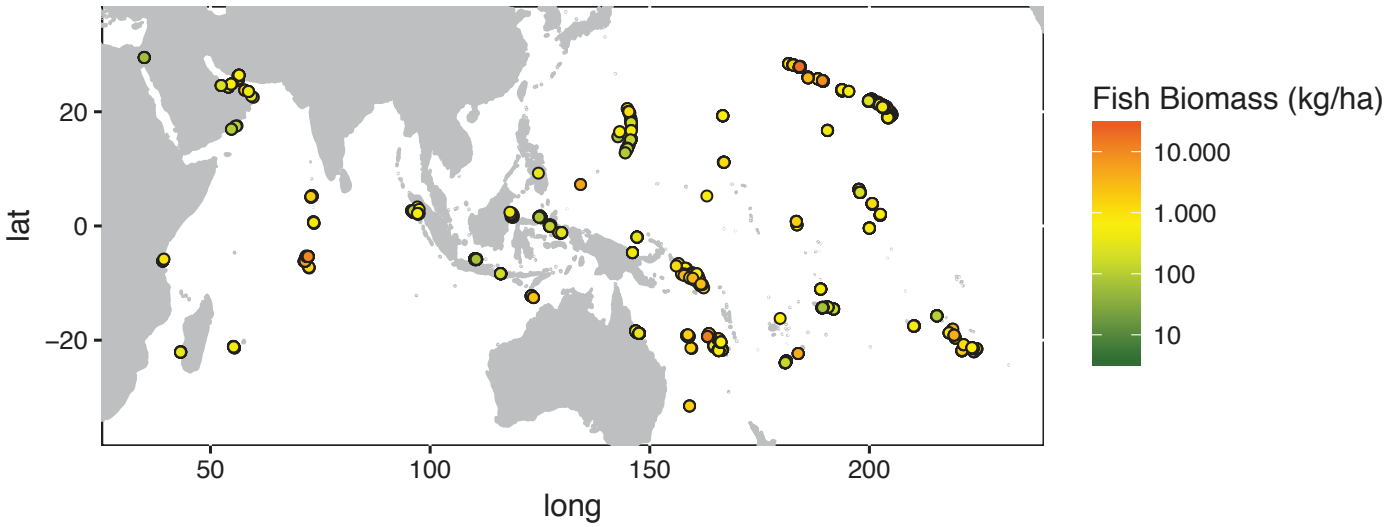


Figure S1 | Map of the reef fish biomass observed in 1,824 reefs located in the Indo-Pacific.

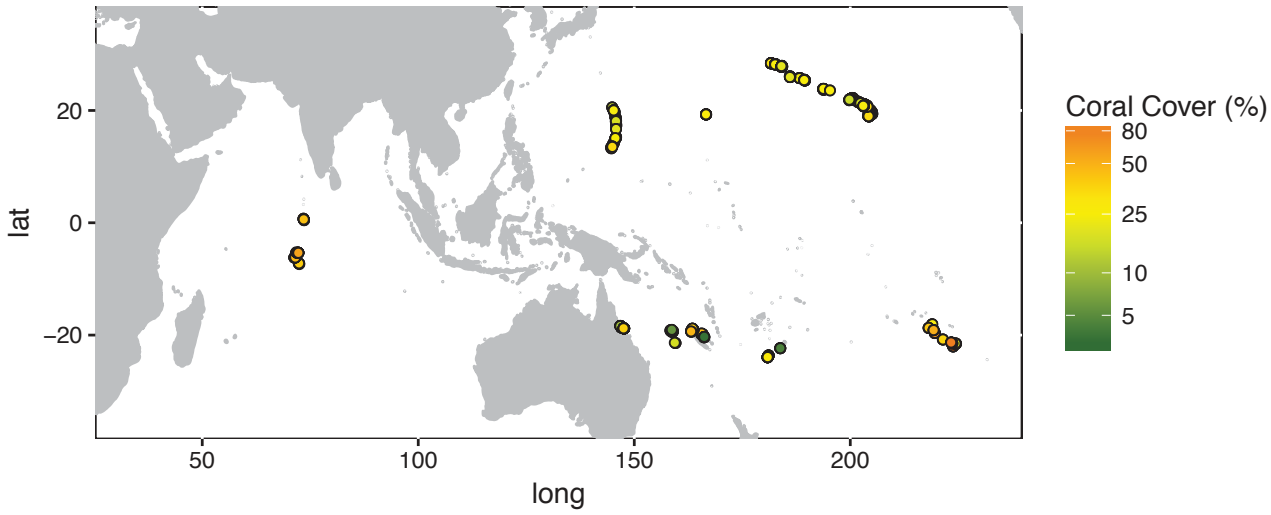


Figure S2 | Map of the live coral cover observed in 741 reefs located in the Indo-Pacific. Information on coral cover was not available for all sites at which reef fish biomass was surveyed.

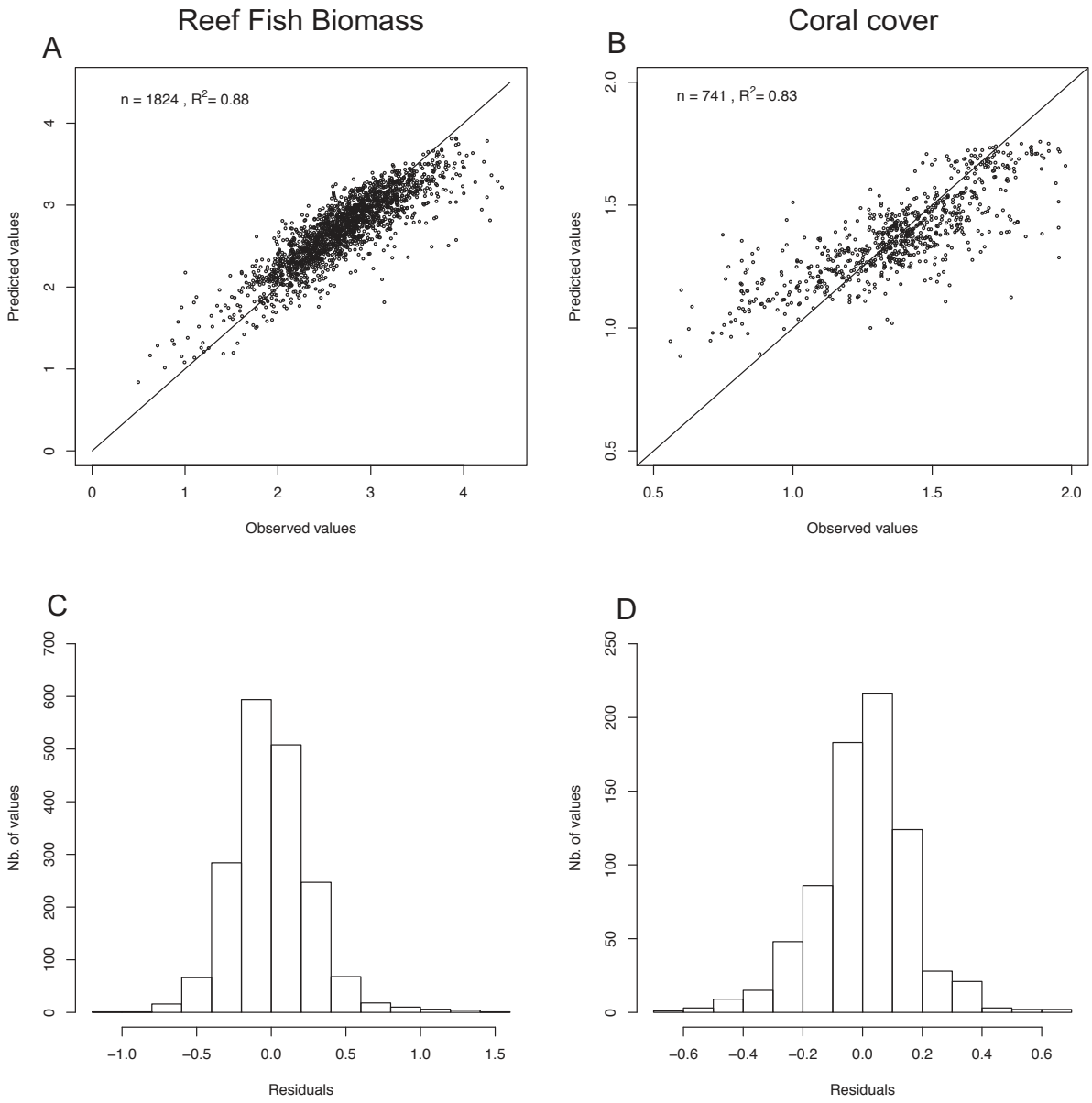


Figure S3 | Accuracy and residuals of the two initial models (fish biomass and coral cover). The accuracy of each model is assessed using the Pearson correlation between predicted and observed values which came to 88% for biomass (A) and 83% for coral cover (B). We checked that residuals of the initial model of fish biomass (C) and coral cover (D) were normally distributed.

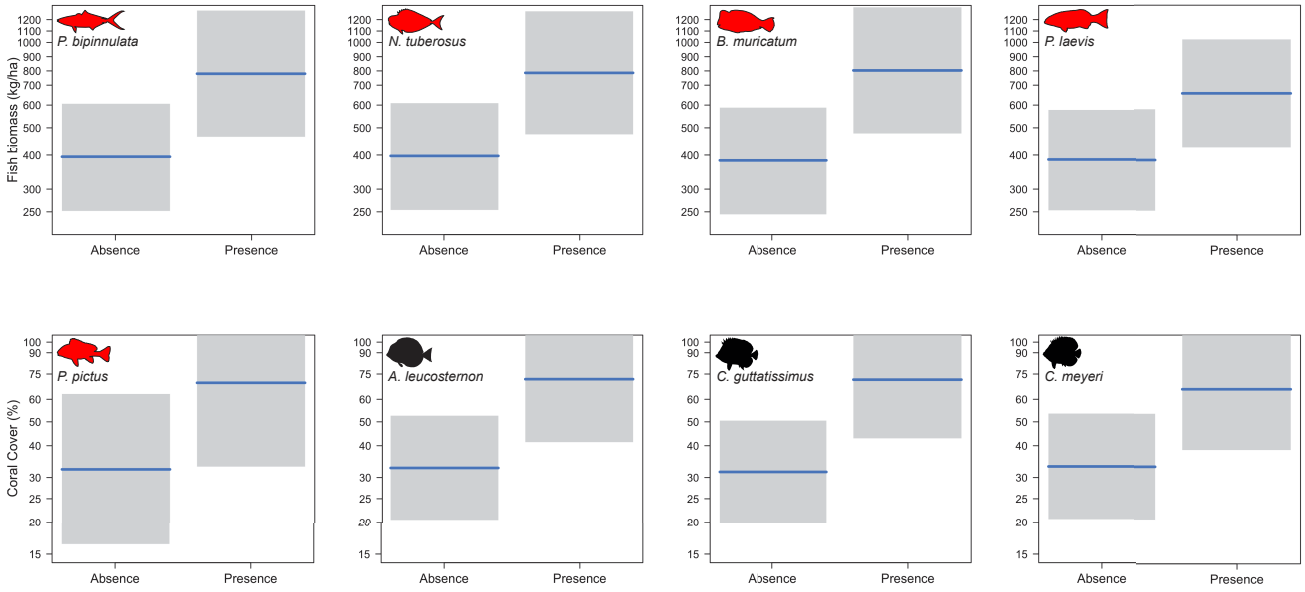


Figure S4 | Net effect of the 4 key fish species linked to the highest levels of fish biomass (top) and live coral cover (bottom). We extracted the pure effects of all the key species and determined which were related to the highest levels of biomass and coral cover respectively, using a partial plot from each LMM while the other variables are held constant.

Table S1 | List of coral reef fish families included in the study and their common name. Families included are: Acanthuridae, Balistidae, Caesionidae, Carangidae, Chaetodontidae, Cirrhitidae, Diodontidae, Ephippidae, Haemulidae, Holocentridae, Kyphosidae, Labridae, Lethrinidae, Lutjanidae, Monacanthidae, Mullidae, Nemipteridae, Pempheridae, Pinguipedidae, Pomacanthidae, Priacanthidae, Pseudochromidae, Scombridae, Serranidae, Siganidae, Sparidae, Sphyraenidae, Synodontidae, Tetraodontidae, Zanclidae.

Fish family	Common family name	Fish family	Common family name
Acanthuridae	Surgeonfishes	Mullidae	Goatfishes
Balistidae	Triggerfishes	Nemipteridae	Coral Breams
Caesionidae	Fusiliers	Pempheridae	Sweepers
Carangidae	Jacks/Trevallies	Pinguipedidae	Sandperches
Chaetodontidae	Butterflyfishes	Pomacanthidae	Angelfishes
Cirrhitidae	Hawkfishes	Priacanthidae	Bigeyes
Diodontidae	Porcupinefishes	Pseudochromidae	Dottybacks
Ephippidae	Batfishes	Scombridae	Mackerels and Tunas
Haemulidae	Sweetlips	Serranidae	Groupers
Holocentridae	Squirrelfishes, Soldierfishes	Siganidae	Rabbitfishes
Kyphosidae	Drummers	Sparidae	Porgies
Labridae	Wrasses and Parrotfishes	Sphyraenidae	Barracuda
Lethrinidae	Emperors	Synodontidae	Lizardfishes
Lutjanidae	Snappers	Tetradontidae	Puffers
Monacanthidae	Filefishes	Zanclidae	Moorish Idol

Table S2 | Relative importance of variables of the fish biomass initial model. The relative importance of each variable is based on the sum of Akaike weights of all the possible models (i.e. all the possible combination of variables) in which the variable is present.

Relative variable importance	
Biodiversity	
Species richness	1
Environmental variables	
Depth	1
Oceanic productivity	1
Habitat	0.94
Socio-economic variables	
Population size	1
Management	1
Tourism	1
HDI	0.72
Reef fish landings	0.71
Gravity of markets	0.66
Voice accountability	0.62
Local population growth	0.39
Gravity of human settlement	0.28
Method	
Sampling area	1
Census method	1

Table S3 | Relative importance of variables of the coral cover initial model. The relative importance of each variable is based on the sum of Akaike weights of all the possible models (i.e. all the possible combination of variables) in which the variable is present.

Relative variable importance	
Biodiversity	
Species richness	1
Environmental variables	
Oceanic productivity	1
Habitat	1
Depth	0.56
Socio-economic variables	
Population size	1
Tourism	1
Local population growth	0.85
HDI	0.74
Gravity of markets	0.48
Reef fish landings	0.44
Management	0.41
Voice accountability	0.37
Gravity of human settlement	0.27
Method	
Census method	1

Table S4 | Details of key fish species for reef fish biomass. AIC of the initial model M_0 (environment, socio-economics and species richness) provides reference Akaike Information Criterion (AIC M_0). Presence of each species has been added to M_0 as binary variable using occurrence (i.e. presence of at least 1 individual). For each species, number of occurrences, coefficient in the model (Coeff.) and AIC of the model accounting for the species (AIC M1) are reported. Comparisons with reference AIC (AIC M0) are also provided (ΔAIC).

Fish species	Nb of occ.	Coeff.	AIC M1	ΔAIC	AIC M0
Caranx ignobilis	98	0.29	1166.6	54.6	1221.2
Lutjanus bohar	448	0.18	1171.4	49.8	1221.2
Plectropomus laevis	129	0.23	1185.7	35.5	1221.2
Aprion virescens	169	0.18	1189.7	31.5	1221.2
Macolor niger	157	0.2	1189.9	31.3	1221.2
Chlorurus microrhinos	314	0.15	1190	31.2	1221.2
Hipposcarus longiceps	163	0.19	1193	28.2	1221.2
Naso tuberosus	51	0.3	1195.9	25.3	1221.2
Lethrinus atkinsoni	74	0.28	1198.3	22.9	1221.2
Bolbometopon muricatum	38	0.32	1199.9	21.3	1221.2
Cheilinus undulatus	134	0.17	1200	21.2	1221.2
Elagatis bipinnulata	32	0.3	1201.5	19.7	1221.2
Naso hexacanthus	113	0.16	1203.1	18.1	1221.2
Caranx melampygus	286	0.11	1207.1	14.1	1221.2
Scarus altipinnis	181	0.13	1208.5	12.7	1221.2
Naso caesius	31	0.27	1209.2	12	1221.2
Parupeneus crassilabris	55	0.2	1212.3	8.9	1221.2
Naso unicornis	380	0.09	1212.3	8.9	1221.2
Lethrinus olivaceus	79	0.16	1212.8	8.4	1221.2
Macolor macularis	107	0.16	1214.7	6.5	1221.2
Lutjanus gibbus	191	0.12	1215	6.2	1221.2
Gymnosarda unicolor	23	0.24	1215.1	6.1	1221.2
Acanthurus albipectoralis	26	0.23	1215.7	5.5	1221.2
Acanthurus lineatus	282	0.09	1215.8	5.4	1221.2
Scarus rubroviolaceus	367	0.08	1216.6	4.6	1221.2
Acanthurus dussumieri	168	0.1	1217	4.2	1221.2

Table S5 | Details of key fish species for live coral cover. AIC of the initial model M_0 (environment, socio-economics and species richness) provides reference Akaike Information Criterion (AIC M_0). Presence of each species has been added to M_0 as binary variable using occurrence (i.e. presence of at least 1 individual). For each species, number of occurrences, coefficient in the model (Coeff.) and AIC of the model accounting for the species (AIC M1) are reported. Comparisons with reference AIC (AIC M0) are also provided (ΔAIC).

Fish species	Nb of occ.	Coeff.	AIC M1	ΔAIC	AIC M0
Chaetodon trifascialis	132	0.22	-106.6	66.4	-40.2
Hemigymnus fasciatus	166	0.17	-82.1	41.9	-40.2
Bodianus loxozonus	35	0.27	-69.1	28.9	-40.2
Zebrasoma scopas	101	0.16	-66.1	25.9	-40.2
Chaetodon guttatissimus	40	0.35	-60.5	20.3	-40.2
Scarus frenatus	158	0.15	-59.1	18.9	-40.2
Chaetodon baronessa	65	0.22	-58.3	18.1	-40.2
Plectorhinchus picus	10	0.33	-55.1	14.9	-40.2
Oxycheilinus unifasciatus	147	0.1	-54.1	13.9	-40.2
Chaetodon meyeri	40	0.29	-54	13.8	-40.2
Chlorurus strongylocephalus	32	0.26	-53.9	13.7	-40.2
Lutjanus gibbus	55	0.16	-53.6	13.4	-40.2
Chaetodon unimaculatus	48	0.16	-52.8	12.6	-40.2
Chaetodon pelewensis	70	0.16	-52.7	12.5	-40.2
Acanthurus leucosternon	44	0.33	-52.6	12.4	-40.2
Ctenochaetus truncatus	36	0.27	-50.6	10.4	-40.2
Chaetodon reticulatus	86	0.18	-50.5	10.3	-40.2
Acanthurus albipectoralis	24	0.2	-49.9	9.7	-40.2
Labrichthys unilineatus	59	0.16	-49.4	9.2	-40.2
Lutjanus bohar	199	0.11	-48.9	8.7	-40.2
Bodianus axillaris	118	0.1	-47.9	7.7	-40.2
Acanthurus thompsoni	88	0.11	-47.3	7.1	-40.2
Scarus chameleon	74	0.11	-47	6.8	-40.2
Paracirrhites nisus	24	0.22	-46.5	6.3	-40.2
Scarus tricolor	31	0.2	-46.2	6	-40.2
Cephalopholis urodeta	145	0.13	-45.2	5	-40.2
Scarus globiceps	76	0.12	-44.7	4.5	-40.2
Cantherhines dumerilii	52	0.11	-44.7	4.5	-40.2

Table S6 | Functional traits of key fish species for reef fish biomass and live coral cover. 23, 25 and 3 fish species are significantly related to biomass (BM), live coral cover (CC) or both (BOTH) of those proxies of coral reef services respectively. Each species is described using six traits: *(1)* size, coded using 3 ordered categories: 10-30cm, 30.1-50cm, >50cm; *(2)* mobility, coded using 3 ordered categories: sedentary, mobile within a reef and mobile between reefs; *(3)* period of activity, coded using 3 ordered categories: diurnal, both diurnal and nocturnal, and nocturnal; *(4)* schooling, coded using 5 ordered categories: solitary, pairing, or living in small (3-20 individuals), medium (20-50 individuals) or large groups (>50 groups); *(5)* vertical position in the water column, coded using 3 ordered categories: benthic, bentho-pelagic and pelagic; *(6)* diet, coded using 7 trophic categories: herbivorous-detritivorous (HD), macro-algal herbivorous (HM), invertivorous targeting sessile invertebrates (IS), invertivorous targeting mobile invertebrates (IM), planktivorous (PK), piscivorous (FC), and omnivorous (OM), i.e. fish for which both vegetal and animal material are important in their diet. Several species can have the same functional traits (trait combinations with the same Funct. Entity ID) and thus, represent the same functional entity. In total, 51 key fish species are described, which represent 35 different functional entities with 6 entities common to both fish biomass and coral cover (highlighted in grey).

ES proxy	Fish Species	Size Class	Mobility	Activity	Schooling	Position	Diet	Funct. Entity ID
BM	*Acanthurus dussumieri*	10-30cm	Mob	Day	SmallG	Bottom	HD	6
BM	*Acanthurus lineatus*	10-30cm	Sed	Day	Sol	Bottom	HD	15
BM	*Aprion virescens*	50-153cm	VMob	Both	SmallG	Low	FC	33
BM	*Bolbometopon muricatum*	50-153cm	VMob	Day	MedG	Bottom	IS	35
BM	*Caranx ignobilis*	50-153cm	VMob	Both	Sol	High	FC	34
BM	*Caranx melampygus*	30-50cm	VMob	Both	SmallG	High	FC	25
BM	*Cheilinus undulatus*	50-153cm	Mob	Day	Sol	Bottom	IM	31
BM	*Chlorurus microrhinos*	30-50cm	Mob	Day	SmallG	Bottom	OM	23
BM	*Elagatis bipinnulata*	50-153cm	VMob	Both	MedG	High	FC	32
BM	*Gymnosarda unicolor*	50-153cm	VMob	Both	Sol	High	FC	34
BM	*Hipposcarus longiceps*	10-30cm	Mob	Day	MedG	Bottom	OM	3
BM	*Lethrinus atkinsoni*	10-30cm	VMob	Night	MedG	Bottom	IM	20
BM	*Lethrinus olivaceus*	30-50cm	VMob	Both	Sol	Bottom	FC	26
BM	*Macolor macularis*	10-30cm	Mob	Both	MedG	High	PK	1
BM	*Macolor niger*	30-50cm	Mob	Both	MedG	High	PK	22
BM	*Naso caesius*	30-50cm	VMob	Day	MedG	High	PK	29
BM	*Naso hexacanthus*	30-50cm	VMob	Day	LargeG	High	PK	27
BM	*Naso tuberosus*	30-50cm	VMob	Day	MedG	High	HM	28
BM	*Naso unicornis*	10-30cm	Mob	Day	SmallG	Bottom	HM	7
BM	*Parupeneus crassilabris*	10-30cm	Mob	Day	SmallG	Bottom	IM	8
BM	*Plectropomus laevis*	50-153cm	Mob	Day	Sol	Bottom	FC	30
BM	*Scarus altipinnis*	10-30cm	Mob	Day	LargeG	Bottom	OM	2
BM	*Scarus rubroviolaceus*	30-50cm	Mob	Day	SmallG	Bottom	OM	23
CC	*Acanthurus leucosternon*	10-30cm	VMob	Day	LargeG	Bottom	HD	18
CC	*Acanthurus thompsoni*	10-30cm	VMob	Day	MedG	Low	PK	19
CC	*Bodianus axillaris*	10-30cm	Mob	Day	Sol	Bottom	IM	9
CC	*Bodianus loxozonus*	10-30cm	Mob	Day	Sol	Bottom	IM	9
CC	*Cantherhines dumerilii*	10-30cm	Mob	Day	Pair	Bottom	IS	4
CC	*Cephalopholis urodeta*	10-30cm	Sed	Both	Sol	Bottom	FC	11
CC	*Chaetodon baronessa*	10-30cm	Sed	Day	Pair	Bottom	IS	12
CC	*Chaetodon guttatissimus*	10-30cm	Sed	Day	Pair	Bottom	IS	12
CC	*Chaetodon meyeri*	10-30cm	Sed	Day	Pair	Bottom	IS	12
CC	*Chaetodon pelewensis*	10-30cm	Sed	Day	Pair	Bottom	IS	12
CC	*Chaetodon reticulatus*	10-30cm	Sed	Day	Pair	Low	IS	13
CC	*Chaetodon trifascialis*	10-30cm	Sed	Day	Pair	Bottom	IS	12
CC	*Chaetodon unimaculatus*	10-30cm	Sed	Day	Pair	Bottom	IS	12
CC	*Chlorurus strongylocephalus*	30-50cm	Mob	Day	SmallG	Bottom	OM	23
CC	*Ctenochaetus truncatus*	10-30cm	Sed	Day	SmallG	Bottom	OM	14
CC	*Hemigymnus fasciatus*	10-30cm	Mob	Day	Sol	Bottom	IM	9
CC	*Labrichthys unilineatus*	10-30cm	Sed	Day	Sol	Bottom	IS	17
CC	*Oxycheilinus unifasciatus*	10-30cm	Mob	Day	SmallG	Bottom	FC	5
CC	*Paracirrhites nisus*	10-30cm	Sed	Day	Sol	Bottom	IM	16
CC	*Plectorhinchus picus*	50-153cm	Mob	Day	Sol	Bottom	IM	31
CC	*Scarus chameleon*	10-30cm	Mob	Day	Sol	Bottom	OM	10
CC	*Scarus frenatus*	10-30cm	Mob	Day	Sol	Bottom	OM	10
CC	*Scarus globiceps*	10-30cm	Mob	Day	Sol	Bottom	OM	10
CC	*Scarus tricolor*	10-30cm	Mob	Day	Sol	Bottom	OM	10
CC	*Zebrasoma scopas*	10-30cm	Mob	Day	SmallG	Bottom	HD	6
BOTH	*Acanthurus albipectoralis*	10-30cm	VMob	Day	MedG	Low	PK	19
BOTH	*Lutjanus bohar*	30-50cm	Mob	Night	MedG	Low	FC	24
BOTH	*Lutjanus gibbus*	30-50cm	Mob	Both	MedG	Bottom	IM	21

Table S7 | Comparative results of potential key species for fish biomass using relative intra-community (left) and intra-specific (right) biomass to define presence (threshold defined as 1%). AIC of the initial model M_0 provides reference Akaike Information Criterion (AIC M0). Presence of each species has been added to M_0 as binary variable using 2 criteria: *(i)* contribution of species to total biomass higher than 1% and *(ii)* the 99th percentile of the biomass distribution of each species. For each species, number of raw occurrences, number of occurrences meeting the biomass threshold, and AIC of the model accounting for the species (AIC M1) are reported. For clarity, only key species are presented and those that are significantly related to fish biomass under the 2 approaches are highlighted in grey. One species had an AIC lower than M0 but did not exceed the performance criterion (ΔAIC > 4) to be considered as key species (underlined).

INITIAL MODEL (M0): AIC = 1221.2			
INTRA-COMMUNITY			
Fish species	Nb of occ.	Nb of occ. (1%)	AIC M1
Caranx ignobilis	98	96	1166.6
Lutjanus bohar	448	332	1185.0
Plectropomus laevis	129	116	1199.3
Chlorurus microrhinos	314	285	1202.3
Bolbometopon muricatum	38	35	1206.1
Naso tuberosus	51	46	1206.6
Macolor niger	157	100	1209.8
Aprion virescens	169	151	1210.9
Hipposcarus longiceps	163	107	1211.5
Naso hexacanthus	113	86	1212.6
Lethrinus atkinsoni	74	58	1213.3
Elagatis bipinnulata	32	28	1214.6
Naso caesius	31	22	1216.7

INTRA-SPECIFIC			
Fish species	Nb of occ.	Nb of occ. (1%)	AIC M1
Caranx ignobilis	98	19	1157.1
Lutjanus gibbus	191	19	1177.5
Macolor niger	157	19	1177.8
Naso hexacanthus	113	19	1183.8
Lethrinus atkinsoni	74	19	1188.2
Bolbometopon muricatum	38	20	1188.4
Hipposcarus longiceps	163	19	1191.6
Scarus altipinnis	181	19	1192.8
Chlorurus microrhinos	314	20	1194
Lutjanus kasmira	202	19	1196
Lutjanus bohar	448	19	1197.3
Plectropomus laevis	129	19	1202.2
Naso tuberosus	51	20	1202.7
Acanthurus blochii	225	19	1202.9
Siganus punctatus	50	19	1203.6
Naso unicornis	380	19	1203.7
Naso caesius	31	19	1204.1
Ctenochaetus striatus	954	19	1205.1
Caranx melampygus	286	19	1205.3
Chlorurus bleekeri	210	19	1206.1
Macolor macularis	107	19	1206.5
Caesio cuning	110	19	1206.7
Chlorurus frontalis	75	19	1206.9
Monotaxis grandoculis	488	19	1206.9
Scarus ghobban	210	19	1208.7
Pterocaesio tile	181	19	1208.9
Acanthurus lineatus	282	19	1208.9
Plectorhinchus orientalis	33	19	1209.4
Elagatis bipinnulata	32	19	1209.9
Naso vlamingii	51	19	1211
Scolopsis ghanam	35	19	1211.2
Lutjanus fulviflamma	107	20	1212.2
Acanthurus xanthopterus	57	20	1212.2
Cheilinus undulatus	134	19	1212.4
Naso brevirostris	155	19	1213.6
Naso lituratus	624	19	1213.6
Parupeneus barberinus	55	20	1213.8
Lethrinus olivaceus	79	23	1213.9
Caesio teres	94	19	1214
Balistoides viridescens	82	19	1214.6
Cetoscarus bicolor	144	19	1214.6
Pterocaesio marri	28	19	1214.9
Scarus rubroviolaceus	367	19	1215.2
Kyphosus vaigiensis	52	19	1215.4
Scarus rivulatus	176	19	1215.5
Epibulus insidiator	428	19	1215.7
Cetoscarus ocellatus	51	19	1215.7
Scarus frenatus	392	19	1215.9
Caesio caerulaurea	55	19	1215.9
Epinephelus polyphekadion	57	21	1216.5
Chaetodon ulietensis	139	19	1216.8
Chlorurus sordidus	1049	19	1216.9
Lutjanus monostigma	84	19	1217
2 < ΔAIC < 4			
Aprion virescens	169	20	1217.9

Table S8 | Comparative results of potential key species for fish biomass using relative intra-community (left) and intra-specific (right) biomass to define presence (threshold defined as 5%). AIC of the initial model M_0 provides reference Akaike Information Criterion (AIC M0). Presence of each species has been added to M_0 as binary variable using 2 criteria: *(i)* contribution of species to total biomass higher than 5% and *(ii)* the 95th percentile of the biomass distribution of each species. For each species, number of raw occurrences, number of occurrences meeting the threshold, and AIC of the model accounting for the species (AIC M1) are reported. For clarity, only key species are presented and those that are significantly related to fish biomass under the 2 approaches are highlighted in grey. Some species did not reach the minimal occurrence required and thus could not be tested using the intra-specific approach (asterisk).

INITIAL MODEL (M0): AIC = 1221.2							
INTRA-COMMUNITY				**INTRA-SPECIFIC**			
Fish species	Nb of occ.	Nb of occ. (5%)	AIC M1	Fish species	Nb of occ.	Nb of occ. (5%)	AIC M1
Caranx ignobilis	98	81	1169.2	*Lutjanus bohar*	448	92	1116.8
Lutjanus bohar	448	238	1186.2	*Chlorurus microrhinos*	314	92	1154.1
Macolor niger	157	48	1207.1	*Caranx ignobilis*	98	92	1156.2
*Platax teira**	22	8	1207.6	*Macolor niger*	157	92	1164.1
*Lethrinus atkinsoni**	74	38	1209.8	*Hipposcarus longiceps*	163	92	1167.3
Plectropomus laevis	129	86	1210.1	*Monotaxis grandoculis*	488	92	1171.2
Naso hexacanthus	113	58	1212.7	*Naso unicornis*	380	92	1183.8
*Bolbometopon muricatum**	38	23	1214.5	*Acanthurus lineatus*	282	92	1186.4
Chlorurus microrhinos	314	167	1215.1	*Plectropomus laevis*	129	92	1186.9
Lutjanus gibbus	191	72	1215.5	*Caranx melampygus*	286	92	1191.8
*Chaetodon flavirostris**	58	3	1216.4	*Ctenochaetus striatus*	954	92	1193.9
*Elagatis bipinnulata**	32	18	1216.9	*Scarus altipinnis*	181	97	1194.7
Hipposcarus longiceps	163	41	1217.2	*Lutjanus gibbus*	191	92	1198.2
				Naso hexacanthus	113	92	1200.1
				Aprion virescens	169	92	1201.1
				Scarus rubroviolaceus	367	95	1204.9
				Cheilinus undulatus	134	92	1205.8
				Pterocaesio tile	181	92	1206.8
				Lutjanus kasmira	202	92	1207.8
				Acanthurus blochii	225	92	1208.5
				Cetoscarus bicolor	144	92	1210.7
				Macolor macularis	107	96	1210.9
				Scarus frenatus	392	92	1211.1
				Zanclus cornutus	532	92	1212.2
				Chlorurus sordidus	1049	92	1212.2
				Heniochus chrysostomus	143	97	1213.6
				Naso lituratus	624	92	1213.8
				Zebrasoma veliferum	295	93	1213.9
				Kyphosus sp.	145	95	1215.2
				Cephalopholis argus	570	92	1215.3
				Acanthurus dussumieri	168	92	1215.3
				Variola louti	139	92	1216.2
				Pomacanthus imperator	137	95	1216.5
				Scarus niger	447	92	1216.9
				Naso brevirostris	155	94	1217.1
				Nb occ. > 90 is required to be tested			
				*Platax teira**	22	NA	NA
				*Lethrinus atkinsoni**	74	NA	NA
				*Bolbometopon muricatum**	38	NA	NA
				*Chaetodon flavirostris**	58	NA	NA
				*Elagatis bipinnulata**	32	NA	NA

Table S9 | Comparative results of potential key species for coral cover using relative intra-community (left) and intra-specific (right) biomass to define presence (threshold defined as 1%). AIC of the initial model M_0 provides reference Akaike Information Criterion (AIC M0). Presence of each species has been added to M_0 as binary variable using 2 criteria: *(i)* contribution of species to total biomass higher than 1% and *(ii)* the 99th percentile of the biomass distribution of each species. For each species, number of raw occurrences, number of occurrences meeting the threshold, and AIC of the model accounting for the species (AIC M1) are reported. For clarity, only key species are presented and those that are significantly related to coral cover under the 2 approaches are highlighted in grey. Some species did not reach the minimal occurrence required and thus could not be tested using the intra-specific approach (asterisk), while some species had an AIC lower than M0 but did not exceed the performance criterion (ΔAIC > 4) to be considered as key species (underlined).

INITIAL MODEL (M0): AIC = -40.2							
INTRA-COMMUNITY				**INTRA-SPECIFIC**			
Fish species	Nb of occ.	Nb of occ. (1%)	AIC M1	Fish species	Nb of occ.	Nb of occ. (1%)	AIC M1
Acanthurus albipectoralis	24	15	-59.9	*Epinephelus fuscoguttatus*	11	9	-55.4
Lutjanus bohar	199	172	-57.1	*Naso hexacanthus*	54	8	-53.1
Bodianus loxozonus	35	7	-53.7	*Lutjanus monostigma*	35	8	-50.3
Plectorhinchus picus	10	9	-50.7	*Lutjanus bohar*	199	8	-49.9
Scarus frenatus	158	132	-47.5	*Acanthurus albipectoralis*	24	8	-47.4
Chlorurus strongylocephalus	32	30	-46.9	*Chaetodon reticulatus*	86	8	-47.1
Macolor niger	67	50	-46.6	*Paracirrhites nisus*	24	11	-46.3
Siganus argenteus	20	11	-44.2	*Plectorhinchus picus*	10	8	-46
				Labroides bicolor	26	14	-45.9
				Thalassoma lutescens	214	8	-44.8
				Hemitaurichthys polylepis	22	8	-44.3
				2 < ΔAIC < 4			
				Chlorurus strongylocephalus	32	8	-35.6
				Bodianus loxozonus	35	6	-36.7
				Scarus frenatus	158	8	-37.3
				Macolor niger	67	8	-37.9
				Siganus argenteus	20	8	-38.1

Table S10 | Comparative results of potential key species for coral cover using relative intra-community (left) and intra-specific (right) biomass to define presence (threshold defined as 5%). AIC of the initial model M_0 provides reference Akaike Information Criterion (AIC M0). Presence of each species has been added to M_0 as binary variable using 2 criteria: *(i)* contribution of species to total biomass higher than 5% and *(ii)* the 95th percentile of the biomass distribution of each species. For each species, number of raw occurrences, number of occurrences meeting the threshold, and AIC of the model accounting for the species (AIC M1) are reported. For clarity, only key species are presented and those that are significantly related to coral cover under the 2 approaches are highlighted in grey. Some species did not reach the minimum occurrence and thus could not be tested using the intra-specific approach (asterisk).

INITIAL MODEL (M0): AIC = -40.2			
INTRA-COMMUNITY			
Fish species	Nb of occ.	Nb of occ. (5%)	AIC M1
*Acanthurus albipectoralis**	24	6	-62.7
Lutjanus bohar	199	131	-55.9
*Siganus argenteus**	20	4	-52.1
Scarus frenatus	158	60	-50.7
Macolor niger	67	28	-49.2

INTRA-SPECIFIC			
Fish species	Nb of occ.	Nb of occ. (5%)	AIC M1
Chaetodon trifascialis	132	42	-71
Acanthurus leucosternon	44	38	-63.7
Chaetodon guttatissimus	40	40	-60.5
Zebrasoma scopas	101	39	-60.4
Chaetodon baronessa	65	44	-58.6
Hemigymnus fasciatus	166	38	-58.2
Chaetodon unimaculatus	48	38	-56.6
Chaetodon meyeri	40	40	-54
Chaetodon reticulatus	86	38	-52.8
Scarus frenatus	158	38	-52.4
Thalassoma lutescens	214	38	-51
Macolor niger	67	38	-50.3
Thalassoma hardwicke	123	39	-48.7
Lutjanus bohar	199	38	-47.1
Chaetodon pelewensis	70	63	-46.0
Naso brevirostris	110	39	-45.8
Lutjanus gibbus	55	38	-44.7
Sargocentron caudimaculatum	39	38	-44.3
Nb occ. > 36 is required to be tested			
*Acanthurus albipectoralis**	24	NA	NA
*Siganus argenteus**	20	NA	NA

10. Résumé substantiel en Français

10.1. Introduction

Les récifs coralliens sont parmi les écosystèmes les plus riches de la planète. Ils couvrent moins de 1% de la surface des océans mais abritent une biodiversité extraordinaire estimée à environ 800 000 (550 000-1 330 000) espèces de plantes multicellulaires et d'animaux, dont 8% seulement sont identifiés (Fisher et al. 2015). Plus généralement, les récifs coralliens subviennent aux besoins nutritionnels, assurent des emplois, des opportunités récréatives, et soutiennent des valeurs esthétiques et spirituelles à des centaines de millions de personnes dans le monde (Burke *et al.* 2011; Kittinger *et al.* 2012; Teh *et al.* 2013; Cinner 2014; Ferrario *et al.* 2014; McClanahan Timothy 2018). Les pêcheries sur les récifs coralliens assurent également plus de la moitié des protéines consommées par les populations humaines dans les régions côtières (FAO 2016) et représentent encore la principale source de protéines pour de nombreuses communautés dans certaines régions insulaires (Kawarazuka & Béné 2011; Teh *et al.* 2013; Charlton *et al.* 2016). Ces pêcheries sont complexes car elles ciblent des centaines d'espèces de poissons et impliquent des stratégies multi-engins tout en présentant de nombreux défis de gestion, en particulier dans les pays en développement (McClanahan *et al.* 2006). Au-delà de l'apport en protéines, les poissons jouent un rôle clé dans le fonctionnement des écosystèmes coralliens. Ils régulent la structure des communautés, sa stabilité, et la dynamique du réseau trophique, et participent aussi au cycle des nutriments et contrôlent la croissance des algues et des macrophytes (Holmlund & Hammer 1999; Bascompte *et al.* 2005).

Or, le changement climatique et le déclin récent des communautés de poissons lié à la surpêche menacent les fonctions et services clés soutenus par les récifs coralliens (Bellwood *et al.* 2004; Hughes *et al.* 2017a; Hughes *et al.* 2017b; Hughes *et al.* 2018), et mettent en péril le bien-être des millions de personnes qui en dépendent directement (Teh *et al.* 2013).

Ainsi, un défi crucial auquel les scientifiques et les gestionnaires sont confrontés aujourd'hui est de mieux comprendre et d'intégrer dans la gestion et la gouvernance des socio-écosystèmes récifaux les relations complexes et multi-échelles entre les humains et les ressources naturelles, particulièrement la biomasse en poissons (Cinner 2014).

Mieux comprendre ces dynamiques sociales et écologiques est primordial afin de préserver durablement les fonctions et les services écosystémiques assurés par les récifs coralliens, c'est pourquoi mon projet de thèse se donne pour objectif de répondre à la question de recherche suivante « Dans quelle mesure et par quels processus les facteurs socio-économiques et écologiques affectent la biomasse en poissons des écosystèmes coralliens ? ».

La thèse a deux objectifs principaux : *(i)* développer de nouvelles métriques intégrant l'accessibilité pour mieux prendre en compte les impacts humains sur les récifs coralliens dans un paysage marin hétérogène et *(ii)* utiliser ces nouvelles métriques pour mieux modéliser les déterminants socio-écologiques de la biomasse en poissons sur les récifs coralliens (Figure 10.1).

Ces objectifs seront déclinés à travers quatre études distinctes dont chacune a sa propre question de recherche :

1. Le temps de trajet depuis les populations humaines est-il un déterminant majeur de la biomasse en poissons sur les récifs coralliens à l'échelle globale ?

2. L'intensité des impacts humains affecte-t-elle l'efficacité des réserves marines à protéger les récifs coralliens notamment leur biomasse en poissons et la présence de prédateurs supérieurs (e.g. requins) ?

3. De quelle manière le temps de trajet au marché influence l'exploitation des ressources en poissons récifaux à l'échelle locale ?

4. Quelles espèces ou quels groupes d'espèces sont nécessaires pour maintenir une forte biomasse en poissons et une couverture corallienne à l'échelle de l'Indopacifique ?

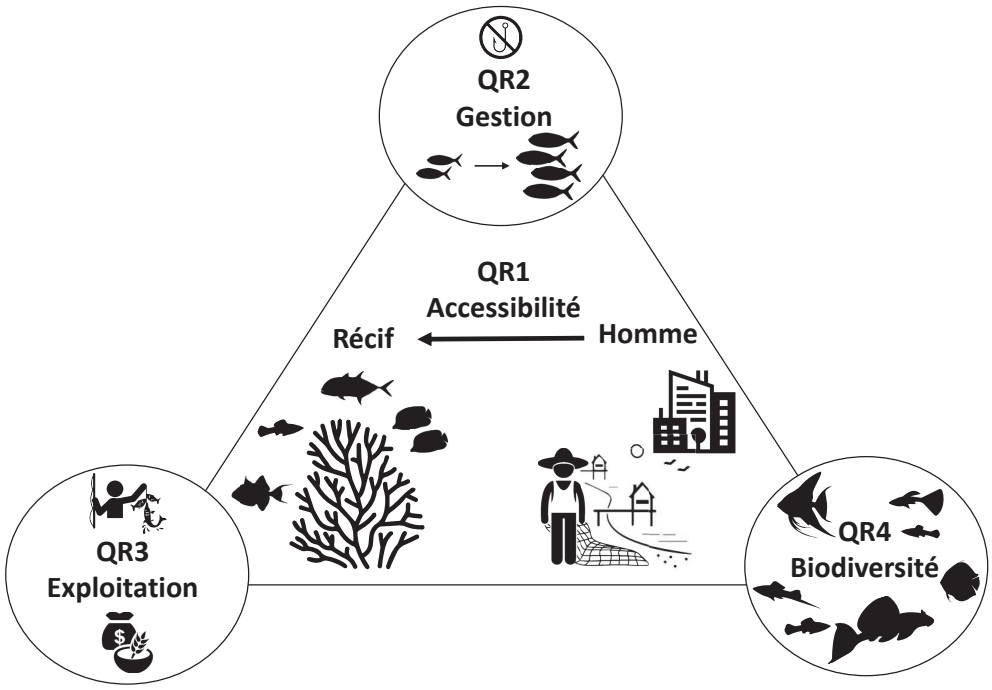


Figure 10.1 | Objectifs principaux de la thèse déclinés en 4 questions de recherche (QR) autour de plusieurs dimensions de la relation homme-récif.

10.2. Redéfinir l'accessibilité des récifs coralliens pour mieux prédire leur biomasse en poissons

Le temps de trajet depuis l'homme est un déterminant majeur de la biomasse en poissons

L'épuisement des ressources naturelles est devenu un problème majeur dans de nombreuses régions du monde, les ressources les plus accessibles étant les plus menacées. En milieu terrestre, l'épuisement des ressources et la perte de biodiversité ont été directement reliés à leur niveau d'accessibilité par l'intermédiaire des réseaux routiers (Laurance *et al.* 2009; Ahmed *et al.* 2014). En revanche, en milieu marin, l'impact sur les ressources naturelles est souvent réduit à une vision Malthusienne qui assimile simplement la pression sur les écosystèmes à la densité humaine avoisinante.

Au travers du **chapitre 3**, la thèse s'est tout d'abord donnée comme objectif de développer une approche capable d'estimer l'accessibilité des récifs coralliens en paysage hétérogène à l'échelle globale. Celle-ci repose sur l'estimation du temps de trajet potentiel depuis les

populations humaines ou les marchés les plus proches en intégrant la complexité des paysages : réseau mondial de routes et chemins, diversité des milieux naturels terrestres et marins. Cette étude a prouvé que 58% des récifs coralliens sont situés à moins de 30 minutes des premières populations humaines. Cette étude a également démontré que cette nouvelle métrique, le temps de trajet, est un déterminant majeur de la biomasse des poissons sur les récifs coralliens (Maire *et al.* 2016).

Bien qu'étant le déterminant majeur de la biomasse de poissons sur les récifs, le temps de trajet présente deux principales limites : *(i)* le temps de trajet ainsi calculé n'intègre aucune information sur la population humaine or un récif situé à 1h d'un village de pêcheurs ou d'une grande agglomération ne sera pas soumis aux mêmes pressions anthropiques directes et indirectes ; *(ii)* estimer le temps de trajet à l'échelle globale repose sur une hypothèse forte qui, dans notre cas, considère que les trajets en mer et sur terre se réalisent au moyen de véhicules motorisés, ce qui n'est pas le cas de nombreux pays en voie de développement où se trouvent une grande partie des récifs.

Pour répondre à la première limite, il paraît indispensable de considérer les populations humaines afin d'avoir une vision plus intégratrice de la potentielle pression humaine qui pèse sur les récifs coralliens, ce sera l'objectif de la partie suivante.

Concernant la seconde limite, une étude locale considérant les récifs du Nord-Ouest de Madagascar montrera l'importance et la complexité de l'accessibilité des ressources récifales par l'homme en paysage naturel et socio-économique hétérogène.

La gravité intègre l'accessibilité et les populations humaines pour mieux expliquer la biomasse en poissons récifaux

De nombreuses métriques quantifiant la pression humaine ont été calculées sur la base de la densité de population tandis que d'autres tiennent compte de l'accessibilité. Très peu combinent ces deux aspects et le concept de gravité vient combler cette lacune. Il s'agit d'un concept couramment utilisé en géographie qui utilise une version modifiée de la loi de Gravitation d'Isaac Newton pour prédire le mouvement des personnes, de l'information et des commodités entre les villes et même les continents. Le modèle de gravité, comme l'appellent les spécialistes des sciences sociales, est basé sur la loi modifiée de gravitation qui tient

compte de la taille de la population de deux endroits et de leur distance. Dans notre cas, nous avons considéré l'attraction des personnes vers les ressources des récifs coralliens en utilisant le temps de trajet nécessaire pour atteindre un récif donné. Ainsi, la gravité d'une population humaine vis à vis d'un récif représente cette densité de population divisée par le temps de trajet au carré qui sépare la population du récif considéré.

L'application de la gravité à l'échelle globale a prouvé que la gravité du marché a l'effet le plus fort et le plus significatif sur la biomasse en poissons récifaux, comparé à la pression démographique, le type de gestion, les conditions environnementales ou le contexte socioéconomique local ou national (Cinner *et al.* 2016). Néanmoins, il reste à déterminer si la gravité humaine affecte les récifs coralliens malgré les mesures de protection mises en place pour contrecarrer ses impacts.

10.3. La gravité des impacts humains réduit les gains de conservation sur les récifs coralliens

Les solutions efficaces face à la crise que connaissent les récifs coralliens (Hughes *et al.* 2003; Pandolfi *et al.* 2003; Bellwood *et al.* 2004; Hughes *et al.* 2017a) dépendent en partie de la compréhension du contexte dans lequel les bénéfices des différentes mesures de gestion peuvent être maximisés (Devillers *et al.* 2015; Pressey *et al.* 2015). Le **chapitre 4** consiste en une analyse globale intégrant près de 1800 récifs tropicaux ayant pour objectif de mesurer les impacts humains sur l'efficacité des réserves marines. L'intensité des impacts humains a été mesurée comme la gravité cumulée de chaque population humaine présente dans l'environnement proche de chaque récif (population divisée par le temps de trajet au récif cumulée dans un rayon de 500 km).

Tout d'abord, l'étude montre que la mise en place de réserves à proximité de l'Homme atténue les pressions humaines, mais ne les élimine pas complètement, notamment celles liées à la pêche. En effet, la gravité des impacts humains diminue l'efficacité des réserves marines, même des réserves intégrales, à maintenir une biomasse en poissons récifaux élevée et une présence de prédateurs apicaux. Plus précisément, la biomasse de poissons dans les réserves marines soumises à des pressions humaines fortes (gravité élevée) tend à être quatre

fois plus faible que la biomasse des réserves où les pressions humaines sont faibles (1150 vs. 270 kg/ha). De même, les prédateurs supérieurs sont absents dans plus de 70 % des récifs coralliens et sont présents sur moins de 1 % des récifs proches de l'Homme. A contrario, leur taux de présence sur les récifs isolés s'élève à 59 %.

Cependant, l'étude a également montré que la différence relative entre les sites ouverts à la pêche et les réserves (appelés les gains de conservation) est plus élevée pour la biomasse de poissons là où les impacts humains sont modérés et pour les prédateurs supérieurs, là où les impacts humains sont faibles.

Ces résultats illustrent de manière concrète le potentiel d'efficacité des actions de conservation : les réserves placées là où les impacts humains sont modérés à élevés peuvent fournir des gains de conservation élevés pour la biomasse de poissons, mais elles sont peu susceptibles de protéger des fonctions écosystémiques clés comme la présence de prédateurs supérieurs, qui sont uniquement présent dans les réserves soumises à de faibles impacts humains. Notre étude suggère donc de maintenir une grande diversité de réserves avec des objectifs très variés et de ne pas négliger la protection des sites éloignés de l'Homme.

10.4. Influence du marché sur les pratiques de pêche et de consommation des communautés côtières du nord-ouest de Madagascar

La dégradation rapide des récifs coralliens à l'échelle mondiale (Hughes *et al.* 2003; Pandolfi *et al.* 2003; Bellwood *et al.* 2004; Hughes *et al.* 2017a) menace leur fonctionnement écologique et finit par mettre en péril le bien-être de millions de personnes qui dépendent directement des récifs pour vivre (Teh *et al.* 2013). Comprendre comment l'accessibilité des sociétés humaines affecte les ressources naturelles est une étape cruciale vers une gestion à long terme des écosystèmes où des actions sont nécessaires pour améliorer leur durabilité écologique et économique.

Le **chapitre 5** a utilisé un cas d'étude dans le nord-ouest de Madagascar pour quantifier l'influence respective des communautés locales et du marché sur les conditions des récifs coralliens, tout en intégrant les actions locales de gestion. Si l'évaluation globale de l'accessibilité dans le domaine marin est une étape essentielle pour mieux comprendre

l'interaction entre les humains et les ressources naturelles, elle présente néanmoins quelques limites lors de son application à une échelle locale. Le premier objectif a donc consisté à développer une méthodologie d'estimation du temps de trajet pour les récifs du Nord-Ouest de Madagascar, basée sur des validations terrain et de définir, à partir des temps de trajet, le marché (point de vente de poissons) le plus proche pour chaque récif. En combinant le temps de trajet avec les données socio-économiques des enquêtes conduites auprès des communautés locales, il a été possible de quantifier l'influence respective des communautés locales et du marché sur les conditions des récifs coralliens et d'évaluer si la proximité du marché influence les pratiques de pêches et de consommation des communautés humaines locales.

L'étude a montré que les communautés les plus éloignées du marché ont plus de personnes engagées dans des activités de pêche, une plus grande dépendance aux ressources marines et un nombre limité de ressources alternatives. Ainsi, toutes ces caractéristiques devraient engendrer une plus forte pression de pêche sur les récifs et donc une biomasse en poissons plus faible à mesure que l'on s'éloigne du marché. Étonnamment, l'étude a révélé le contraire et donc des biomasses en poissons plus élevées sur les récifs distants du marché. Ainsi, les marchés impactent la biomasse de poissons des récifs avec un effet encore plus fort que l'effet direct des communautés de pêcheurs, y compris sur les récifs gérés localement.
Une meilleure évaluation de l'accessibilité des sociétés humaines (marché et village) apparaît donc comme une étape nécessaire vers une gestion à long terme des pêcheries récifales. Enfin, l'accès au marché est désormais un indicateur clé mesuré lors des suivis réalisés par la *Wildlife Conservation Society (WCS)* et les partenaires *Blue Ventures* et *Conservation International.*

10.5. Identifier les espèces associées au fonctionnement des écosystèmes via l'approche *Community-Wide Scan*

Dans le contexte de changements globaux et de perte de biodiversité, le retour des récifs à leurs configurations passées n'est plus une option. En revanche, la prise en compte des nouveaux scénarios de l'Anthropocène nécessite une meilleure compréhension des multiples facteurs influençant la réponse des écosystèmes (Hughes *et al.* 2003; Pandolfi *et al.* 2003; Bellwood *et al.* 2004; Hughes *et al.* 2017a). Une gestion efficace repose sur une meilleure compréhension des liens qui existent entre les communautés écologiques et la myriade de services qu'elles soutiennent (Cardinale *et al.* 2012; Cheung *et al.* 2016; Ricketts *et al.* 2016; Ratcliffe *et al.* 2017). Déterminer si de nombreuses espèces fonctionnellement complémentaires ou seulement un sous-ensemble d'espèces clés sont nécessaires au maintien du fonctionnement et des services écosystémiques est une question cruciale en écologie des communautés et en conservation de la biodiversité. Néanmoins, l'identification de telles espèces clés reste difficile, en particulier dans les tropiques où de nombreuses espèces coexistent et peuvent potentiellement soutenir des processus identiques ou différents. Le **chapitre 6** propose de développer une nouvelle approche, le *Community-Wide Scan* (CWS), analogue à l'analyse génomique, pour identifier les espèces de poissons qui contribuent de manière significative, au-delà des effets socio-environnementaux et de richesse spécifique, à la biomasse et à la couverture corallienne des récifs de l'Indopacifique. L'étude a montré que seul un nombre limité d'espèces de poissons (51 sur 400, environ 13%), appartenant à divers groupes fonctionnels et lignées évolutives, est fortement et positivement associé à la biomasse de poissons et à la couverture corallienne. Beaucoup de ces espèces n'ont pas encore été identifiées comme fonctionnellement importantes et pourraient donc être impliquées dans des mécanismes biologiques inconnus, mais néanmoins prépondérants, et permettraient ainsi de maintenir des récifs coralliens sains et productifs. Le fait qu'un nombre limité d'espèces soient significativement corrélées à des niveaux élevés de biomasse et de couverture corallienne soutient l'idée que le maintien à long terme des services écosystémiques nécessiterait une large gamme de fonctions particulières au-delà du simple nombre d'espèces (Soliveres *et al.* 2016; Gross *et al.* 2017). Ces résultats appellent à davantage de stratégies de gestion ciblées telles que l'interdiction de pêche de certaines

espèces considérées comme essentielles pour l'écosystème (Bozec *et al.* 2016). De plus, le maintien de la multifonctionnalité nécessiterait également une approche « portefeuille » qui pourrait réduire le risque d'extinction locale des espèces clés tout en sécurisant le niveau de biodiversité des communautés (Webster *et al.* 2017). Le CWS a donc le potentiel de révéler des espèces essentielles au fonctionnement et aux services des écosystèmes, mais également de guider les stratégies de gestion ainsi que de futures expérimentations permettant de révéler les processus écologiques sous-jacents.

10.6. Conclusion et perspective

Évaluer la capacité des mesures de gestion à bénéficier aux populations humaines et aux écosystèmes nécessite au préalable un meilleure compréhension des impacts humains sur les récifs coralliens et leurs ressources. Ainsi, la mise en œuvre du temps de trajet et de la gravité représente la première étape essentielle et semble offrir de nombreuses applications. La thèse a contribué à un certain nombre d'avancées pour mieux protéger et comprendre les récifs coralliens en tant que systèmes dynamiques complexes : *(i)* une grande diversité de réserves (proche et éloignés des hommes) est à privilégier afin d'optimiser les gains de conservation pour la biomasse totale en poissons et les fonctions clés telles que celles soutenues les prédateurs supérieurs; *(ii)* la proximité d'un marché est un indicateur clé à intégrer dans les programmes de gestion des petites pêcheries récifales car il permet de mieux appréhender les pratiques des communautés locales dans l'exploitation des ressources marines et; *(iii)* au-delà des conditions environnementales et anthropiques, certaines espèces de poissons soutiendraient de manière disproportionnée par rapport à d'autres espèces, le fonctionnement et les services des écosystèmes et pourraient donc constituer des objectifs ciblés de protection.

Enfin, le développement du temps de trajet et de la gravité présente de nombreuses applications. En effet, l'usage de scénarios futurs intégrant la construction de nouvelles routes ou la motorisation mais également les prédictions de croissance démographique, permettrait d'identifier les récifs qui dans les années à venir, seraient soumis à une forte pression anthropique potentiellement d'un certain seuil de durabilité de l'usage des ressources. Ainsi,

il pourrait être possible de mieux anticiper les futurs impacts humains en développant des alternatives (changement des tracés des futures routes) ou en instaurant de nouvelles mesures de gestion et de protection en amont de l'urbanisation.

La thèse s'est particulièrement intéressée aux déterminants de la biomasse en poissons car c'est une ressource cruciale pour les communautés humaines qui en dépendent. Cependant, de nombreux services écosystémiques reposent sur des fonctions essentielles exercées par certains poissons récifaux qui ne sont pas pris en compte lorsque l'on considère uniquement la biomasse. Déterminer de quelle manière les impacts humains affectent la composition des communautés de poissons et plus précisément leur structure trophique, reste une question non résolue.

11. Publications arising during PhD candidature

Publications derived from thesis chapters

Maire, E., Villéger, S., Graham, N., Hoey, A., Cinner, J., Ferse, S., Aliaume, C., Booth, D., Feary, D., Kulbicki, M., Sandin, S., Vigliola, L. & Mouillot, D. (2018). Community-wide scan flags fish species associated to coral reef services globally. *Proc. R. Soc. B.* 20181167, doi: 10.1098/rspb.2018.1167

Cinner, J.E., **Maire, E.**, Huchery, C., MacNeil, M.A., Graham, N.A.J., Mora, C. et al. (2018). The gravity of human impacts mediates coral reef conservation gains. Proceedings of the National Academy of Sciences, 115 (27) E6116-E6125, doi: 10.1073/pnas.1708001115

Maire, E., Cinner, J., Velez, L., Huchery, C., Mora, C., Dagata, S., Vigliola, L., Wantiez, L., Kulbicki, M., & Mouillot, D. (2016). How accessible are coral reefs to people? A global assessment based on travel time. *Ecology Letters*, 19, 351:360, doi: 10.1111/ele.12577

Other peer-reviewed articles published during PhD candidature

Villéger, S., **Maire, E.** & Leprieur, F. On the risks of using dendrogram to measure functional diversity and multidimensional space to measure phylogenetic diversity: a comment on Sobral et al. (2017). *Ecology Letters*, 20: 554-557, doi:10.1111/ele.12750

Cinner, J.E., Huchery, C., MacNeil, M.A., Graham, N.A.J., McClanahan, T.R., Maina, J., **Maire E.** et al. (2016). Bright spots among the world's coral reefs. *Nature*, 535, 416–419, doi:10.1038/nature18607

ECOLOGY LETTERS

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IDEA AND PERSPECTIVE

How accessible are coral reefs to people? A global assessment based on travel time

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Abstract

The depletion of natural resources has become a major issue in many parts of the world, with the most accessible resources being most at risk. In the terrestrial realm, resource depletion has classically been related to accessibility through road networks. In contrast, in the marine realm, the impact on living resources is often framed into the Malthusian theory of human density around ecosystems. Here, we develop a new framework to estimate the accessibility of global coral reefs using potential travel time from the nearest human settlement or market. We show that 58% of coral reefs are located < 30 min from the nearest human settlement. We use a case study from New Caledonia to demonstrate that travel time from the market is a strong predictor of fish biomass on coral reefs. We also highlight a relative deficit of protection on coral reef areas near people, with disproportional protection on reefs far from people. This suggests that conservation efforts are targeting low-conflict reefs or places that may already be receiving *de facto* protection due to their isolation. Our global assessment of accessibility in the marine realm is a critical step to better understand the interplay between humans and resources.

Keywords

Accessibility, coral reefs, marine protected areas, social–ecological, travel time.

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INTRODUCTION

Natural resources, such as forests and fisheries, are becoming severely depleted; especially those that are more accessible to people (Mora *et al*. 2011; Cinner *et al*. 2013; Barber *et al*. 2014). For example numerous studies have linked increased accessibility through road building to deforestation (Laurance *et al*. 2009) and biodiversity erosion (Ahmed *et al*. 2014). Accessibility is also shown to be a main driver of ecosystem recovery. Distance to primary roads enhances recovery of secondary forests after abandonment of agriculture in Puerto Rico (Crk *et al*. 2009). In terrestrial systems, there is thus considerable attention on accessibility management, mainly via road networks at both local (Dobson *et al*. 2010) and global scales (Laurance *et al*. 2014).

In contrast, considerably less research has focused on accessibility in marine ecosystems, though it has been shown to strongly determine their conditions (e.g. fish biomass and biodiversity) and functioning (Morato *et al*. 2006; Cinner *et al*. 2013). For example in Nicaragua, the development of a road into a remote fishing area altered both price and price variability of fish, which led to more intensive overexploitation (Schmitt & Kramer 2009). Likewise, several studies have shown proximity to market to be the strongest predictor of overfishing on coral reefs (Cinner & McClanahan 2006; Cinner *et al*. 2012, 2013).

Measuring the extent to which global marine resources are accessible to humans has been generally limited to examining the linear distance between fishing grounds and markets or ports (e.g. Watson *et al*. 2015). However, for most coastal ecosystems and artisanal fisheries, this linear distance does not capture ragged coastlines, road networks and other features that can affect the time it takes to travel to a fishing ground. The availability of new analytical tools and high-resolution geo-referenced landscape data now allows for global travel time analyses.

Here, we undertake the first global assessment of the human accessibility of an entire marine ecosystem: coral reefs. Coral reefs are an important study system for exploring accessibility because millions of people depend on their resources (Teh *et al*. 2013; Cinner 2014) and because their services are valued more than for any other ecosystem on earth; on average at $350,000/ha/year (De Groot *et al*. 2012). Yet reefs are located on varied coastal and oceanic places with different levels of infrastructure development (roads, markets) and thus are likely to show great variability in their degree of accessibility

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by people. Using a novel metric of 'potential travel time' between people and reefs we ask the following questions: (1) How accessible are the world's coral reefs to people? (2) Is accessibility to people through travel time a better predictor of reef fish biomass than classical measures of human impact? (3) Are marine conservation efforts representatively protecting reefs near and far from people?

GLOBAL ACCESSIBILITY OF CORAL REEFS FROM HUMAN POPULATIONS

Potential travel time as a new measure of accessibility – more than linear distance

Linear distance between fisheries and human settlements can fail to capture differences in accessibility incurred by road networks, landscape heterogeneity and coastline tortuosity. The existence of a road along the coast, for instance could facilitate faster access to a given coral reef than the direct travel by boat (Fig. 1a). To account for all these drivers of differential accessibility, we adapted the geographical concept of 'friction of distance' to develop a metric we refer to as 'potential travel time'. We first assigned speeds required to cross 24 different types of land cover for each cell of our global 1 km-resolution grid (e.g. 60 km h^{-1} on a road, 30 km h^{-1} on a track, 20 km h^{-1} on the ocean; see details in Supplemental methodological procedures and Table S1). These estimates were adapted from a global assessment of travel time between major cities (Nelson 2008) and represent the minimum travel time required to cross each type of surface, assuming that road and maritime travels are made by motorised vehicles. Road speed depends on road type while off road travel is foot based. Since these values can vary depending on available technology, infrastructures and vehicles we called our metric 'potential travel time'. We then used the Dijkstra's algorithm through the *accCost* function (R Development Core Team 2014) to determine the minimum cumulative cost in time between every coral reef in the world (27,212 coral reef cells) and (1) the nearest human settlement of any size (any populated pixel given by the finest resolution global human distribution grid, see Fig. S1), and (2) the nearest major market (considered as a national capital, a provincial capital, a major population centre, or landmark city; see Supplemental methodological procedures) since both have been shown to impact reef resources and functioning (Cinner *et al*. 2013; Advani *et al*. 2015).

We related the linear geographical distance and potential travel time from the nearest major market (Fig. 1b). Not surprisingly, linear distance and travel time are correlated globally (R^2 = 0.9); a reef far from people cannot be reached with limited travel time while a reef close to people (< 10 km) is always accessible with < 4 h travel time. However, a given linear distance value may correspond to a wide range of potential travel times (Fig. 1c). For any 10km-window along a whole linear distance gradient from 0 to 500 kilometres between a given reef and the nearest market, the range of travel time is highly variable. For example a range of linear distance to market between 105 and 115 kilometres (represented as red bar in Fig. 1c) corresponds to potential travel time ranging from 2 to 13 h. This result highlights the importance of integrating the landscape heterogeneity in accessibility assessments since considering travel on a unique surface may produce a coarse and unrealistic estimation of time required to reach reefs. Travelling only off-road, i.e. through the vegetation, only on road or only on the ocean provide over-simplified scenarios that are almost never met (Fig. 1b). Most of the pathways to reach the reefs combine road and maritime travel, preventing any simplification. Even if linear distance may appear to be a good surrogate for estimating potential travel time to reach the reefs globally (Fig. 1b), a map of residuals from predicted values shows that, relative to potential travel time, linear distance tends to underestimate accessibility in populated areas where roads are present and overestimates accessibility in more remote places (Fig. S2). This likely has to do with the potential travel time metric's recognition of reduced travel time on roads.

High but variable accessibility of coral reefs around the world

Our global assessment of coral reefs accessibility shows that 58% of coral reefs (15,609 out of 27,212 coral reef cells) are located at < 30 min travelling time from the nearest human settlement (Fig. 2). On average, each reef can be reached within 1 h 50 (SD = 4 h 15). The bulk of reefs are highly accessible in the Caribbean, the Coral Triangle, the Western Indian Ocean and the Pacific Islands. However, some areas like the Chagos Archipelago, the Spratly Islands, the Chesterfield Islands, the northwest Hawaiian Islands and the Coral Sea have reefs at more than 12 h travel time from the nearest human settlement. None of Caribbean coral reefs are more than 13 h from people (Fig. 2 a1 & b1).

Accessibility of coral reefs from major markets is high relative to the nearest human settlement (mean = 10 h), but is highly variable around the world (SD = 9 h). Our analysis shows that 25% (6,790 pixels) of reefs are located at < 4 h from the nearest major market, whereas 31% (8,428 pixels) of reefs are more than 12 h from the nearest market. Caribbean coral reefs appear much more accessible from markets than their Indo-Pacific counterparts (Fig. 2 a2 & b2).

To take into account the variability of available boat technology, we re-assessed global accessibility using slow (10 km h^{-1}) and fast (40 km h^{-1}) boat speeds. Accessibility of coral reefs from the nearest population ranges between 3 h 40 (SD = 8 h 30) and 1 h 10 (SD = 3 h), and from the nearest market between 17 h (SD = 17 h 30) and 6 h 10 (SD = 4 h 40) using slow vs. fast boats respectively (Fig. S3 and S4). Future applications should consider variable travel speeds according to per capita Gross Domestic Product to reflect different levels of infrastructure and technology in developed vs. developing countries. Yet this country-scale assessment was beyond the scope of our initial exploration of travel time.

TRAVEL TIME FROM MARKET AS A KEY DRIVER OF CORAL REEF CONDITIONS

There is considerable effort to better understand the multi-scale drivers of change in coral reef ecosystems through

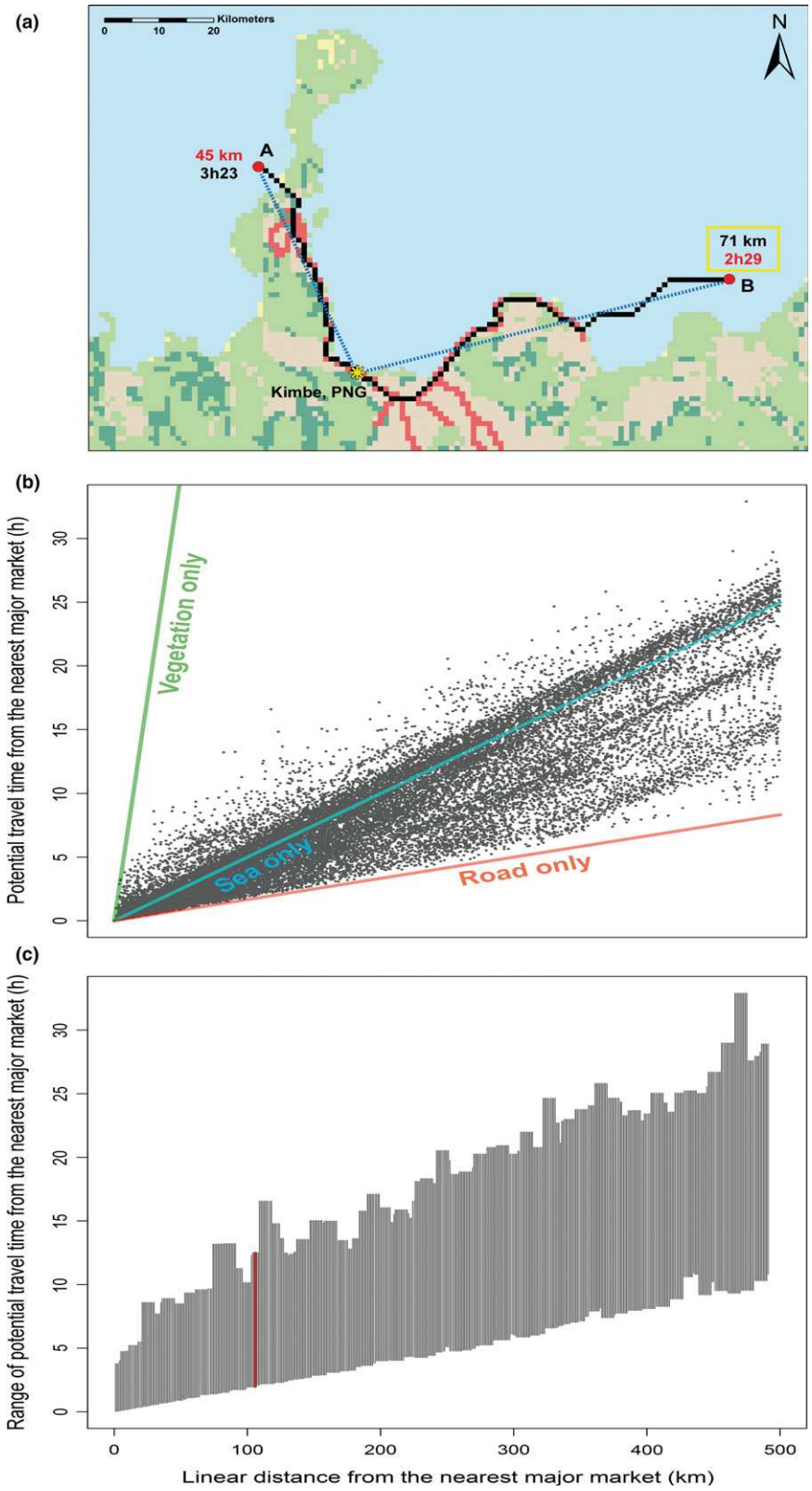

Figure 1 Potential travel time as a measure of accessibility. Accessibility is defined as the travel time to a location using land (road and land cover) or water (navigable river, lake and ocean) based travels and represents the 'cost' of travelling in time across a specific surface (e.g. land, sea, forest, etc.). As an illustration, the major market in Papua New Guinea, Kimbe (yellow asterisk), and two reef sites (red points) were considered (a). We calculated the linear distance and the travel time from the nearest market for 23,940 cells of coral reefs globally (b). Linear distance and travel time are highly correlated (R^2 = 0.9) but a small range of linear distance values (10 kilometres) may correspond to a wide range of potential travel time values (c). Travel time is a combination of road (red line), off road (green line) and maritime (blue line) travels.

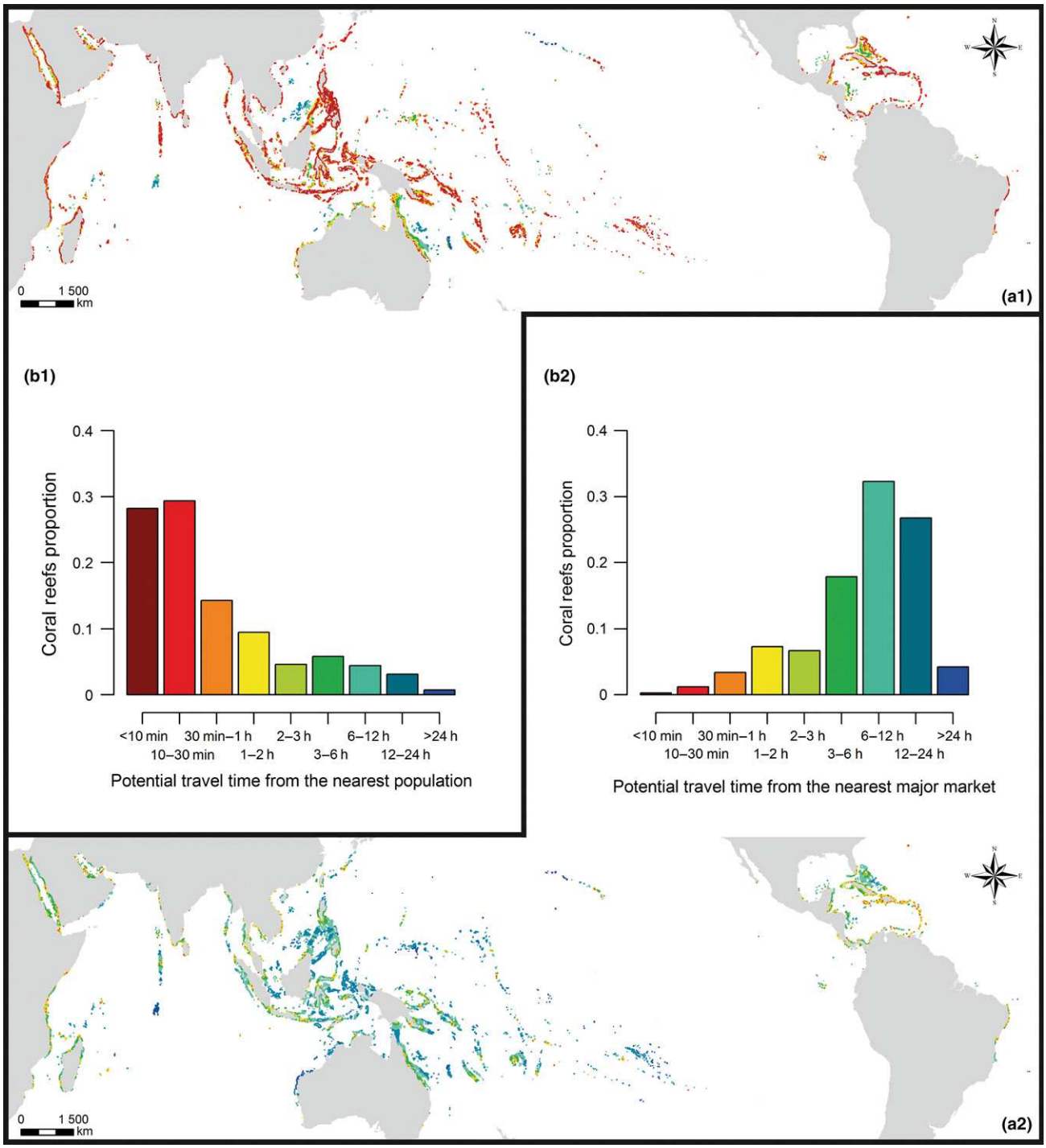

Figure 2 Accessibility of any coral reef from people (nearest market and nearest human settlement) around the world. Global coral reefs are extremely close to people (a1 & b1); 58% of reefs located at < 30 min travelling from the nearest human settlement while 25% of reefs are located at < 4 h from the nearest major market (a2 & b2). Only few areas appear as remote reefs (further away than 12 h travelling from human settlements) like the Chagos Archipelago, the Spratly Islands, the Chesterfield Islands and the Hawaiian Islands.

predictive modelling from local to global scales. For instance patterns of biomass and biodiversity across coral reef assemblages have been explained by several non-mutually exclusive processes that involve the roles of energy (Tittensor *et al.* 2010), climate (Pellissier *et al.* 2014), habitat (Rogers *et al.* 2014), biogeography (Parravicini *et al.* 2013), humans (Mora *et al.* 2011) and environmental stochasticity (Dornelas *et al.* 2006). A key goal of this body of research is to identify drivers of change that can be used as policy levers to positively influence the future conditions of coral reefs (Cinner & Kittinger 2015). We suggest that the availability of travel time estimation to reach the reefs from markets or populations

may help to decipher the many dimensions of human influence on ecosystem conditions when integrated to models in combination with other commonly used predictors (e.g., environment and habitat). Coral reef conditions (biomass or biodiversity) and functioning (e.g. herbivory) are classically related to the density of local human populations (Bellwood *et al*. 2012; Williams *et al*. 2015) and more recently to the linear distance to humans (Advani *et al*. 2015) or markets (Brewer *et al*. 2012; Cinner *et al*. 2013). Here, we test whether potential travel time from market is a better predictor of reef fish biomass than local human density and linear distance to market in a case study from New Caledonia.

We used 1,357 Distance Sampling Underwater Visual Census (UVC) surveys of fish communities (Fig. 3a) to quantify the relative influences of environment, habitat and human impact on fish biomass (Supplemental methodological procedures, Table S2, Fig. S5). Human impact is assessed through three potential proxies: (1) the density of people within a buffer of 20 km around each UVC survey, (2) the linear distance between each UVC survey and the major market located in the regional capital of Noumea and (3) the travel time to reach each UVC survey from the market. We use generalised linear models (GLM) and boosted regression tree (BRT) models to predict fish biomass and rank the different explanatory variables according to their Akaike weight (AIC_w) and their relative contribution respectively (see Supplemental methodological procedures). We demonstrate that humans shape the level of reef fish biomass since each proxy of human impact has a significant effect beyond that of habitat and environment (Table 1). Then we show that potential travel time from the market is the strongest predictor of fish biomass since its AIC_w is 1 (essential variable in all best GLM sub-models) and its relative contribution to the BRT model is 28% surpassing that of all other competing variables (Fig. 3b). In contrast, human density and linear distance to market have lower AIC_w values (0.33 and 0.44 respectively) and contribute to BRT models at, respectively, the fourth (11%) and third rank (13%) suggesting their marginal influence on fish biomass compared to travel time. Finally the most parsimonious model ('best' in Table 1), based on variable selection using the AIC criterion, only retains potential travel time from the market as the sole human driver of fish biomass on New Caledonian reefs. This GLM model explains 45% of variation in fish biomass across reefs. However, the BRT model, which takes into account variable interactions and thresholds effects, explains up to 70% of this variation highlighting potential interplay between human, environmental and habitat drivers. When extracting the 'pure' effect of travel time from the market on fish biomass using a partial plot from the GLM we observe a saturating relationship (Fig. 3c). Low biomass values (< 100 kg ha^{-1}) are mostly found when travel time is lower than 10 h (Fig. 3c). All remote reefs (Fig. 3a) have a fish biomass higher than 500 kg ha^{-1}, which has been suggested as a potential threshold to maintain healthy and functioning coral reefs (McClanahan *et al*. 2011; MacNeil *et al*. 2015).

Table 1 Comparison of candidate models predicting reef fish biomass as a function of environmental, habitat and human impact variables across the coral reefs of New Caledonia

Model	AIC	R^2	F
Null	2085	0	
Environment + Habitat	1544	0.37	LR-test
Environment + Habitat + Human density	1449	0.41	98.854*
Environment + Habitat + Linear distance	1413	0.43	138.3*
Environment + Habitat + Travel time	1352	0.45	206.2*
Best	1350	0.45	

*P-value < 0.001. We calculated the Aikaike Information Criterion (AIC) and the total adjusted R-squared (R^2) for each model and sub-model (see Supplemental methodological procedures and Table S2). A likelihood ratio test (LR-test and F-value) between the 'Environment+Habitat' model and each enriched model with one aspect of human influence (population, linear distance or travel time) shows the significance of adding human impact variables. The 'Best' model is the most parsimonious according to the AIC criterion containing only travel time and some selected environmental variables (mean depth, surface cover of live coral, surface cover of macroalgae, the reef type and island type).

DISPROPORTIONNAL ISOLATION OF MARINE PROTECTED AREAS FROM PEOPLE

While numerous approaches can be used to sustain marine resources (Costello *et al*. 2008; Gelcich *et al*. 2008; Worm *et al*. 2009; Cinner *et al*. 2012), Marine Protected Areas (MPAs) are widely recognised as a key management tool (Gaines *et al*. 2010; Veitch *et al*. 2012; MacNeil *et al*. 2015). As in terrestrial systems, scientists have voiced concerns that protected areas are being disproportionally placed in remote areas, away from human impacts, and consequently are 'residual reserves' with limited benefits for biodiversity since not adverting direct exploitation (Mora & Sale 2011; Devillers *et al*. 2014; Watson *et al*. 2014). However, remote MPAs offer reference conditions to evaluate management measures or time to recovery (MacNeil *et al*. 2015), and can be emblematic so making publicity for marine protection worldwide (Singleton & Roberts 2014). Our goal is not to discuss the value of remote MPAs but to assess the degree to which remote areas receive disproportional protection, or whether the 1,140 coral reef MPAs we reported (Fig. S6) are unevenly distributed along gradients of accessibility based on travel time.

Intersecting the 1,140 MPAs globally with our 10 × 10 km coral reef grid, we first identify which coral reef cells are protected (6,935 among the 27,212 cells) and to which MPA they belong (Supplemental methodological procedures). For each protected coral reef cell, we then calculate the potential travel time from the nearest human settlement and major market. To examine whether protected coral reefs around the world are disproportionally farther from people, we estimate the deviance between the accessibility of protected reefs and the global distribution of coral reef accessibility for five categories of potential travel time: ≤ 10, 10–30 min, 30 min–2 h, 2–12 h, > 12 h. We then compare the proportion of reefs protected relative to the global distribution of reefs in each travel time category (Fig. 4). Relative to the global distribution of reefs, the proportion of reefs receiving protection is lower near people. We find an average 'deficit' of −19% lower protection on reefs that have a potential travel time lower than 2 h. However, reefs further from people (potential travel time higher than 2 h) are disproportionally protected. This relative 'sur-

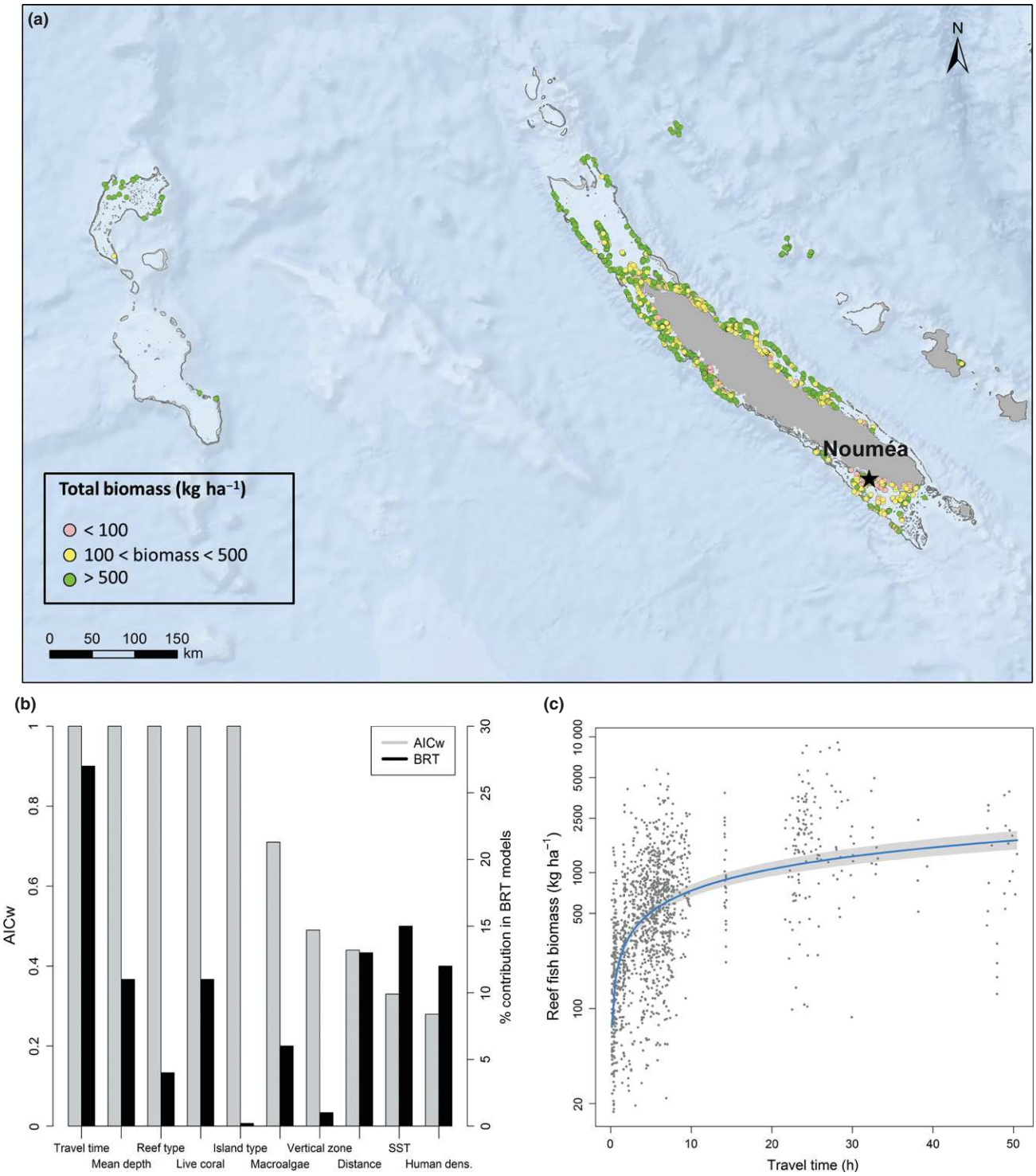

Figure 3 Potential travel time as the main driver of fish biomass. Fish biomass estimates from 1,357 Underwater Visual Census (UVC) surveys performed across coral reefs of New Caledonia (a). The relative influences of predictor variables (environment, habitat and human impact) are assessed using the weighted Akaike Information Criterion (AIC_w) from generalised linear models and the relative contribution from boosted regression tree models (b). The partial plot (c) shows the 'pure' relationship between potential travel time and reef fish biomass, i.e. while considering the other predictor variables.

plus' of protection is even more marked for isolated coral reefs (potential travel time > 12 h) with more than twice (127%) the proportion of protected coral reefs compared to the global distribution (Fig. 4a). Importantly, this disproportional protection of isolated reefs is much less pronounced when using travel time from markets (Fig. 4b).

This trend of protecting inaccessible reefs tends to emerge because of complex ecological, socioeconomic and political

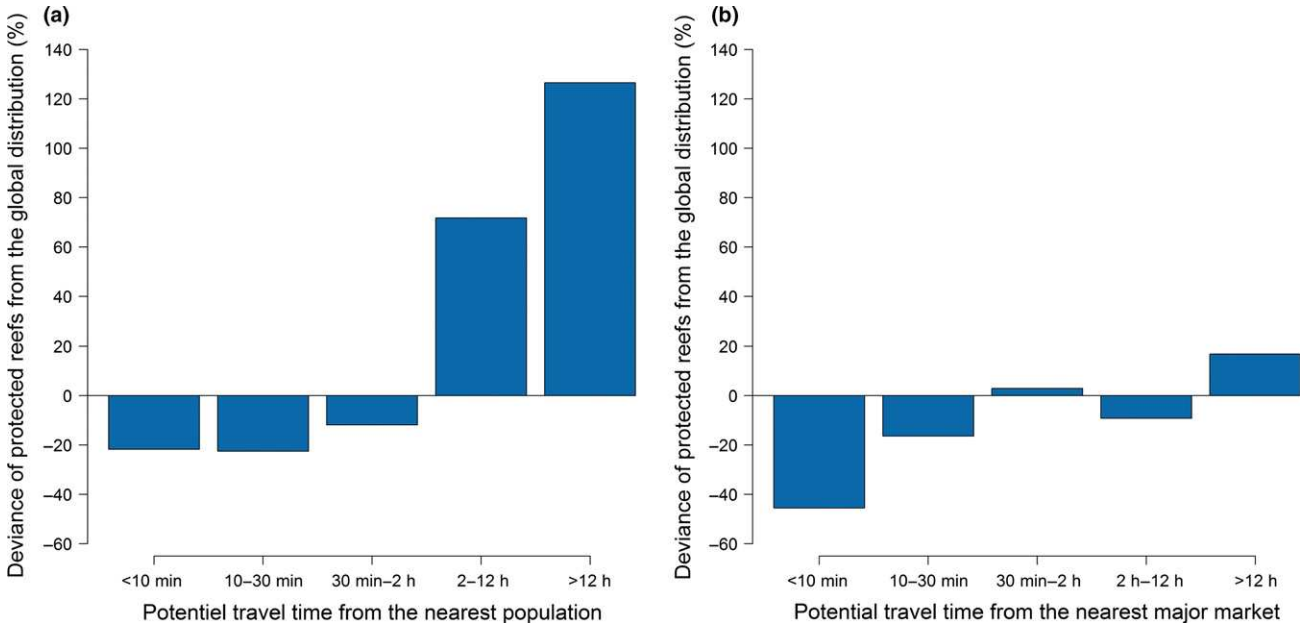

Figure 4 Deficit and surplus of protection for global coral reefs. The proportion of reefs receiving a deficit or a surplus of protection relative to the distribution of reefs globally is assessed along a gradient of isolation (≤ 10 min, 10–30 min, 30 min-2 h, 2–12 h, >12 h) using travel time from the nearest population (a) or the nearest market (b).

trade-offs that aim to maximise conservation benefits while minimising costs to the people engaged in natural resources exploitation (McNeill 1994; Pressey *et al*. 1993; Jones 1999; Stewart *et al*. 2003). Indeed, some fishers are very unlikely to support development of no-take MPAs, particularly in their primary fishing grounds (McClanahan *et al*. 2012), so locating MPAs further away from people can be a sensible strategy for reducing opposition from fishers but with questionable conservation benefits (Singleton & Roberts 2014; Wilhelm *et al*. 2014). The concern with the pattern of disproportionally protecting inaccessible areas that we quantified is that conservation targets (such as 10% protection of oceans by 2020) can be met without actually reducing human impacts on the seascape (i.e. because MPAs get placed in locations which are already *de facto* protected because of their inaccessibility; Devillers *et al*. 2014). Our results suggest that in situations where MPAs are located where they do little to actually reduce human impacts, complementary tools such as gear restrictions and user rights may help to sustain reef fisheries in accessible areas (Costello et al. 2008; Gelcich *et al*. 2008; McClanahan *et al*. 2011; Cinner *et al*. 2012; MacNeil *et al*. 2015) with less opposition from fishers (McClanahan *et al*. 2012).

FUTURE DIRECTIONS

To sustain coral reef ecosystems, we need to understand the complex interactions between people and reefs. Our development of a global measure of potential travel time is an important step towards this objective, and we suggest three areas where future applications could be beneficial: (1) using travel time as a proxy for fishing effort to identify refuges and analyse extinction risk, (2) assessing financial cost and profitability for artisanal reef fisheries and (3) assessing potential impacts of expanding road networks. To facilitate these and other applications, we provide our global potential travel time estimates for coral reefs as a spatial layer at 10 km-resolution upon request or for a set of coordinates.

Species accessibility and refuges on coral reefs

The extent to which a species is under fishing pressure is classically estimated through either its catch rates (Bejarano *et al*. 2013) or its geographical overlap with fishing effort (Comeros-Raynal *et al*. 2012). The former is a direct measure of extraction but is unavailable in many data-poor fisheries while the latter is an indirect estimate which is challenging to downscale (Teh *et al*. 2013). Alternatively, the potential travel time to reach the reefs from markets or people, certainly in interaction with other social–economic aspects, can provide a standardised way to approximate fishing pressure with a host of potential applications. These could include: (1) identifying refuges where the geographical ranges of threatened or endangered species may overlap with inaccessible areas; and (2) providing a standardised index of potential exposure to fishing threats to include in evaluations of vulnerability or extinction risk (Parravicini *et al*. 2014).

Assessing profitability and costs of fishing coral reefs

Travel time is a first step towards the assessment of travel cost in terms of energetic or monetary units. Beyond time and distance, travel cost also depends on the type of vessel (size, engine, etc.), labour costs, infrastructure (road, harbour, etc.), and the price of fuel (including government subsidies). Estimating travel costs would require detailed data currently

unavailable for a global analysis but could be well suited to a downscaled analysis. Ultimately, based on expected yields and seafood prices, isoclines or contours of profitability could be drawn for artisanal fisheries on coral reefs. Such estimates and maps may also serve to define reefs where accessibility is too restricted to host profitable fisheries, show where short travel time and low travel cost from humans may promote overexploitation, and even highlight potential consequences of fisheries fuel subsidies. The travel cost to reach any reef from a market or a village would make a valuable management tool to better map artisanal fisheries effort, yields and economic outcomes in what is generally a data-poor fisheries.

Future impacts of road building on coral reefs accessibility

The global network of roads is rapidly expanding under multiple needs of accessibility to resources, industries and infrastructures. Most of the 25 million kilometres of new roads anticipated by 2050 will be built in developing countries to sustain their social and economic development, but this could have profound impacts on biodiversity (Laurance *et al*. 2014). The spread of this road network in the last terrestrial wilderness areas (e.g. Amazon) and its ecological consequences have been widely documented particularly the accentuated depletion of natural resources (Barber *et al*. 2014). Comparatively the impact of road construction on marine ecosystems remains largely overlooked (Schmitt & Kramer 2009). Travel time provides a framework to assess scenarios of future road development on reef systems, highlighting potential ecological consequences and trade-offs associated with specific plans. Development of new and faster roads along the coasts will increase the accessibility of some reefs to humans (Fig. 1a), likely resulting in overfishing and potential impacts on corals (Mumby 2006; Hughes *et al*. 2007). Travel time calculations using future scenarios of road building may help to identify reefs that are particularly at risk and develop potential alternatives that could still meet socioeconomic goals with less environmental impact.

CONCLUSION

Better understanding the dynamics of coral reef social–ecological systems is one of the most critical challenges that scientists and managers are facing today (Cinner 2014). The severity of human impacts on reef systems has been widely acknowledged, though the causes of, and solutions to, these impacts are debated (Hughes *et al*. 2010; Rogers *et al*. 2015). It is clear that human population size and density are major drivers of change on reefs (Mora *et al*. 2006, 2011; Bellwood *et al*. 2012; Williams *et al*. 2015), but in addition to these demographic pressures, drivers such as market integration and poverty also shape the ways that people use and govern coral reefs (Cinner *et al*. 2009, 2013). However, these drivers of unsustainable exploitation are often poorly considered by both scientists and policy makers, leading to insufficient governance and diminished outcomes. A critical step is to better understand, and integrate into governance, the complex, multi-scale interrelationship between humans and coral reefs with accessibility being critical.

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AUTHORSHIP

J.C., C.M. and D.M. conceived the project; all authors designed the study; S.D., L.V., L.W. and M.K. collected the data. E.M., L.V. and C.H. performed the analyses; E.M., J.C. and D.M. wrote the first draft and all authors contributed substantially to revisions.

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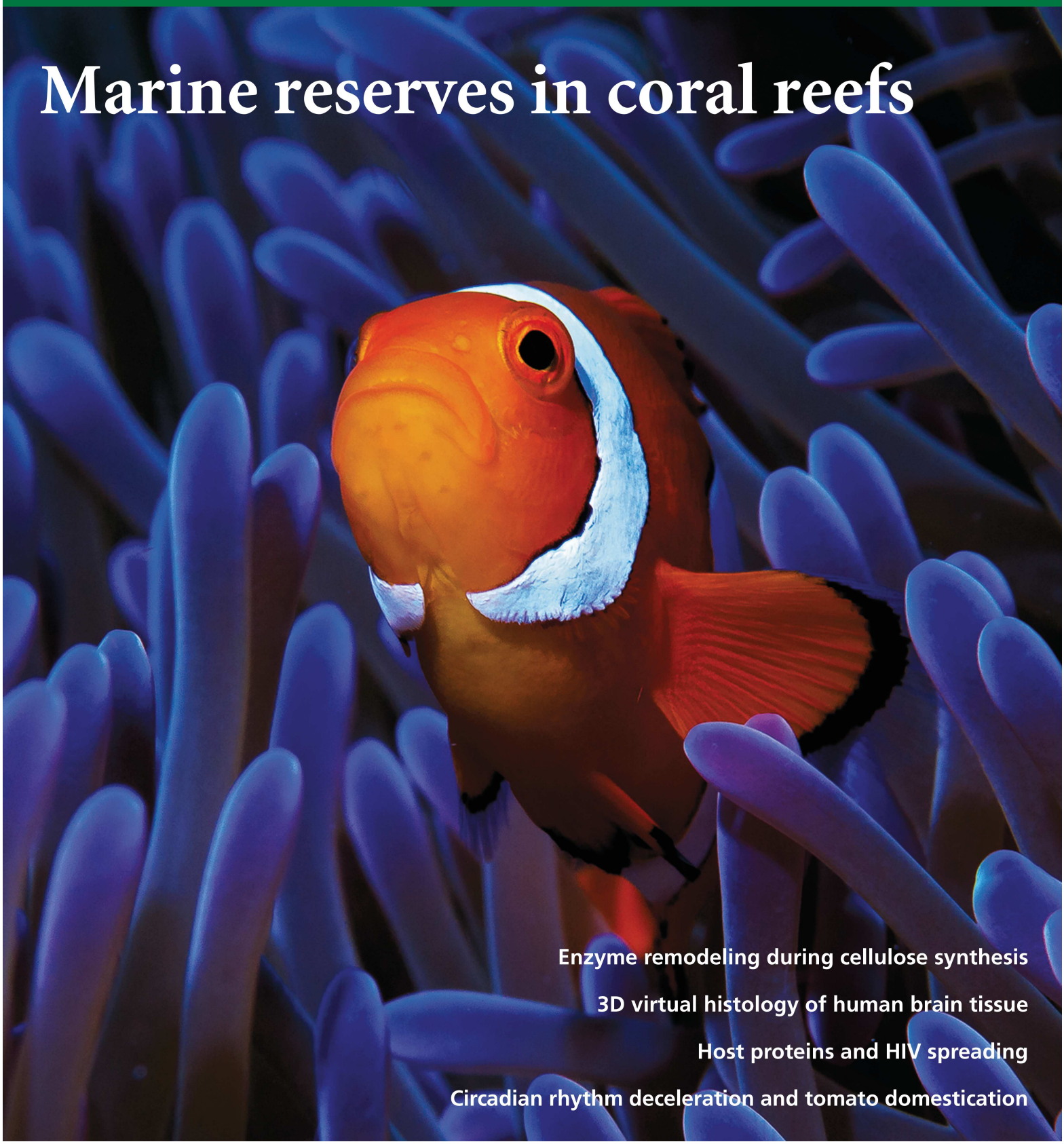
Marine reserves in coral reefs



Enzyme remodeling during cellulose synthesis

3D virtual histology of human brain tissue

Host proteins and HIV spreading

Circadian rhythm deceleration and tomato domestication

Gravity of human impacts mediates coral reef conservation gains

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Coral reefs provide ecosystem goods and services for millions of people in the tropics, but reef conditions are declining worldwide. Effective solutions to the crisis facing coral reefs depend in part on understanding the context under which different types of conservation benefits can be maximized. Our global analysis of nearly 1,800 tropical reefs reveals how the intensity of human impacts in the surrounding seascape, measured as a function of human population size and accessibility to reefs ("gravity"), diminishes the effectiveness of marine reserves at sustaining reef fish biomass and the presence of top predators, even where compliance with reserve rules is high. Critically, fish biomass in high-compliance marine reserves located where human impacts were intensive tended to be less than a quarter that of reserves where human impacts were low. Similarly, the probability of encountering top predators on reefs with high human impacts was close to zero, even in high-compliance marine reserves. However, we find that the relative difference between openly fished sites and reserves (what we refer to as conservation gains) are highest for fish biomass (excluding predators) where human impacts are moderate and for top predators where human impacts are low. Our results illustrate critical ecological trade-offs in meeting key conservation objectives: reserves placed where there are moderate-to-high human impacts can provide substantial conservation gains for fish biomass, yet they are unlikely to support key ecosystem functions like higher-order predation, which is more prevalent in reserve locations with low human impacts.

marine reserves | fisheries | coral reefs | social-ecological | socioeconomic

Significance

Marine reserves that prohibit fishing are a critical tool for sustaining coral reef ecosystems, yet it remains unclear how human impacts in surrounding areas affect the capacity of marine reserves to deliver key conservation benefits. Our global study found that only marine reserves in areas of low human impact consistently sustained top predators. Fish biomass inside marine reserves declined along a gradient of human impacts in surrounding areas; however, reserves located where human impacts are moderate had the greatest difference in fish biomass compared with openly fished areas. Reserves in low human-impact areas are required for sustaining ecological functions like high-order predation, but reserves in high-impact areas can provide substantial conservation gains in fish biomass.

The world's coral reefs are rapidly degrading (1–3), which is diminishing ecological functioning and potentially affecting the well-being of the millions of people with reef-dependent livelihoods (4). Global climate change and local human impacts (such as fishing) are pervasive drivers of reef degradation (1, 5). In

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Data deposition: A gridded global gravity data layer is freely available at dx.doi.org/10.4225/28/5a0e7b1b3cc0e.

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response to this "coral reef crisis," governments around the world have developed a number of reef conservation initiatives (1, 6, 7). Our focus here is on the efficacy of management tools that limit or prohibit fishing. Management efforts that reduce fishing mortality should help to sustain reef ecosystems by increasing the abundance, mean body size, and diversity of fishes that perform critical ecological functions (8–10). In practice, however, outcomes from these reef-management tools have been mixed (5, 11–13).

A number of studies have examined the social, institutional, and environmental conditions that enable reef management to achieve key ecological outcomes, such as sustaining fish biomass (5, 14, 15), coral cover (16), or the presence of top predators (17). These studies often emphasize the role of: (*i*) types of key management strategies in use, such as marine reserves where fishing is prohibited, or areas where fishing gears and/or effort are restricted to reduce fishing mortality (8, 18); (*ii*) levels of compliance with management (12, 19, 20); (*iii*) the design characteristics of these management initiatives, for example the size and age of reserves, and whether they are placed in remote versus populated areas (11, 21); and (*iv*) the role of social drivers, such as markets, socioeconomic development, and human demography that shape people's relationship with nature (14, 22).

In addition to examining when key ecological conditions are sustained, it is also crucial to understand the context under which conservation gains can be maximized (23, 24). By conservation gains, we are referring to the difference in a conservation outcome (e.g., the amount of fish biomass) when some form of management (i.e., a marine reserve or fishery restriction) is implemented relative to unmanaged areas. These conservation gains can be beneficial for both people and ecosystems. For example, increased fish biomass inside marine reserves is not only related to a range of ecosystem states and processes (18), but can also result in spillover of adults and larvae to surrounding areas, which can benefit fishers (25–27). The potential to achieve conservation gains may depend on the intensity of human impacts in the surrounding seascape (23, 24), yet these effects have never been quantified.

Here, we use data from 1,798 tropical coral reef sites in 41 nations, states, or territories (hereafter "nation/states") in every major coral reef region of the world to quantify how expected conservation gains in two key ecological outcomes are mediated by the intensity of human impact, namely: (*i*) targeted reef fish biomass (i.e., species generally caught in fisheries) and (*ii*) the presence of top predators (*Materials and Methods* and *SI Appendix*, Table S1). To quantify human impact at each site, we draw from a long history of social science theory and practice to develop a metric referred to as "gravity" (*Box 1*). The concept of gravity (also called interactance) has been used in economics and geography to measure economic interactions, migration patterns, and trade flows since the late 1800s (28–30). We adapt this approach to examine potential interactions with reefs as a function of how large and far away the surrounding human population is (*Box 1*). At each site, we also determined the status of reef management, grouped into either: (*i*) openly fished, where sites are largely unmanaged and national or local regulations tend to be poorly

Box 1

Drawing on an analogy from Newton's Law of Gravitation, the gravity concept predicts that interactions between two places (e.g., cities) are positively related to their mass (i.e., population) and inversely related to the distance between them (31). The gravity concept is often considered one of the most successful and long-enduring empirical models in economics and geography (31), but has rarely been directly applied in a natural resource management setting and holds much promise in informing reef conservation and management. Application of the gravity concept in a reef governance context posits that human interactions with a reef are a function of the population of a place divided by the squared time it takes to travel to the reefs (we used travel time instead of linear distance to account for the differences incurred by traveling over different surfaces, such as water, roads, tracks) (14, 32) (see Fig. 1 and *SI Appendix*, Table S2). Here, we build upon previous work (14) by developing a new indicator that examines the cumulative human gravity of all populated places within a 500-km radius of a given reef, which aims to capture both market and subsistence pressures on reef fish biomass. We tested the predictive power of a series of gravity metrics with varying radii (50 km, 250 km, 500 km) and exponents of travel time (travel time, travel time^2, travel time^3) (*Materials and Methods* and *SI Appendix*, Table S3). A key limitation of our global gravity metric is that we are unable to capture local variations in efficiencies that may affect fishing mortality per capita, such as fishing fleet technology or infrastructure (e.g., road) quality.

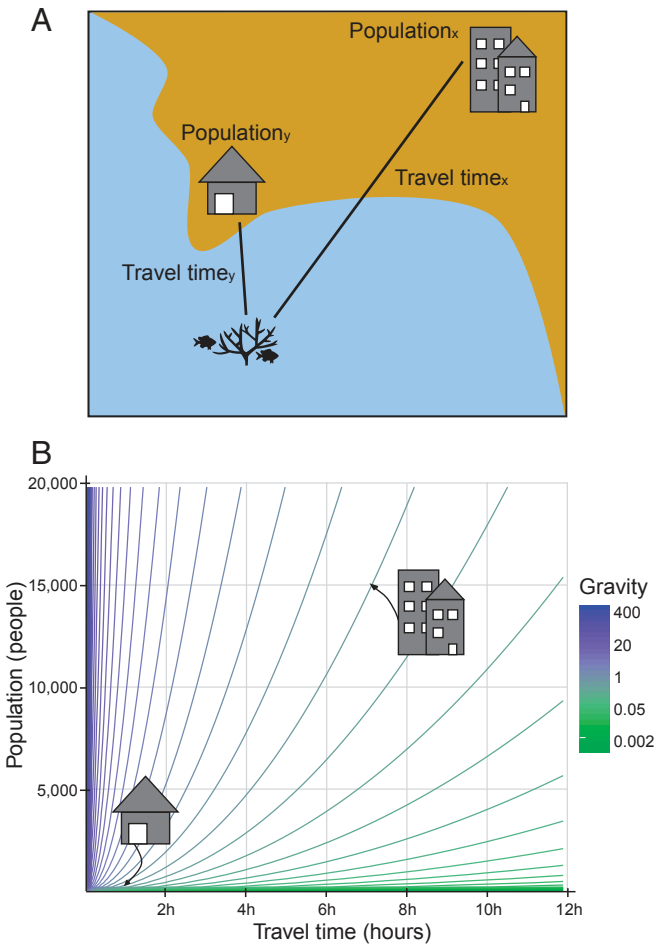

Fig. 1. Operationalizing gravity. (*A*) Applied to coral reefs, our heuristic of the gravity concept captures interactions between people and coral reef fish as a function of the population of a place divided by the squared time it takes to travel to the reefs (i.e., travel time). (*B*) Gravity isoclines along gradients of population size and travel time illustrate how gravity values could be similar for places that have large populations but are far from the reefs (e.g., population$_x$ = 15,000 people, travel time$_x$ = 7 h, gravity$_x$ = 306) as to those with small populations that are close to the reef (e.g., population$_y$ = 300 people, travel time$_y$ = 1 h, gravity$_y$ = 300). For ease of interpretation, we have illustrated travel time here in hours, but we use minutes in the main text.

complied with; (*ii*) restricted fishing, where there are actively enforced restrictions on the types of gears that can be used (e.g., bans on spear guns) or on access (e.g., marine tenure systems that restrict fishing by "outsiders"); or (*iii*) high-compliance marine reserves, where fishing is effectively prohibited (*Materials and Methods*). We hypothesized that our ecological indicators would decline with increasing gravity in fished areas, but that marine reserves areas would be less sensitive to gravity. To test our hypotheses, we used general and generalized linear mixed-effects models to predict target fish biomass and the presence of top predators, respectively, at each site based on gravity and management status, while accounting for other key environmental and social conditions thought to influence our ecological outcomes (14) (*Materials and Methods*). Based on our models, we calculated expected conservation gains along a gravity gradient as the difference between managed sites and openly fished sites.

Our analysis reveals that human gravity was the strongest predictor of fish biomass (Fig. 2 and *SI Appendix*, Fig. S1). Fish biomass consistently declined along a human gravity gradient, a trend particularly evident at the nation/state scale (Fig. 2 *C*–*E*). However, this relationship can vary by management type (Fig. 2 and *SI Appendix*, Fig. S1). Specifically, we found that biomass in reserves demonstrated a flatter (but still negative) relationship with gravity compared with openly fished and restricted areas (Fig. 2*B*). Interestingly, this differential slope between reserves and fished areas (Fig. 2*B*) was due to a strong interaction between gravity and reserve age such that older reserves contributed more to biomass in high-gravity situations than in low-gravity ones (*SI Appendix*, Fig. S1). This is likely due to fish stocks at high-gravity sites being heavily depleted and requiring decades to recover, whereas low-gravity sites would likely require less time to reach unfished biomass levels (8). Thus, given average reserve age in our sample (15.5 y), biomass in reserves did not decline as rapidly with gravity compared with fished and restricted areas (Fig. 2*B*). In the highest-gravity locations, modeled fish biomass in marine reserves was approximately five times higher than in fished areas (270 kg/ha compared with 56 kg/ha) (Fig. 2*B*). At the reef site scale, there was considerable variability in reef fish biomass, particularly at low gravity (Fig. 2 *F*–*H*). For example, at the lowest-gravity locations, biomass levels in reserves spanned more than three orders-of-magnitude (Fig. 2*F*). Importantly, there was never extremely high biomass encountered in high-gravity locations. Our estimate of target fish biomass included top predators. As a supplemental analysis, we also examined target fish biomass with the biomass of top predators excluded, which displays a similar trend, but with lower fish biomass in reserves at low gravity compared with when top predators are included (*SI Appendix*, Fig. S2).

A key finding from our study is that top predators were encountered on only 28% of our reef sites, but as gravity increases, the probability of encountering top predator on tropical coral reefs dropped to almost zero (<0.005), regardless of management (Fig. 3). The probability of encountering top predators was strongly related to gravity and the type of management in place, as well as sampling methodology and area surveyed (Fig. 3 and *SI Appendix*, Fig. S1). At low gravity, the probability of encountering a top predator was highest in marine reserves (0.59) and lowest in fished areas (0.14), when controlling for sampling and other environmental and social drivers (Fig. 3 and *SI Appendix*, Fig. S1).

Our study demonstrates the degree to which fish communities inside marine reserves can be affected by human impacts in the broader seascape (Figs. 2 and 3). Critically, high-compliance marine reserves in the lowest-gravity locations tended to support more than four times more fish biomass than the highest-gravity reserves (1,150 vs. 270 kg/ha, respectively) (Fig. 2*B*). Similarly, the modeled probability of encountering a top predator decreased by more than 100-fold from 0.59 in low-gravity reserves to 0.0046 in the highest-gravity reserves (Fig. 3*B*). Our study design meant that it was not possible to uncover the mechanisms responsible for this decline of ecological condition indicators within marine reserves along a gravity gradient, but this pattern of depletion is likely related to: (*i*) human impacts in the surrounding seascape (fishing, pollution, and so forth) affecting ecological processes (recruitment, feeding behavior, and so forth) within reserves (33, 34); (*ii*) almost every marine reserve is likely to have some degree of poaching, even where compliance is considered high (20, 35) and the cumulative impacts from occasional poaching events is probably higher in high-gravity situations; (*iii*) the life history of top predators, such as old age of reproduction and small clutch size for some (e.g., sharks), which makes then particularly susceptible to even mild levels of exploitation (36); and (*iv*) high-gravity marine reserves in our sample possibly being too young or too small to provide substantial conservation gains (11, 37). We conducted a supplementary analysis to further examine this latter potential explanation. Because of collinearity, we could not directly account for reserve size in our model, but conducted a supplemental analysis where we separated reserves into small (≤28 km^2) and large (*Materials and Methods* and *SI Appendix*, Fig. S3). We found that the biomass and probability of encountering top predators was higher in large compared with small reserves, but surprisingly, we found a flatter slope for small compared with large reserves (*SI Appendix*, Fig. S3). However, there were no large high-compliance reserves in high-gravity areas in our sample, likely due to the social and political difficulties in establishing large reserves near people (38). Because there is little overlap between large and small reserves along the gravity gradient in our sample, we are unable to distinguish the effects of reserve size from those of gravity, but this is an important area for future research. Additionally, we modeled how the relationship between gravity and our ecological outcomes changed with reserve age, comparing outcomes using the average reserve age (15.5 y) to those from reserves nearly twice as old (29 y, which was the third quartile of our global distribution in reserve age). Older reserves were predicted to sustain an additional 180 kg/ha (+66%) of fish biomass at the highest levels of gravity compared with average age reserves. However, the effects of reserve age on the probability of encountering a top predator was less marked: the modeled probability of encountering a top predator in older reserves (29 y) was only 0.01, compared with <0.005 for average age (~15 y) reserves, suggesting that small reserves common in high-gravity situations can support high levels of biomass, but are unlikely to sustain top predators, even when they are mature.

Although absolute fish biomass under all management categories declined with increasing gravity (Fig. 2*B*), the maximum expected conservation gains (i.e., the difference between openly fished and managed) differed by management type along the gravity gradient (Fig. 4*A*). Interestingly, the conservation gains for restricted fishing is highest in low-gravity situations, but rapidly declines as human impacts increase (Fig. 4*A*) (39). For marine reserves, biomass conservation gains demonstrated a hump-shaped pattern that peaked at very low gravity when predators were included in the biomass estimates (Fig. 4*A*, solid blue line). When top predators were excluded from biomass estimates, conservation gains peaked at intermediate gravity levels, and were higher in high gravity compared with low gravity (Fig. 4*A*, dotted blue line). Our results highlight how the expected differences between openly fished and marine reserves change along a gravity gradient, given a range of other social and environmental conditions that are controlled for within our model (*SI Appendix*, Fig. S1). Thus, differences in these trends are relative to average conditions, and individual reserves may demonstrate larger or smaller biomass build-up over time, which can vary by fish groups or families (e.g., ref. 40).

In an effort to minimize costs to users, many marine reserves, particularly the large ones, tend to be placed in remote locations that experience low human pressure (24, 41). However, critics of marine reserves in remote locations suggest that limited resources could be better spent protecting areas under higher threat that could potentially yield greater conservation gains (23, 24, 42). Our results make explicit the types of benefits—and the limitations—to placing reserves in high versus low human-impact locations. We found that for nontop predator reef fishes,

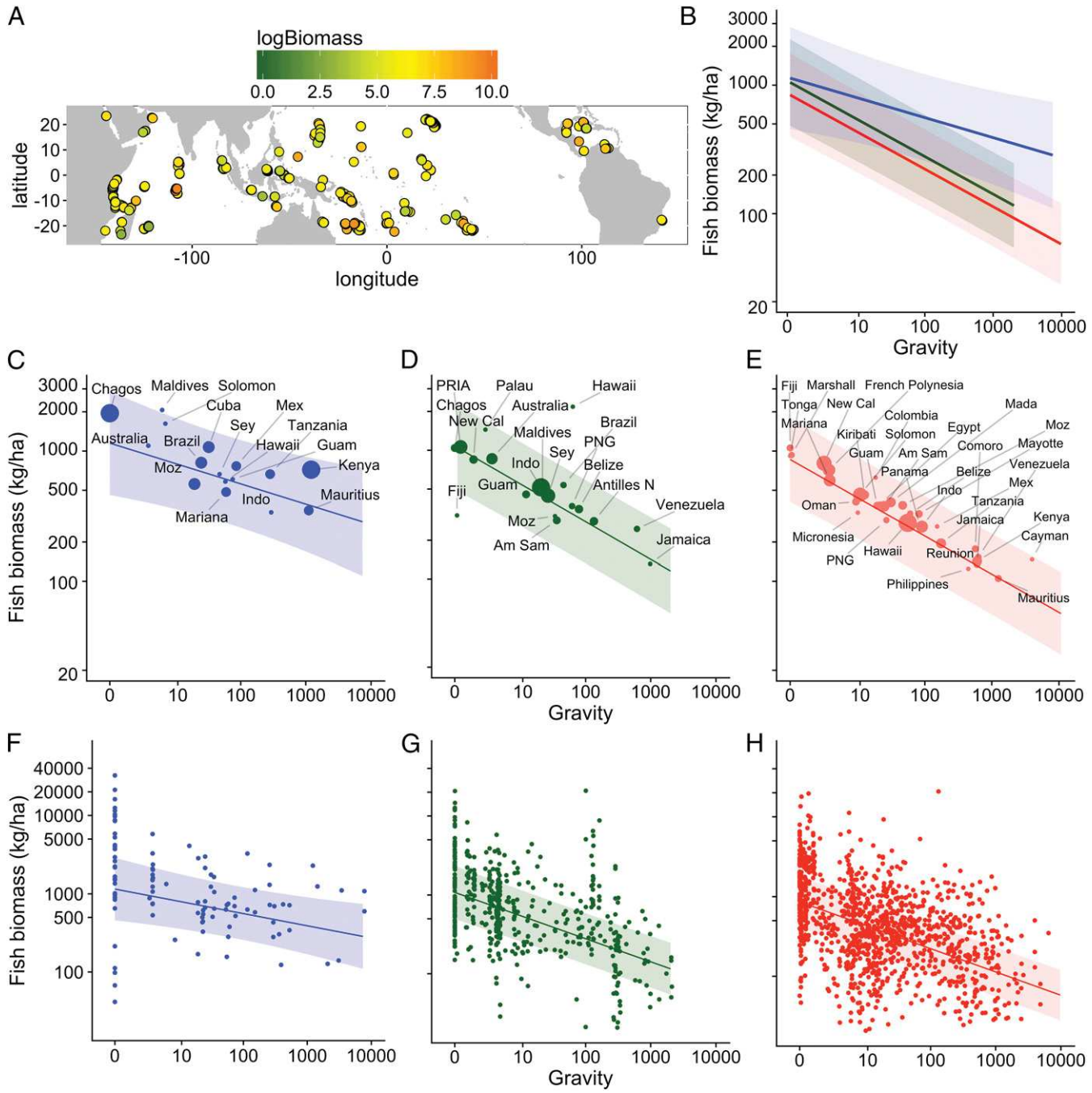

Fig. 2. Model-predicted relationships between human gravity and reef fish biomass under different types of fisheries management. (*A*) Map of our study sites with color indicating the amount of fish biomass at each site. (*B*) Model-predicted relationships of how reef fish biomass declines as gravity increases by management type. Partial plots of the relationship between biomass and gravity under different types of management at the nation/state (*C–E*), and reef site (*F–H*) scale; openly fished (red), restricted (green), and high-compliance marine reserves (blue). Shaded areas represent 95% confidence intervals. Bubble size in *C–E* reflect the number of reef sites in each nation/state, scaled for each management type (such that the largest bubble in each panel represent the highest number of sites per nation/state for that type of management) (*SI Appendix*, Table S5). Nation/state name abbreviations for *F–H* are in *SI Appendix*, Table S5.

substantial conservation gains can occur at even the highest-gravity locations but that optimal gains are obtained at moderate gravity (Fig. 4*A*). Our results also show that low-gravity marine reserves (and to a lesser extent low-gravity fisheries restrictions) are critical to support the presence of top predators (Fig. 3). However, the expected conservation gains for top predators declines rapidly with gravity in both marine reserves and restricted areas (Fig. 4*B*). Our results illustrate a critical ecological trade-off inherent in the placement of marine reserves: high-gravity reserves can have the substantial conservation gains for fish biomass, yet they are unlikely to support key ecosystem functions like predation, even with high levels of compliance. This highlights the importance of having clear objectives for conservation initiatives and recognizing the trade-offs involved (43, 44).

Our analysis does not allow us to uncover the mechanisms behind why we might observe the greatest differences in top predators between marine reserves and fished areas in low-gravity locations. A plausible explanation is that top predators, such as sharks, are

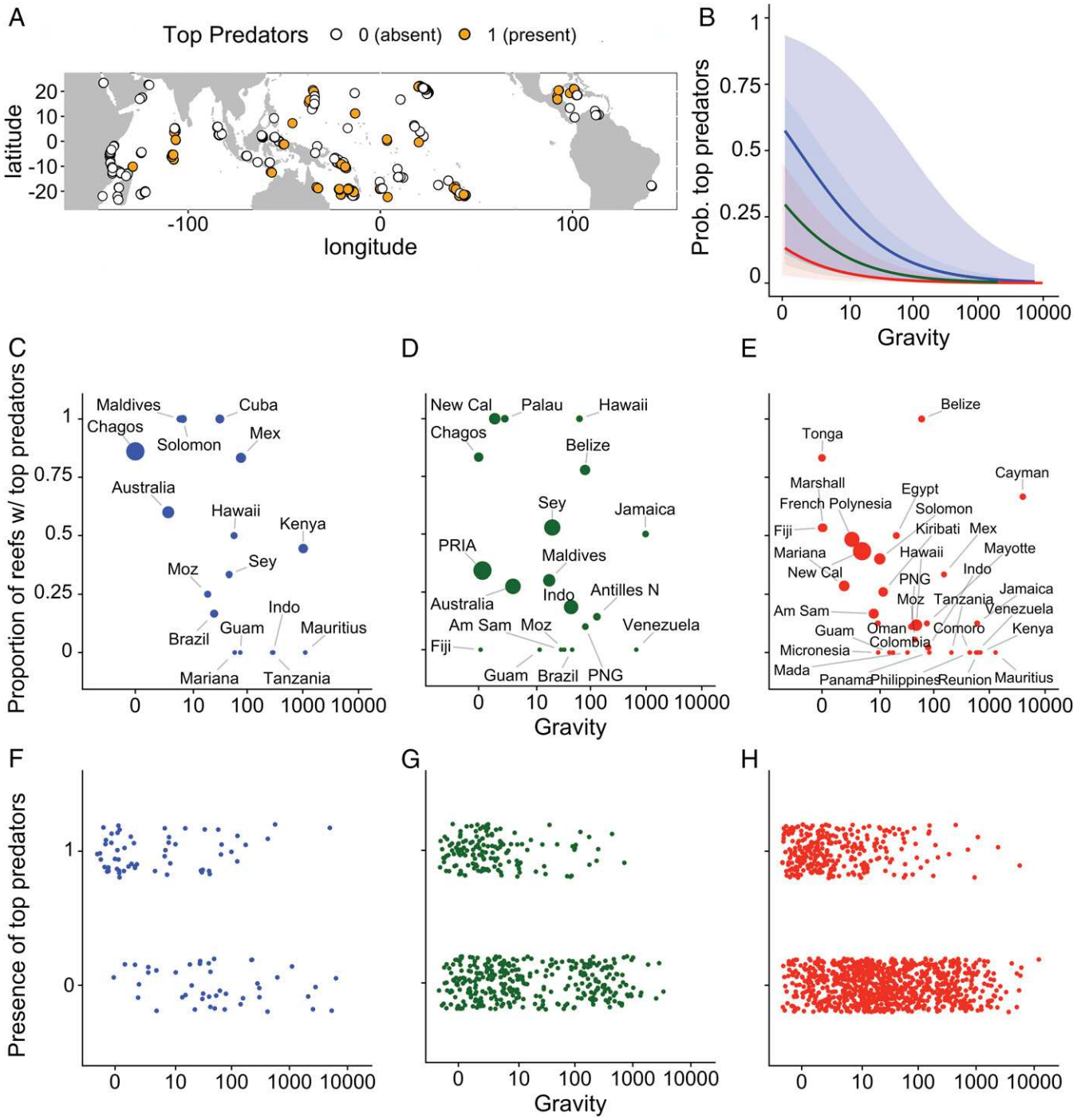

Fig. 3. Model-predicted relationships between human gravity and the probability of encountering top predators under different types of fisheries management. (*A*) Map of our study sites indicating the presence of top predators. (*B*) Model-predicted relationships of how the probability of encountering predators declines as gravity increases. Shaded areas represent 95% confidence intervals. The presence of top predators along a gravity gradient under different types of management at the nation/state (*C–E*) and site (*F–H*) scale; openly fished (red), restricted (green), and high-compliance marine reserves (blue). Bubble size in *C–E* reflect the number of reef sites in each nation/state, scaled for each management type (such that the largest bubble in each panel represent the highest number of sites per nation/state for that type of management) (*SI Appendix*, Table S5). Nation/state name abbreviations for *F–H* in *SI Appendix*, Table S5.

particularly vulnerable to fishing (17) and are exposed to some fishing even in the most remote fished areas, driven by the extremely high price for shark fins [shark fins can fetch US$960/kg in wholesale markets (45), compared with only $43/kg for parrotfish in European supermarkets (46)]. Thus, even small amounts of fishing in remote openly fished areas may be depleting top predators, which creates a large difference between low-gravity–fished areas and marine reserves. This difference may diminish along the gravity because top predators tend to have large home ranges (37), and there were only small reserves in high-gravity locations (*SI Appendix*, Fig. S3), which may mean that existing high-gravity reserves are not likely big enough to support the large home ranges of many predators (37, 47).

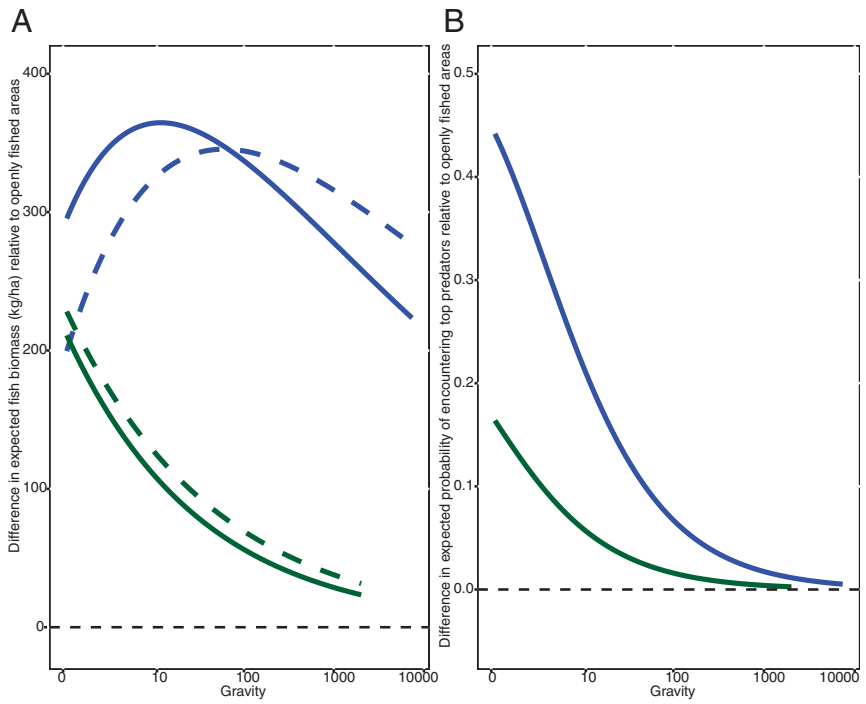

Fig. 4. The conservation gains (i.e., the difference between openly fished sites and managed areas) for high-compliance marine reserves (blue line) and restricted fishing (green line) for (*A*) target fish biomass (solid lines include biomass of top predators, dotted lines exclude top predator biomass as per *SI Appendix*, Fig. S2), and (*B*) the probability of encountering top predators change along a gradient of gravity.

Successful conservation also depends on a range of social considerations (48). For example, gear restrictions often have greater support from local fishers (49) and are usually implemented over greater reef areas than marine reserves. We show here that there are conservation gains produced by gear restrictions, although they are low relative to marine reserves (Fig. 4). Thus, in locations where a lack of support makes establishing marine reserves untenable, gear restrictions may still provide incremental gains toward achieving some conservation goals (8), particularly for specific fish groups and families (39).

As a supplemental analysis, we examined the conservation gains for biomass of nontarget species (*SI Appendix*, Figs. S1*D* and S4). This supplemental analysis addresses whether the effects of gravity on reef fish communities are from fishing or other impacts, such as sedimentation or pollution. We found very different patterns for nontarget species compared with target species, suggesting the relationship between target fish biomass and gravity (*SI Appendix*, Fig. S1) is primarily driven by fishing pressure.

Overall, our results demonstrate that the capacity to not only sustain reef fish biomass and the presence of top predators, but also the potential to achieve conservation gains, may be highly dependent on the level of human impact in the surrounding seascape. It is therefore essential to consider the global context of present and future human gravity in coral reef governance. Consequently, we calculated gravity of human impacts for every reef cell globally using a 10- × 10-km grid across the world's coral reefs (Fig. 5). Critically, the distribution of gravity varies substantially among regions, with the central and eastern Indo-Pacific demonstrating lower-gravity values. Even within a region, there can be substantial variability in gravity values. For example, the Central Indo-Pacific has highly contrasting gravity patterns, with Southeast Asian reefs (Fig. 5 *A*, *3*) generally showing extremely high-gravity values while Australian and Melanesian reefs (Fig. 5 *A*, *4*) are dominated by relatively low-gravity values.

The ways in which gravity will increase over time, and how the impacts of gravity on reef systems can be reduced, is of substantial concern for coral reef governance. The potential benefits of protecting locations that are currently remote could increase over time as human populations and the accessibility of reefs change (50). Demographic projections of high migration and fertility rates in some countries suggest substantial increases in coastal human populations in developing countries, where the majority of coral reefs are located (5, 51–53). Development projects that address high rates of fertility through improvements in women's education, empowerment, and the expansion of family-planning opportunities have successfully reduced fertility rates (54, 55). Such initiatives, when partnered with resource management, have the potential to be beneficial to both people and reefs. Demographic changes, such as increased migration in coastal areas, are also expected to be coupled with coastal development and road building that will increase the accessibility of reefs. For example, previously uninhabited areas have become more accessible, as evidenced by China's recent Belt and Roads Initiative and island-building enterprise in the South China Sea (56–58). Investments in sustainable planning of coastal development and road building could help to minimize unnecessary increases in reef accessibility. Importantly, stemming increases in gravity is only part of the potential solution space: it will also be important to dampen the mechanisms through which gravity operates, such that a given level of gravity can have a lesser impact on reef systems (1). People's environmental behavior is fundamentally driven by their social norms, tastes, values, practices, and preferences (59), all of which can be altered by policies, media, and other campaigns in ways that could change the local relationship between gravity and reef degradation.

Gravity Future Directions

Our gravity index (*Materials and Methods* and *Box 1*) makes several key assumptions that could potentially be refined in further applications. First, our application of gravity held friction constant across each specific type of surface (i.e., all paved roads had the same friction value). Future applications of more localized studies could vary travel time to reflect the quality of road networks, topographic barriers to access (such as cliffs), and the availability of technology. Similarly, future applications could also aim to incorporate local information about fishing fleet efficiency. Second, our adaptation of the gravity model (31) is unidirectional, assuming a constant level of attraction from any reef (i.e., gravity varies based on human population size, but not

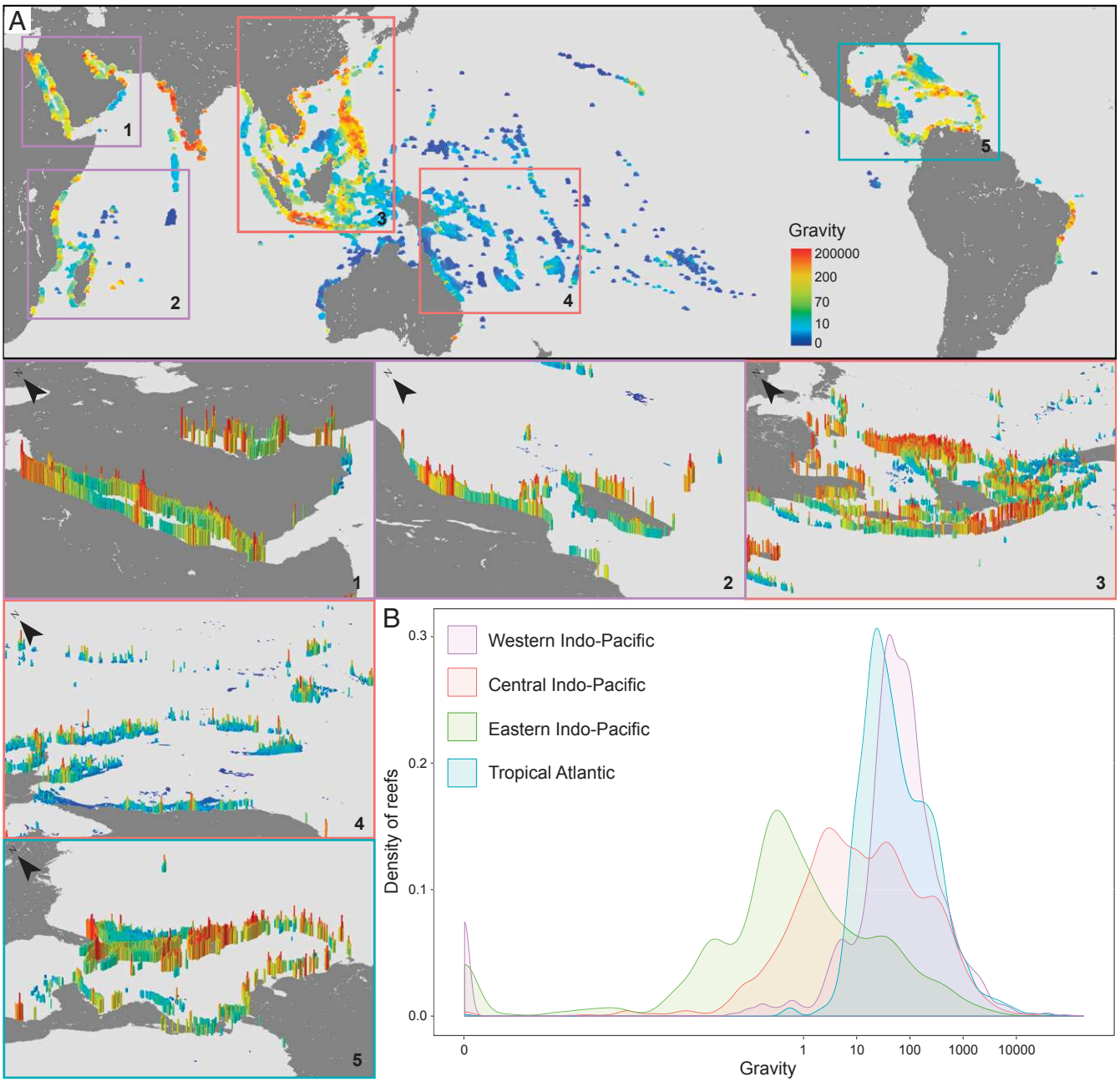

Fig. 5. Distribution of gravity on the world's coral reefs. (*A*) Map of gravity calculated for every coral reef in the world ranging from blue (low gravity) to red (high gravity). The four coral reef realms (70) are delineated. *Insets* highlight gravity for key coral reef regions of the world: (*1*) Red Sea, (*2*) Western Indian Ocean, (*3*) Southeast Asia, (*4*) Great Barrier Reef of Australia and the South Pacific, (*5*) Caribbean. For visual effect, gravity values in *Inset* maps are also given vertical relief, with higher relief indicating higher gravity values. (*B*) Distribution of gravity values per coral reef realm.

on the quality or quantity of fish on a specific reef). Reefs with more fish, or higher fish value, could be more attractive and exert a higher pull for exploitation (60). Likewise, societal values and preferences can also make certain fish more or less attractive. Our adaptation of gravity was designed to examine the observed conditions of reefs as a function of potential interactions with markets and local settlements, so our modification of the concept for this application was appropriate. However, future applications wishing to predict where reefs may be most vulnerable might wish to consider incorporating fish biomass or composition (i.e., potential market price of reef fish) in the gravity equation. Third, our database was not designed to look at ecological changes in a single location over time. However, future applications could examine whether ecological recovery in reserves (8) depends on the level of gravity present. To this end, we provide a global dataset of gravity for every reef pixel globally (*Materials and Methods*).

We demonstrate that human impacts deplete reef fish stocks and how certain types of management can mediate but not eliminate these pressures. In an era of increasing change, the global network of marine reserves may not safeguard reef fish communities from human impacts adequately enough to ensure key ecological functions, such as predation, are sustained. Efforts must be made to both reduce and dampen key drivers of change (1, 61), while maintaining or improving the well-being of reef-dependent people. Importantly, we find evidence that both

remote and human-surrounded reserves can produce different types of conservation gains. Ultimately, multiple forms of management are needed across the seascape to sustain coral reef fishes and the people who depend upon them.

Materials and Methods

Scales of Data. Our data were organized at three spatial scales: reef site (n = 1,798), reef cluster (n = 734), and nation/state (n = 41).

Reef site is the smallest scale, which had an average of 2.4 surveys (transects), hereafter referred to as "reef."

For reef cluster (which had an average of 2.4 ± 2.4 reef sites), we clustered reefs together that were within 4 km of each other, and used the centroid to estimate reef cluster-level social and environmental covariates. To define reef clusters, we first estimated the linear distance between all reef sites, then used a hierarchical analysis with the complete-linkage clustering technique based on the maximum distance between reefs. We set the cut-off at 4 km to select mutually exclusive sites where reefs cannot be more distant than 4 km. The choice of 4 km was informed by a 3-y study of the spatial movement patterns of artisanal coral reef fishers, corresponding to the highest density of fishing activities on reefs based on GPS-derived effort density maps of artisanal coral reef fishing activities (62). This clustering analysis was carried out using the R functions "hclust" and "cutree."

A larger scale in our analysis was "nation/state" (nation, state, or territory, which had an average of 44 ± 59 reef clusters), which are jurisdictions that generally correspond to individual nations (but could also include states, territories, overseas regions), within which sites were nested for analysis.

Targeted fish biomass. Reef fish biomass estimates were based on visual counts in 1,798 reef sites. All surveys used standard belt-transects, distance sampling, or point-counts, and were conducted between 2004 and 2013. Where data from multiple years were available from a single reef site, we included only data from the year closest to 2010. Within each survey area, reef-associated fishes were identified to species level, their abundance counted, and total length (TL) estimated, with the exception of one data provider who measured biomass at the family level. To make estimates of targeted biomass from these transect-level data comparable among studies, we did the following. (*i*) We retained families that were consistently studied, commonly targeted, and were above a minimum size cut-off. Thus, we retained counts of >10 cm diurnally active, noncryptic reef fish that are resident on the reef (14 families), excluding sharks and semipelagic species (*SI Appendix*, Table S1). We calculated total biomass of targeted fishes on each reef using standard published species-level length–weight relationship parameters or those available on FishBase (63). When length–weight relationship parameters were not available for a species, we used the parameters for a closely related species or genus. For comparison, we also calculated nontarget fish biomass (*SI Appendix*, Table S1). (*ii*) We directly accounted for depth and habitat as covariates in the model (see *Environmental Drivers*, below). (*iii*) We accounted for differences among census methods by including each census method (standard belt-transects, distance sampling, or point-counts) as a covariate in the model. (*iv*) We accounted for differences in sampling area by including total sampling area for each reef (m^2) as a covariate in the model.

Top predators. We examined the presence/absence of eight families of fish considered top predators (*SI Appendix*, Table S1). We considered presence/absence instead of biomass because biomass was heavily zero inflated.

Gravity. We first developed a gravity index for each of our reef sites where we had in situ ecological data. We gathered data on both population estimates and a surrogate for distance: travel time.

Population estimates. We gathered population estimates for each 1- by 1-km cell within a 500-km radius of each reef site using LandScan 2011 database. We chose a 500-km radius from the reef as a likely maximum distance fishing activities for reef fish are likely to occur.

Travel time calculation. The following procedure was repeated for each populated cell within the 500-km radius. Travel time was computed using a cost–distance algorithm that computes the least "cost" (in minutes) of traveling between two locations on a regular raster grid. In our case, the two locations were the centroid of the reef site and the populated cell of interest. The cost (i.e., time) of traveling between the two locations was determined by using a raster grid of land cover and road networks with the cells containing values that represent the time required to travel across them (32) (*SI Appendix*, Table S2), we termed this raster grid a "friction-surface" (with the time required to travel across different types of surfaces analogous to different levels of friction). To develop the friction-surface, we used global datasets of road networks, land cover, and shorelines:

Road network data were extracted from the Vector Map Level 0 (VMap0) from the National Imagery and Mapping Agency's (NIMA) Digital Chart of the World (DCW). We converted vector data from VMap0 to 1 km resolution raster.

Land cover data were extracted from the Global Land Cover 2000 (64).

To define the shorelines, we used the GSHHS (Global Self-consistent, Hierarchical, High-resolution Shoreline) database v2.2.2.

These three friction components (road networks, land cover, and shorelines) were combined into a single friction surface with a Behrmann map projection (an equal area projection). We calculated our cost-distance models in R using the *accCost* function of the "*gdistance*" package. The function uses Dijkstra's algorithm to calculate least-cost distance between two cells on the grid taking into account obstacles and the local friction of the landscape (65). Travel time estimates over a particular surface could be affected by the infrastructure (e.g., road quality) and types of technology used (e.g., types of boats). These types of data were not available at a global scale but could be important modifications in more localized studies.

Gravity computation. To compute gravity, we calculated the population of the cell and divided that by the squared travel time between the reef site and the cell. We summed the gravity values for each cell within 500 km of the reef site to get the "total gravity" within 500 km. We used the squared distance (or in our case, travel time), which is relatively common in geography and economics, although other exponents can be used (31) (Table S3).

We also developed a global gravity index for each 10- × 10-km grid of reef in the world (*Box 1*), which we provide as an open-access dataset. The procedure to calculate gravity was similar to above with the only difference being in the precision of the location; the former was a single data point (reef site), while the latter was a grid cell (reef cell). For the purpose of the analysis, gravity was log-transformed and standardized.

We also explored various exponents (1–3) and buffer sizes (50, 250, and 500 km) to build nine gravity metrics. The metric providing the best model, so with the lowest Akaike Information Criterion (AIC), was that with a squared exponent for travel time and a 500-km buffer (*SI Appendix*, Table S3).

Management. For each observation, we determined the prevailing type of management, including the following. (*i*) Marine reserve (whether the site fell within the borders of a no-take marine reserve): we asked data providers to further classify whether the reserve had high or low levels of compliance. For this analysis, we removed sites that were categorized as low-compliance reserves (n = 233). (*ii*) Restricted fishing: whether there were active restrictions on gears (e.g., bans on the use of nets, spearguns, or traps) or fishing effort (which could have included areas inside marine protected areas that were not necessarily no take). Or (*iii*) openly fished: regularly fished without effective restrictions. To determine these classifications, we used the expert opinion of the data providers, and triangulated this with a global database of marine reserve boundaries (66). We also calculated size (median = 113.6 km^2, mean = 217,516 km^2, SD = 304,417) and age (median = 9, mean = 15.5 y, SD = 14.5) of the no-take portion of each reserve. Reserve size was strongly related to our metric of gravity and could not be directly included in the analysis. We conducted a supplemental analysis where we separated reserves into small (≤28 km^2) and large (>65 km^2) based on a natural break in the data to illustrate: (*i*) how biomass and the presence of top predators might differ between small and large reserves; and (*ii*) how large reserves are absent in our sample in high gravity.

Other Social Drivers. To account for the influence of other social drivers that are thought to be related to the condition of reef fish biomass, we also included the following covariates in our model.

Local population growth. We created a 100-km buffer around each site and used this to calculate human population within the buffer in 2000 and 2010 based on the Socioeconomic Data and Application Centre gridded population of the world database. Population growth was the proportional difference between the population in 2000 and 2010. We chose a 100-km buffer as a reasonable range at which many key human impacts from population (e.g., land-use and nutrients) might affect reefs (67).

Human development index. Human development index (HDI) is a summary measure of human development encompassing a long and healthy life, being knowledgeable, and having a decent standard of living. In cases where HDI values were not available specific to the state (e.g., Florida and Hawaii), we used the national (e.g., United States) HDI value.

Population size. For each nation/state, we determined the size of the human population. Data were derived mainly from the national census reports CIA fact book (https://www.cia.gov/library/publications/the-world-factbook/rankorder/2119rank.html), and Wikipedia (https://en.wikipedia.org/wiki/Main_Page). For the purpose of the analysis, population size was log-transformed.

Environmental Drivers.

Depth. The depth of reef surveys was grouped into the following categories: <4 m, 4–10 m, >10 m to account for broad differences in reef fish community structure attributable to a number of interlinked depth-related factors. Categories were necessary to standardize methods used by data providers and were determined by preexisting categories used by several data providers.

Habitat. We included the following habitat categories. (*i*) Slope: the reef slope habitat is typically on the ocean side of a reef, where the reef slopes down into deeper water. (*ii*) Crest: the reef crest habitat is the section that joins a reef slope to the reef flat. The zone is typified by high wave energy (i.e., where the waves break). It is also typified by a change in the angle of the reef from an inclined slope to a horizontal reef flat. (*iii*) Flat: the reef flat habitat is typically horizontal and extends back from the reef crest for tens to hundreds of meters. (*iv*) Lagoon/back reef: lagoonal reef habitats are where the continuous reef flat breaks up into more patchy reef environments sheltered from wave energy. These habitats can be behind barrier/fringing reefs or within atolls. Back reef habitats are similar broken habitats where the wave energy does not typically reach the reefs and thus forms a less continuous "lagoon style" reef habitat. Due to minimal representation among our sample, we excluded other less-prevalent habitat types, such as channels and banks. To verify the sites' habitat information, we used the Millennium Coral Reef Mapping Project hierarchical data (68), Google Earth, and site depth information.

Productivity. We examined ocean productivity for each of our sites in milligrams of C per square meter per day (mg C m^{-2} d^{-1}) (www.science.oregonstate.edu/ocean.productivity/). Using the monthly data for years the 2005–2010 (in hdf format), we imported and converted those data into ArcGIS. We then calculated yearly average and finally an average for all these years. We used a 100-km buffer around each of our sites and examined the average productivity within that radius. Note that ocean productivity estimates are less accurate for nearshore environments, but we used the best available data. For the purpose of the analysis, productivity was log-transformed.

Climate stress. We included an index of climate stress for corals, developed by Maina et al. (69), which incorporated 11 different environmental conditions, such as the mean and variability of sea-surface temperature.

Analyses. We first looked for collinearity among our covariates using bivariate correlations and variance inflation factor estimates. This led to the exclusion of several covariates (not described above): (*i*) Biogeographic Realm (Tropical Atlantic, western Indo-Pacific, Central Indo-Pacific, or eastern Indo-Pacific); (*ii*) Gross Domestic Product (purchasing power parity); (*iii*) Rule of Law (World Bank governance index); (*iv*) Control of Corruption (World Bank governance index); (*v*) Voice and Accountability (World Bank governance index); (*vi*) Reef Fish Landings; (*vii*) Tourism arrivals relative to local population; (*viii*) Sedimentation; and (*ix*) Marine Reserve Size. Other covariates had correlation coefficients 0.7 or less and Variance Inflation Factor scores less than 5 (indicating multicollinearity was not a serious concern). Care must be taken in causal attribution of covariates that were significant in our model, but demonstrated collinearity with candidate covariates that were removed during the aforementioned process. Importantly, the covariate of interest in this study, gravity, was not strongly collinear with candidate covariates except reserve size ($r = -0.8$, $t = 3.6$, df = 104, $P = 0.0004$).

To quantify the relationships between gravity and target fish biomass, we developed a general linear-mixed model in R, using a log-normal distribution for biomass. To quantify the relationships between gravity and presence/absence of top predators, we developed a generalized linear-mixed model with a binomial family and a logit link function. For both models, we set reef cluster nested within nation/state as a random effect to account for the hierarchical nature of the data (i.e., reef sites nested in reef clusters, reef clusters nested in nation/states). We included an interaction between gravity and reserve age, as well as all of the other social and environmental drivers and the sampling method and total sampling area as covariates. We also tested interactions between gravity and management and used AIC to select the most parsimonious model. For fish biomass, the interaction between gravity and reserve age had AIC values >2 lower than the interaction between gravity and management (and a combination of both interactions). For the top predator models, both interactions were within 2 AIC values, so we chose the interaction with reserve age for consistency. All continuous covariates were standardized for the analysis, and reserve age was then normalized such that nonreserves were 0 and the oldest reserves were 1. In summary, our models thus predicted target fish biomass or probability of top predators being observed at the reef site scale with an interaction between gravity and reserve age, while accounting within the random factors for two bigger scales at which the data were collected (reef cluster, and nation/state) (*SI Appendix*), and key social and environmental characteristics expected to influence the biomass of reef fish (14). In addition to coefficient plots (*SI Appendix*, Fig. S1), we conducted a supplemental analysis of relative variable importance (*SI Appendix*, Table S4).

We ran the residuals from the models against size of the no-take areas of the marine reserves and no patterns were evident, suggesting it would explain no additional variance in the model. Trend lines and partial plots (averaged by site and nation/state) are presented in the figures (Figs. 2 *B–H* and 3*H*). We plotted the partial effect of the relationship between gravity and protection on targeted fish biomass and presence of top predators (Figs. 2 *B–G* and 3 *B–G*) by setting all other continuous covariates to 0 because they were all standardized and all categorical covariates to their most common category (i.e., 4–10 m for depth, slope for habitat, standard belt transect for census method). For age of reserves, we set this to 0 for fished and restricted areas, and to the average age of reserves (15.5 y) for reserves.

To examine the expected conservation gains of different management strategies, we calculated: (*i*) the difference between the response of openly fished areas (our counterfactual) and high-compliance marine reserves to gravity; and (*ii*) the difference between the response of openly fished areas and fisheries restricted areas to gravity. For ease of interpretation, we plotted conservation gains in kilograms per hectare (kg/ha; as opposed to log[kg/ha]) (Fig. 4*A*). A log-normal (linear) model was used to develop the slopes of the biomass (*i*) fished, (*ii*) marine reserve, and (*iii*) fisheries restricted areas, which results in the differences between (*i*) and (*ii*) and between (*i*) and (*iii*) being nonlinear on an arithmetic scale (Fig. 4*A*).

We plotted the diagnostic plots of the general linear-mixed model to check that the model assumptions were not violated. To check the fit of the generalized linear-mixed model, we used the confusion matrix (tabular representation of actual versus predicted values) to calculate the accuracy of the model, which came to 79.2%.

To examine homoscedasticity, we checked residuals against fitted values. We checked our models against a null model, which contained the model structure (i.e., random effects), but no covariates. We used the null model as a baseline against which we could ensure that our full model performed better than a model with no covariate information. In all cases our models outperformed our null models by more than 2 AIC values, indicating a more parsimonious model.

All analyses were undertaken using R (3.43) statistical package.

Data Access. A gridded global gravity data layer is freely available at dx.doi.org/10.4225/28/5a0e7b1b3cc0e. The ecological data used in this report are owned by individual data providers. Although much of these data (e.g., NOAA CRED data, and Reef Life Surveys) are already open access, some of these data are governed by intellectual property arrangements and cannot be made open access. Because the data are individually owned, we have agreed upon and developed a structure and process for those wishing access to the data. Our process is one of engagement and collaboration with the data providers. Anyone interested can send a short (one-half to one page) proposal for use of the database that details the problem statement, research gap, research question(s), and proposed analyses to the Principle Investigator and database administrator Joshua.cinner@jcu.edu.au, who will send the proposal to the data providers. Individual data providers can agree to make their data available or not. They can also decide whether they would like to be considered as a potential coauthor if their data are used. The administrator will then send only the data that the providers have agreed to make available.

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Community-wide scan identifies fish species associated with coral reef services across the Indo-Pacific

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Determining whether many functionally complementary species or only a subset of key species are necessary to maintain ecosystem functioning and services is a critical question in community ecology and biodiversity conservation. Identifying such key species remains challenging, especially in the tropics where many species co-occur and can potentially support the same or different processes. Here, we developed a new community-wide scan (CWS) approach, analogous to the genome-wide scan, to identify fish species that significantly contribute, beyond the socio-environmental and species richness effects, to the biomass and coral cover on Indo-Pacific reefs. We found that only a limited set of species (51 out of approx. 400, approx. 13%), belonging to various functional groups and evolutionary lineages, are strongly and positively associated with fish biomass and live coral cover. Many of these species have not previously been identified as functionally important and thus, may be involved in unknown, yet important, biological mechanisms that help sustain healthy and productive coral reefs. CWS has the potential to reveal species that are key to ecosystem functioning and services and to guide management strategies as well as new experiments to decipher underlying causal ecological processes.

1. Introduction

Within the context of global changes and biodiversity loss, effective ecosystem management relies on a better understanding of the causal pathways between ecological communities and the myriad of services they sustain [1–4]. Experiments that manipulate community compositions have unambiguously demonstrated the positive effect of species diversity on ecosystem functioning over short and long timescales [5–8]. Recent studies have also convincingly shown that natural species-rich communities are more productive and can deliver higher rates of ecosystem services than impoverished communities [9,10]. Beyond the mere number of species, the diversity of species traits and evolutionary histories has been shown to promote ecosystem functioning in both controlled experiments and natural communities [11–14]. In parallel, another

line of evidence suggests that particular species are key to ecosystem functioning as they contribute disproportionally to certain processes when present [15–19]. However, identifying these key species remains highly challenging in diverse ecosystems, such as tropical reefs or rainforests, where many species co-occur and can have multiple or unique contributions to ecosystem functions and services [17,20].

To tackle this challenge, ecologists can now use the increasing availability of extensive and standardized databases that have compiled environmental, social and ecological information across space and time [9,21]. This emergence of large social-ecological databases parallels what happened 20 years ago in genetics with advances in genome sequencing generating millions of genetic variants for individual loci. To identify genetic variants among this myriad of sequences that are more frequent in people with a particular disease or traits of biomedical significance, genome-wide scans or genome-wide association studies (GWAS) were developed [22]. Such an approach is powerful to relate a given biological feature or trait to its underlying genetics, based on the simple idea that if a genetic variant increases the frequency of a given trait it should be more frequent in individuals with this trait than expected by chance [23]. Although this approach does not attribute causality, it can uncover previously unsuspected, yet important, potential biological mechanisms and pathways [24]. Although similar approaches have not been used in ecology, they hold much promise in empirical community ecology where only a few, among dozens or even hundreds of species (the ecological equivalents of genetic variants) can disproportionally drive ecosystem functioning and the delivery of services (the equivalents of diseases, traits or phenotypes) [17,19,25]. This approach could also reveal the unknown level of ecological pleiotropy in communities, i.e. the propensity that a single species can be key to many ecological functions and services [26,27]. This term was initially coined by Strauss & Irwin [28] [29] by analogy to genetic pleiotropy, where one gene can influence two or more seemingly unrelated phenotypic traits. Under ecological pleiotropy a few species, so only a small fraction of biodiversity, may underpin many different ecosystem functions or services and would deserve particular conservation actions.

Identifying functionally important or key species is particularly challenging in biodiverse ecosystems, due largely to the complexity of interactions between species and with their environment including human disturbances. For example, despite the large body of research on coral reefs, the identification of fish species that disproportionally drive ecosystem functioning is still in its infancy [15,30]. The functional importance of most coral reef fishes is still poorly understood, and no study has scanned entire fish communities to detect potential links with ecosystem functioning and services at large scale. Here, we develop a new community-wide scan (CWS) approach, analogous to the GWAS approach, to identify key fish species that are linked to the delivery of services on coral reef ecosystems. Here 'key' has a different meaning than 'keystone' which corresponds to a 'species whose effect is large, and disproportionately large relative to its abundance' [31]. We define key species as those consistently and significantly associated, i.e. above a certain statistical threshold, to a certain level of ecosystem functioning or services.

More precisely, we propose a statistical framework and use empirical data from 1824 Indo-Pacific coral reefs hosting approximately 400 fish species to determine species whose presence is disproportionately related to fish biomass and live coral cover which insure, for instance, fisheries yield [32] and coastal protection [33], respectively. We then place those key species on a reef fish phylogeny, and in a functional trait space [34] to show the extent of species traits and evolutionary lineages that are necessary to sustain these two services on coral reefs. Identifying key species can provide new research priorities to elucidate ecological processes by which such candidate species positively affect coral reefs and to motivate a diversification of management options to maintain fish communities and their associated services in the face of a highly uncertain future.

2. Material and methods

(a) General framework

The community-wide scan (CWS) framework to identify species that are associated with higher levels of ecosystem services involves three steps (figure 1): (i) collecting environmental, socioeconomic, species presence and/or abundance, and indicators of ecosystem services data across many sites; (ii) modelling a given (or several) ecosystem service as a function of this large set of predictor variables (socioeconomic, environmental conditions and species richness). The accuracy and parsimony of this comprehensive initial, or reference, model (M_0) is validated according to its R^2 and its Akaike information criterion (AIC_{M0}), respectively; (iii) testing the effect of each species separately on each ecosystem service beyond the effect of previous variables including species richness. For this, the presence of a given candidate species in a community (coded as a binary variable) is added as an explanatory variable to M_0. The resulting model M_1, so the importance of the candidate species to explain variations of a given ecosystem service, is evaluated according to its AIC (AIC_{M1K}). A species is declared as a potential key contributor to the ecosystem service if ΔAIC ($AIC_{M0} - AIC_{M1k}$) greater than 4 and if its partial effect is positive (figure 1).

(b) Coral reef data

(i) Coral reef services

The proxies for coral reef services we considered are fish biomass and live coral cover which support, among many others, food security, shoreline protection and recreational value [32,33,35,36]. We used data from 1824 coral reefs in 26 nations/states located across the Indo-Pacific which include fish biomass (electronic supplementary material, figure S1) and live coral cover (electronic supplementary material, figure S2) estimates (see details in the electronic supplementary material).

(ii) Initial models and species candidates

For each of the 1824 reefs located in the Indo-Pacific we collected and used 12 relevant social and environmental variables (listed below), together with the occurrence, abundance and size of 739 reef fish species [21]. To build the initial model (M_0) and estimate the reference AIC_{M0} we modelled fish biomass and live coral cover using linear mixed models (LMMs) with the complete set of socioeconomic and environmental conditions plus species richness as predictor variables. For each of the 739-fish species present in this dataset, we estimated the number of reefs where a given fish species was present. To avoid results only influenced by a few reefs we chose to remove rare species. Rarity can be seen as a relative (compared to other species) or absolute (compared to the number of sampled reefs) concept while cutoffs are always subjective [37,38]. Here, we excluded species present on

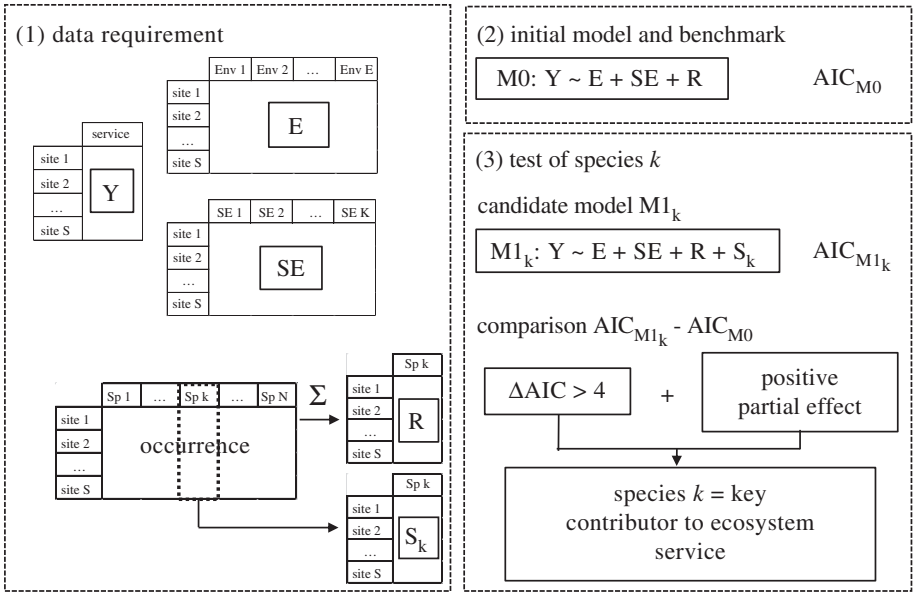

Figure 1. Statistical framework to assess the significant potential contribution of species to ecosystem services beyond the effects of environmental and socio-economic conditions and species richness. (1) Collecting datasets: for a (large) set of sites, variables describing a given ecosystem service (Y), environmental (E) and socioeconomic conditions (SE), and the occurrence of species. Species richness (R) is computed for each site from the sites-species matrix as well as the vector (Sk) with presence–absence of each species in sites. (2) The goal is to model a given ecosystem service (Y) according to environmental (E) and socio-economic conditions (SE) and species richness (R); to check its relevance according to its explanatory power and to save its AIC_{M0} as a reference for the next step. (3) The goal is to identify species key for the studied ecosystem service (Y) adding each candidate species (presence–absence, S_k) as an additional explanatory variable to M0 to compute model M1 and its associated AIC (AIC_{M1k}). Finally, a species is declared as a key potential contributor to the ecosystem service if ΔAIC ($AIC_{M0} - AIC_{M1k}$) > 4 and if its partial effect is positive (positive coefficient in the model).

less than 1% of the reefs (i.e. 18 and 7 reefs for fish biomass and coral cover dataset, respectively), so we retained 381 species which corresponds to roughly half (51%) of the species pool, a conservative threshold to define rarity [37]. These 381 fish species belonged to 116 genera and 30 families were considered as potential candidate species.

(iii) Identifying potential key contributors to ecosystem services

Each of the 381 species was tested as candidate for improving prediction of reef fish biomass and live coral cover given the socioeconomic and environmental conditions at each study site. More precisely, we tested presence of each candidate species as an additional explanatory binary variable to M_0 to compute model M_1 and its associated AIC (AIC_{M1K}). Finally, a species was identified as a potential key contributor to a given ecosystem service if, when included, ΔAIC greater than 4 and if its partial effect was positive (positive coefficient in the model). The binary variable describing the presence/absence of a species was strictly related to its occurrence in our study (i.e. presence of at least 1 individual) but could be also determined using any relative abundance threshold (figure 1 and electronic supplementary material).

(iv) Environmental and socioeconomic variables

The variables included in the models were environmental: (1) oceanic productivity, (2) habitat type, (3) depth and socioeconomic: (4) management (5) local human population growth rate, (6) gravity of local population, (7) gravity of markets, (8) levels of human development (human development index), (9) human population size, (10) levels of tourism, (11) degree of voice and accountability of citizens and (12) reef fish landings (details are provided in the electronic supplementary material).

(v) Statistical analyses

We first built two linear mixed models (LMM), which predicted fish biomass and live coral cover respectively, while accounting for the different scales at which the data were collected as random effects (reef site, location and nation/state, electronic supplementary material), with 12 key environmental and socioeconomic variables expected to influence reef conditions [21,39] and fish species richness as fixed effects (electronic supplementary material). To evaluate the fit of the two linear mixed models, we checked the relationship between observed and predicted values. Model validation and quality control procedures are described in the electronic supplementary material.

In order to quantify the potential net benefit of each identified key species, we extracted the net effect of each key species for biomass and live coral cover using a partial plot from linear mixed models while the other variables were held constant.

We next investigated whether reefs with several key species show high levels of fish biomass and live coral cover. To control for the effects of species richness we compared modelled estimates of fish biomass and live coral between reefs while increasing the number of key species. We estimated the number of key species present on each reef and chose the richest quartile as a threshold (i.e. four and six key species for biomass and live coral cover respectively). We next created three categories of reefs: those with no key species, those with at least one key species but below the richness threshold (four and six for biomass and live coral cover, respectively) and those with more key species than the threshold.

(vi) Functional space and entities

The 381 candidate fish species were functionally described using six traits: (1) size, (2) mobility, (3) period of activity, (4) schooling, (5) vertical position in the water column and (6) diet. Values for these six traits were taken from the global trait database on tropical reef fishes from Mouillot *et al.* [40] (electronic supplementary material). The 381 candidate species represented 240 functional entities and most functional entities comprise species from different genera [40].

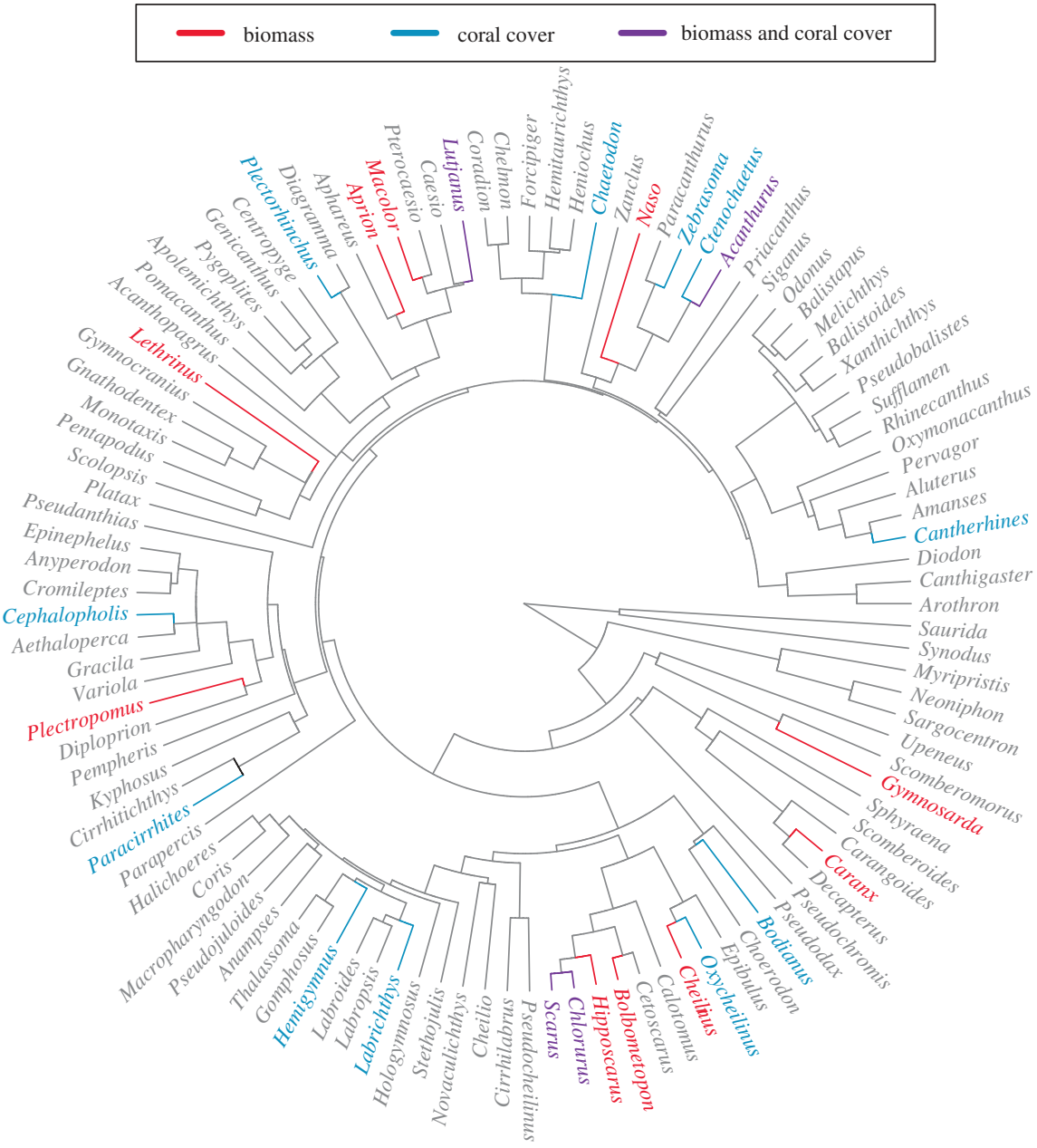

Figure 2. Positions of key species for biomass (red), live coral cover (blue) or both of them (purple) represented as their corresponding fish genera in the Tree of Life of Coral Reef Fishes, adapted from Near *et al*. [42]. The 26 key species for biomass represent 16 genera while the 28 key species for coral cover represent 15 genera with 4 common genera. *Elagatis* and *Parupeneus* genera are missing.

We assessed functional richness (FRic), i.e. the functional space occupied by the key fish species for biomass and coral cover respectively, using the convex hull volume index proposed by Cornwell *et al*. [41]. This volume corresponds to the amount of multidimensional (four in our case) functional space filled by key species, where axes are defined by species traits.

(vii) Fish phylogeny

We used a phylogeny of Acanthomorph fishes [42] which covers all 30 reef fish families of the present study (electronic supplementary material, table S1). Some fish genera (e.g. *Elagatis* and *Parupeneus*) recorded on reefs were missing in this phylogeny.

3. Results

(a) Predictability of fish biomass and coral cover

The two initial (M0) models explained 79% and 61% of the variance in fish biomass and live coral cover, respectively (electronic supplementary material, figure S3). The residuals of the two models were normally distributed (electronic supplementary material, figure S3). In total, eight and six variables had the highest importance (Akaike weight = 1) in predicting fish biomass and live coral cover, respectively (electronic supplementary material, tables S2, S3). Fish species richness, oceanic productivity, population size, tourism and census method were the main predictors of both fish biomass and coral cover. Depth, management and sampling area were also important predictors of fish biomass while habitat type was important in predicting coral cover (electronic supplementary material, tables S2, S3).

(b) Key species associated with reef fish biomass

Among the 381 fish species considered as candidates, only 26 species (7%) were significantly related to fish biomass beyond the initial set of variables ($\Delta AIC > 4$ and positive effect), after considering their presence (at least one

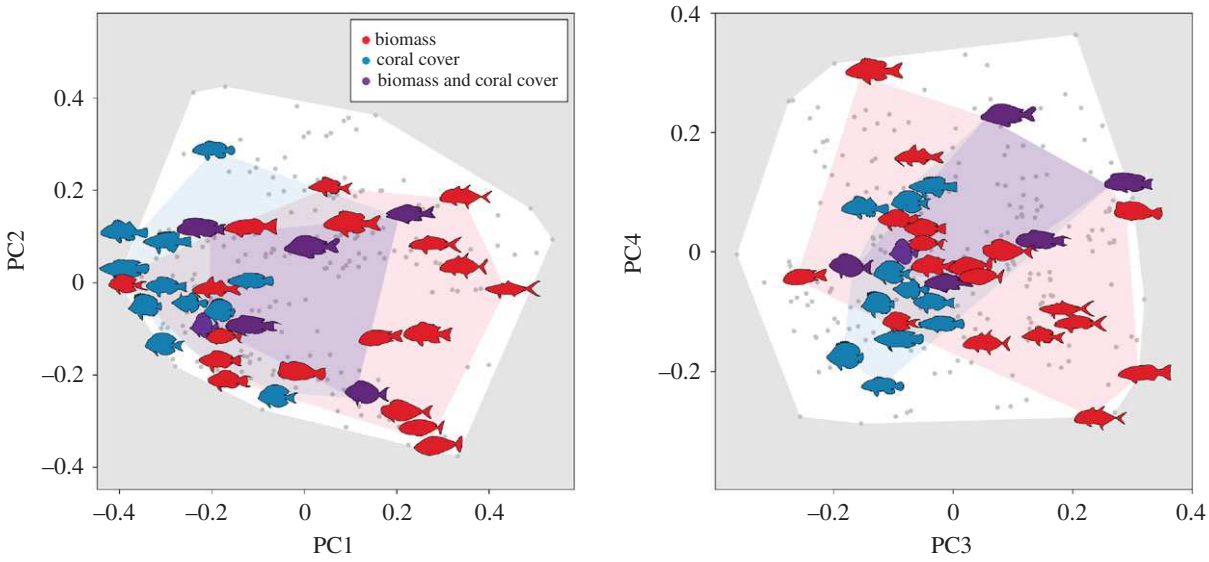

Figure 3. In total, 51 fish species which correspond to 35 out of 240 functional entities (15%) have been identified as strongly related to high biomass (18 red shapes), high live coral cover (11 blue shapes) or both of them (6 purple shapes). The positions those 35 functional entities in the four-dimensional functional space are defined according to species trait values. Fish shapes were chosen to illustrate the main genus of the species comprised in each functional entity, other functional entities are represented with grey dots. Coloured areas represent the functional volume filled by the functional entities strongly related to high biomass (red, FRic = 0.2), high live coral cover (blue, FRic = 0.05), both of them (purple, FRic = 0.01) or all functional entities (e.g. all species, white) present in the dataset.

individual) (electronic supplementary material, table S4). Those 26 key species covered a wide breadth of phylogenetic lineages (figure 2), representing 16 out of 116 genera and 8 out of 30 families (i.e. Acanthuridae, Carangidae, Labridae, Lethrinidae, Lutjanidae, Mullidae, Scombridae, Serranidae).

When considering functional traits, we found that those 26 key species represented 24 different functional entities (electronic supplementary material, table S6) demonstrating a very low functional redundancy with 1.1 species per functional entity (median = 1; range: 1–2). In addition, key species had contrasting functional traits with all body sizes (from 10 cm to greater than 50 cm) and all diets (seven trophic categories) represented (electronic supplementary material, table S6). Together these 26 key species filled 20% of the whole functional space defined by the 240 functional entities corresponding to the 381 candidate species (FRic = 0.20; figure 3).

(c) Key species associated with live coral cover

We found that 28 reef fish species out of 381 (7%) were significantly and positively related to coral cover ($\Delta AIC > 4$), after considering their presence (electronic supplementary material, table S5). Those 28 key species also encompassed a wide breadth of phylogenetic lineages (figure 2), representing 15 out of 116 genera and 8 out of 30 families (i.e. Acanthuridae, Chaetodontidae, Cirrhitidae, Haemulidae, Labridae, Lutjanidae, Monacanthidae, Serranidae).

When considering functional traits, we found that the 28 key fish species were distributed among 17 different functional entities (electronic supplementary material, table S6). Key fish species with regard to coral cover showed some degree of functional redundancy with, on average, 1.6 key species per functional entity (median = 1; range: 1–6 species). This higher functional redundancy translated into a more restricted functional space filled by these key species (only 5% with FRic = 0.05; figure 3). Species of all sizes (from 10 cm to greater than 50 cm) and almost all diets (six diet categories out of seven) were significantly associated with live coral cover. However, large mobile predators and large herbivorous fishes were not considered as key for live coral cover (electronic supplementary material, table S6).

(d) Low overlap between key species with regard to fish biomass and coral cover

The two sets of key species associated with total fish biomass and live coral cover (26 and 28 key species, respectively) each represented less than 10% of the 381 fish species tested as candidates. Only three species (*Acanthurus albipectoralis, Lutjanus bohar, Lutjanus gibbus)* were common to both sets while four genera (*Acanthurus, Chlorurus, Lutjanus and Scarus*) and four families (Acanthuridae, Labridae, Lutjanidae and Serranidae) presented key species significantly associated with the two reef services (figure 2, electronic supplementary material, table S6).

Only six functional entities were common and significantly associated with both biomass and live coral cover (figure 3), namely small and medium herbivores, small planktivores, medium and large fishes targeting mobile invertebrates and meso-predators (electronic supplementary material, table S6).

(e) The net benefit of key species for fish biomass and live coral cover

When present, each key species belonged to a community with a median level of fish biomass higher (560 kg ha^{-1}, range: 439–773 kg ha^{-1}) than the median biomass observed when absent (370 kg ha^{-1}, range: 337–385 kg . ha^{-1}). Similarly, live coral cover was estimated at a median value of 50% (range: 36–82%) when each key species was present against 34% (range: 26–38%) when absent (figure 4). For clarity, we only presented the net effect of the four most

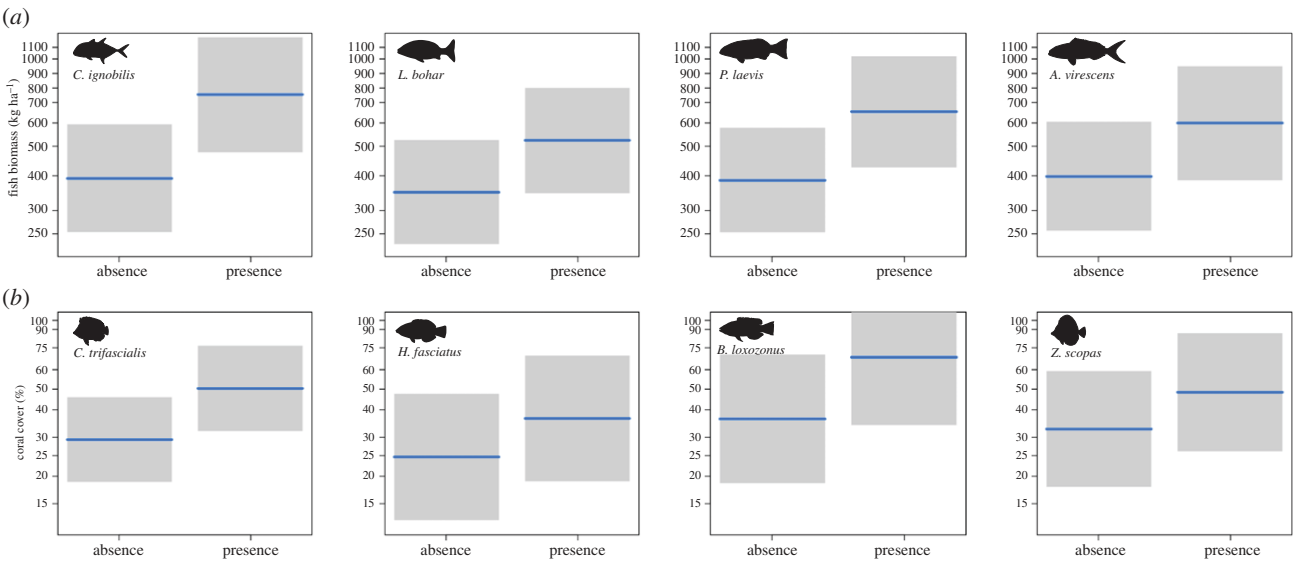

Figure 4. Net effect of the four most significant (lowest AIC) key fish species when present for fish biomass (*a*) and live coral cover (*b*) (among the 26 and 28 key species, respectively) using a partial plot from the linear mixed models while the other variables are held constant. When present, each key species is linked to a median level of biomass and live coral cover significantly ($p < 0.05$) higher than the level observed where absent. (Online version in colour.)

significant key species (lowest AIC, electronic supplementary material, tables S4, S5) associated with biomass and live coral cover (figure 4). Importantly, these four most significant key species (lowest AIC) were not necessarily related to the highest level of biomass and coral cover (electronic supplementary material, figure S4).

It is not only individual key species, but also the accumulation of key species that was linked to high levels of ecosystem services. For instance, reefs with more than four key species reached a median level of biomass of 1,150 kg ha^{-1} (range: 362–3,715 kg ha^{-1}), i.e. three times the median biomass observed (370 kg ha^{-1}, range: 86–1,380 kg ha^{-1}) in reefs with an intermediate number of key species (from 1 to 3 key species) and more than seven times higher than the median level of fish biomass reached in reefs having no key species (156 kg ha^{-1}, range: 12–812 kg ha^{-1}). Although less pronounced, reefs with at least six key fish species showed a median live coral cover of 40% (range: 20–68%) while reefs with no key species had a median level of 31% (range: 18–54%) live coral cover (figure 5).

4. Discussion

(a) Sustaining healthy and productive coral reefs

Even if the purpose of the present study was not to disentangle effects of anthropogenic, environmental and biodiversity drivers on fish biomass and coral cover, we found consistent results (electronic supplementary material, tables S2, S3) with previous large-scale studies highlighting the primary importance of human density, species richness and ocean productivity on fish biomass and coral cover [43–45].

In the present study, many different fish species (approx. 400 candidate species) were scanned and only 26 and 28 species were identified as significantly and positively related to fish biomass and live coral cover, respectively, with only three species being common to both. In total, these 51 species (i.e. approx. 13% of the species pool tested) represent 35 distinct functional entities (out of 240, i.e. 15%) that are widespread in the functional space. While large-bodied species may be expected to disproportionately contribute to fish biomass, our results indicate that only 25% (7 out of 26, electronic supplementary material, table S6) of key species for fish biomass were large-bodied (greater than 50 cm), which is directly comparable to the percentage of large-bodied species among the initial candidate species (24% or 91 fish species out of 381). In addition, 35% of key species for fish biomass were smaller than 30 cm (9 out of 26, electronic supplementary material, table S6). The positive association with fish biomass is thus independent of body size.

It comes as no surprise that some key fish species identified in this study have already attracted considerable interest in coral reef ecology. Herbivorous fish support coral reef resilience by preventing coral–algal phase shifts [17,29,46–49], and, therefore, may contribute to the maintenance of high coral cover and fish biomass. In particular, scarine parrotfishes (i.e. *Bolbometopon*, *Chlorurus*, *Hipposcarus* and *Scarus*, electronic supplementary material, tables S4–S6) play critical roles as grazers and bioeroders of the reef substratum [50,51], and their abundances have strong positive effects on cover of corals and hence accretion rates of the reef [52]. Further, grazing and detritivorous acanthurids (i.e. *Acanthurus* and *Ctenochaetus*, electronic supplementary material, tables S4–S6) intensely graze epilithic algal turfs [49,53], while benthic-feeding unicornfishes (i.e. *Naso*, electronic supplementary material, tables S4, S6) play a significant role in macroalgal removal [30,54].

By contrast, some key species identified in the present study have not previously been identified as playing significant roles. While predation is a key process shaping prey behaviour and populations [55], structuring ecological communities [56] and promoting nutrient capacity [57], no individual predator species have been expressly identified. Here, we show that predatory species like *Aprion*, *Caranx*, *Cephalopholis*, *Elagatis*, *Gymnosarda*, *Lethrinus*, *Lutjanus*, *Oxycheilinus* and *Plectropomus* (figure 4, electronic supplementary material, S4 Tables S4, S5) may play a critical role for fish biomass and live coral cover, although the exact pathways through which they act remain to be elucidated.

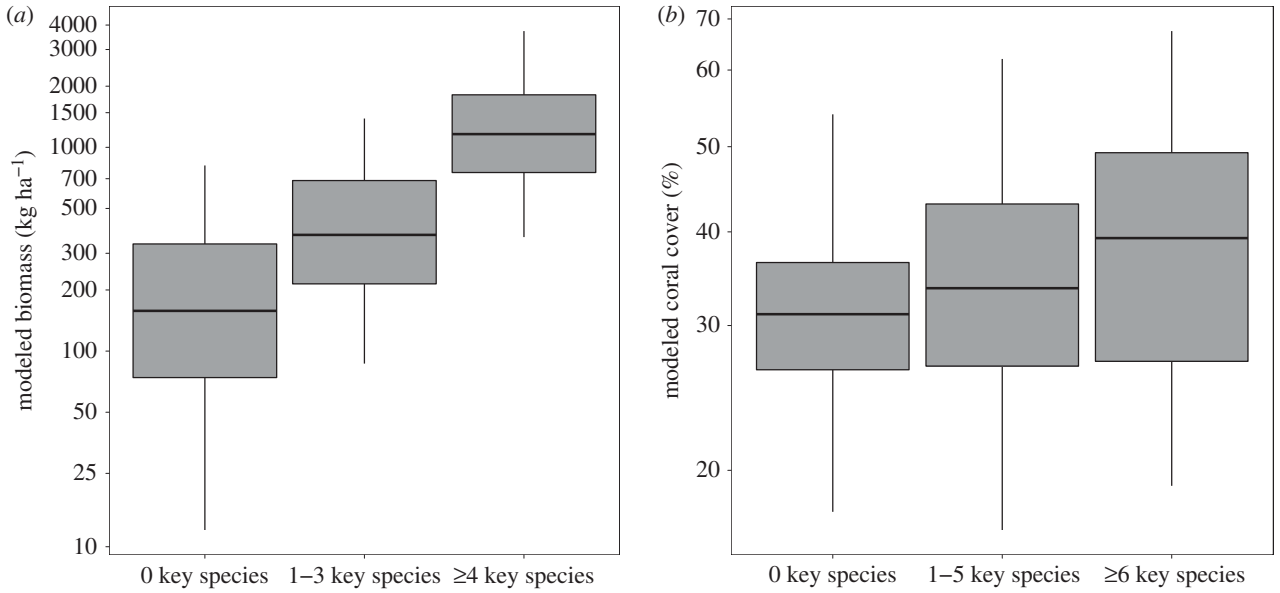

Figure 5. The accumulation of key species co-occurring on coral reefs is positively related to fish biomass (*a*) and live coral cover (*b*). To control for positive effect of species richness on ecosystem functioning, we compared modelled estimates of fish biomass and live coral between reefs while increasing the number of co-occurring key species. Reef with the highest number of co-occurring key species reached higher levels of biomass (1150 kg ha^{-1}) and coral cover (40%) than their counterparts having no key species (156 kg ha^{-1}, 31%, respectively). Distributions are represented using 95% confidence intervals.

(b) Low ecological pleiotropy on coral reefs

The finding that a limited number of functionally and evolutionary different species are positively related to high levels of fish biomass and coral cover (figures 2, 3, electronic supplementary material, S4) supports the idea that sustaining ecosystem services may require a large breadth of particular attributes beyond the number of species [14,58]. The limited overlap between the two sets of species significantly associated with two reef services (three species, four genera and six functional entities) suggests a low level of ecological pleiotropy [28], i.e. that a single species, genus or functional entity cannot be key to many independent ecosystem functions and services. Extended to the community level, we show that ecological pleiotropy, the opposite of functional redundancy, is not the norm on coral reefs. This finding may explain why the multi-functionality of ecosystems relies more strongly on biodiversity than do single functions [6,14,58,59], because some species play unique and thus irreplaceable roles in ecosystems [25,60]. However, it is important to keep in mind that the results may change depending on which traits and functions are considered in the analysis, and a number of yet unknown but relevant traits or functions not considered here could be included in future studies. We suggest that this ecological pleiotropy reconciles two opposing views in biodiversity and ecosystem functioning (BEF) research because many complementary species groups and lineages, and hence a large amount of biodiversity, are necessary to sustain ecosystem multi-functionality and associated services. Rather than providing multiple functions individually, those key species appear to provide high benefits in terms of fish biomass and live coral cover once combined (figure 5). Maintaining habitat heterogeneity and high regional species diversity is thus a major component of management and conservation. Our results call for more species-focused management strategies such as the banning of fishing species considered as key for the ecosystem [17]. Additionally, sustaining multi-functionality also requires a broader portfolio approach which may reduce local extinction risk by securing the biodiversity level in an increasingly uncertain future [61].

(c) Community-wide scan as a flexible framework to link biodiversity to ecosystem functioning and services

The CWS approach can be adapted for a wide range of ecosystems, combinations of taxa or interactions and services. Here, we only tested the presence of key species, while it would be possible to look for key species groups (pairs or more), key evolutionary lineages or even key biotic interactions. Since those interactions are potentially multiple in species-rich communities they cannot be experimentally tested but they can emerge from empirical data using the CWS approach. The way candidates are tested can be modified while respecting independence between predicted and explanatory variables. As positive effects of some species may only be revealed beyond particular thresholds, presence data can also be determined by any abundance threshold such as a minimum number of individuals, cover rate, biomass or level of interactions.

On coral reefs, defining species presence based on distribution of its biomass across study area (using upper percentiles or deciles) can promote the inclusion of small-bodied species but can also discriminate against species that are not commonly encountered or have skewed biomass distributions (electronic supplementary material, tables S7–S10). Rather, defining species presence according to its relative biomass in communities can be applied independently of the species biomass distribution. However, we found consistent results between these two procedures because the majority of species detected as key species using the intracommunity approach are also significant using the intraspecific approach, reinforcing the robustness of our findings.

CWS studies can also be considered as initial forays into a better understanding of the complex relationships between

particular species, species groups or interactions and ecosystem processes or services. Some false-positives, species being detected as key while they are not, may be revealed. Furthermore, no causality is determined in this approach; the main merit is to identify unsuspected and statistically significant positive associations. The logical progression would be to conduct experiments focusing on potential key species with the ultimate aim of highlighting the underlying ecological or biological processes that potentially sustain healthy and productive ecosystems.

5. Conclusion

The CWS approach has the potential to reveal unsuspected contributions to ecosystem functioning and its associated services, especially in complex and biodiverse ecosystems where the detection of such contributions remains challenging. The CWS approach holds much promise in empirical BEF studies where only a few species, functional or phylogenetic groups, can disproportionally drive ecosystem functioning and the delivery of services. Our framework offers a new and flexible way to analyse the ongoing massive empirical data relating biodiversity to ecosystem functioning and services with the potential to reconcile two opposing views: species identity versus diversity. Given the growing interest in the assessment and consequences of the ongoing extinction crisis on ecosystem functioning, such a framework is extremely timely and widely applicable.

Ethics. The study procedures were approved by the Institutional Review Board at the University of Montpellier.

Data accessibility. Fish biomass and coral cover dataset, fish presence and fish functional traits on Dryad: http://dx.doi.org/10.5061/dryad.45dc7qj [62].

Authors' contributions. E.M., S.V., N.A.J.G. and D.M. conceived the study; E.M. developed and ran the analyses, wrote the first draft of the manuscript and all the authors made substantial contributions.

Competing interests. The authors declare no competing interests.

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LETTER

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Bright spots among the world's coral reefs

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Ongoing declines in the structure and function of the world's coral reefs[1,2] require novel approaches to sustain these ecosystems and the millions of people who depend on them[3]. A presently unexplored approach that draws on theory and practice in human health and rural development[4,5] is to systematically identify and learn from the 'outliers'—places where ecosystems are substantially better ('bright spots') or worse ('dark spots') than expected, given the environmental conditions and socioeconomic drivers they are exposed to. Here we compile data from more than 2,500 reefs worldwide and develop a Bayesian hierarchical model to generate expectations of how standing stocks of reef fish biomass are related to 18 socioeconomic drivers and environmental conditions. We identify 15 bright spots and 35 dark spots among our global survey of coral reefs, defined as sites that have biomass levels more than two standard deviations from expectations. Importantly, bright spots are not simply comprised of remote areas with low fishing pressure; they include localities where human populations and use of ecosystem resources is high, potentially providing insights into how communities have successfully confronted strong drivers of change. Conversely, dark spots are not necessarily the sites with the lowest absolute biomass and even include some remote, uninhabited locations often considered near pristine[6]. We surveyed local experts about social, institutional, and environmental conditions at these sites to reveal that bright spots are characterized by strong sociocultural institutions such as customary taboos and marine tenure, high levels of local engagement in management, high dependence on marine resources, and beneficial environmental conditions such as deep-water refuges. Alternatively, dark spots are characterized by intensive capture and storage technology and a recent history of environmental shocks. Our results suggest that investments in strengthening fisheries governance, particularly aspects such as participation and property rights, could facilitate innovative conservation actions that help communities defy expectations of global reef degradation.

Despite substantial international conservation efforts, diversity and abundance continue to decline within many of the world's ecosystems[1,7]. Most conservation approaches aim to identify and protect places of high ecological integrity under minimal threat[8]. Yet, with escalating social and environmental drivers of change, conservation actions are also needed where people and nature coexist, especially where human effects are already severe[9]. Here, we highlight an approach for implementing conservation in coupled human–natural systems focused on identifying and learning from outliers—places that are performing substantially better than expected, given the socioeconomic and environmental conditions they are exposed to. By their very nature, outliers deviate from expectations, and consequently can provide novel insights into confronting complex problems where conventional solutions have failed. This type of positive deviance, or bright spot analysis has been used in fields such as business, health, and human development to uncover local actions and governance systems that work in the context of widespread failure[10,11], and holds much promise in informing conservation.

To demonstrate this approach, we compiled data from 2,514 coral reefs in 46 countries, states, and territories (hereafter 'nations/states') and developed a Bayesian hierarchical model to generate expected conditions of how standing reef fish biomass (a key indicator of resource availability and ecosystem functions[12]) was related to 18 key environmental variables and socioeconomic drivers (Fig. 1; Extended Data Tables 1–4; Extended Data Figs 1–3; Methods). Drawing on a broad body of theoretical and empirical research in the social sciences[13–15] and ecology[2,6,16] on coupled human–natural systems, we quantified how reef fish biomass (Fig. 1a) was related to distal social drivers such as markets, affluence, governance, and population (Fig. 1b, c), while controlling for well-known environmental conditions such as depth,

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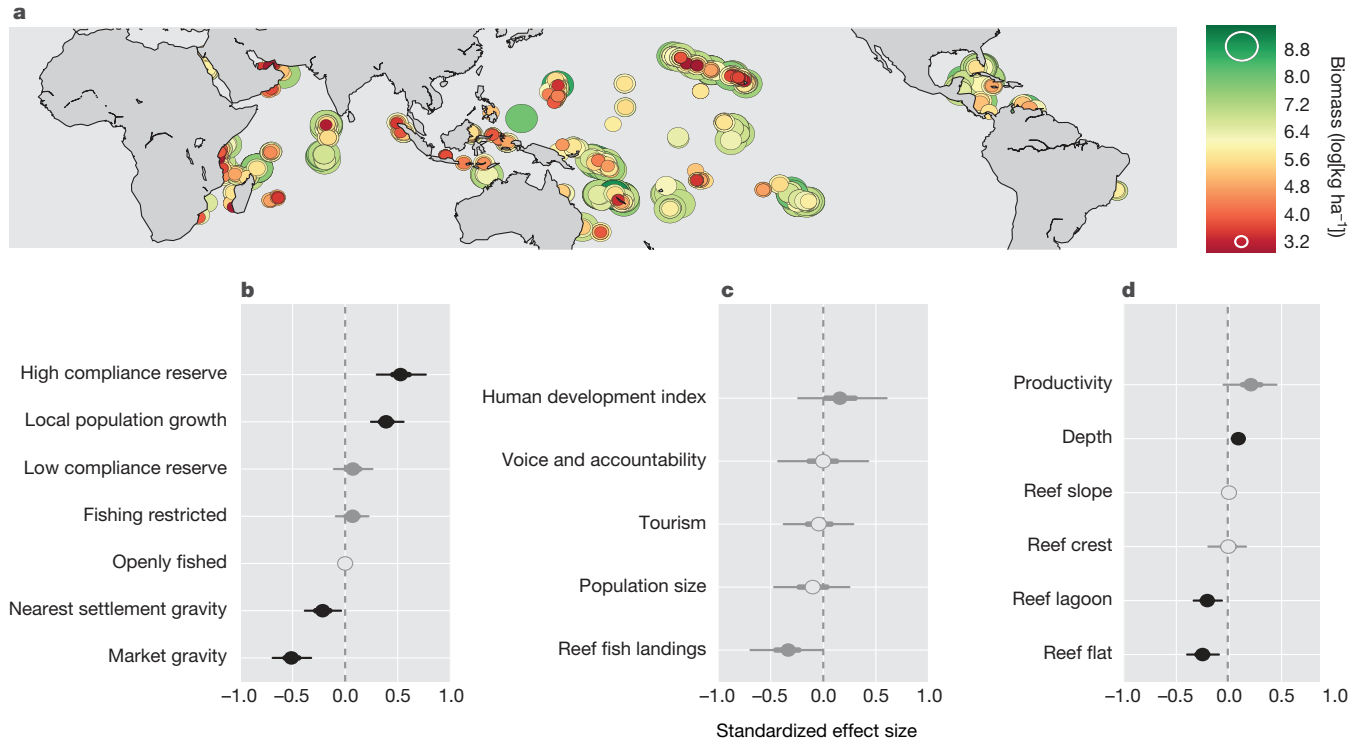

Figure 1 | Global patterns and drivers of reef fish biomass. a, Reef fish biomass among 918 study sites. Points vary in size and colour proportional to the amount of fish biomass. **b–d**, Standardized effect size of local-scale social drivers, nation/state-scale social drivers, and environmental covariates, respectively. Parameter estimates are Bayesian posterior median values, 95% uncertainty intervals (UI; thin lines), and 50% UI (thick lines). Black dots indicate that the 95% UI does not overlap 0; grey closed circles indicates that 75% of the posterior distribution lies to one side of 0; and grey open circles indicate that the 50% UI overlaps 0.

habitat, and productivity (Fig. 1d) (Extended Data Table 1; Methods). In contrast to many global studies of reef systems that are focused on demonstrating the severity of human effects[6], our examination seeks to uncover potential policy levers by highlighting the relative role of specific social drivers. A key finding from our global analysis is that our metric of potential interactions with urban centres, called market

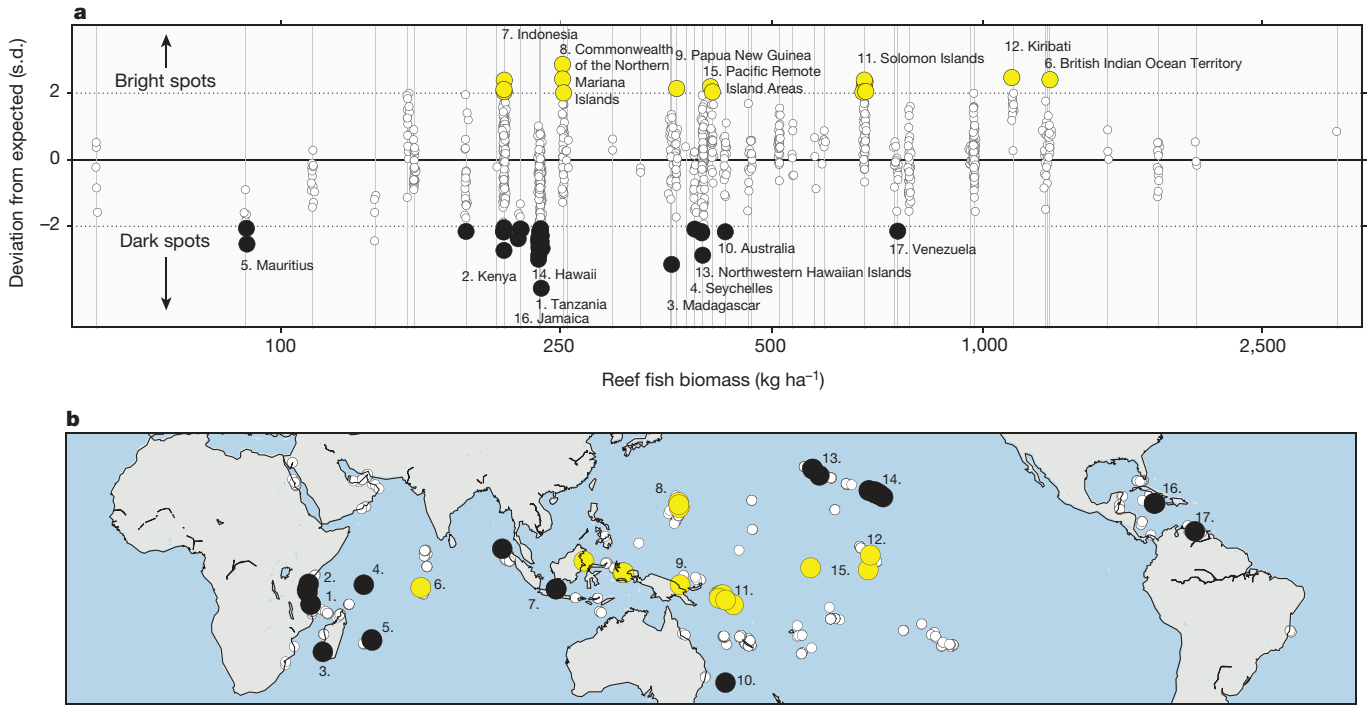

Figure 2 | Bright and dark spots among the world's coral reefs. a, Each site's deviation from expected biomass (*y* axis) along a gradient of nation/state mean biomass (*x* axis). The 50 sites with biomass values >2 standard deviations above or below expected values were considered bright (yellow) and dark (black) spots, respectively. Each grey vertical line represents a nation/state; those with bright or dark spots are labelled and numbered. There can be multiple bright or dark spots in each nation/state. **b**, Map highlighting bright and dark spots with large circles, and other sites in small circles. Numbers correspond to panel **a**.

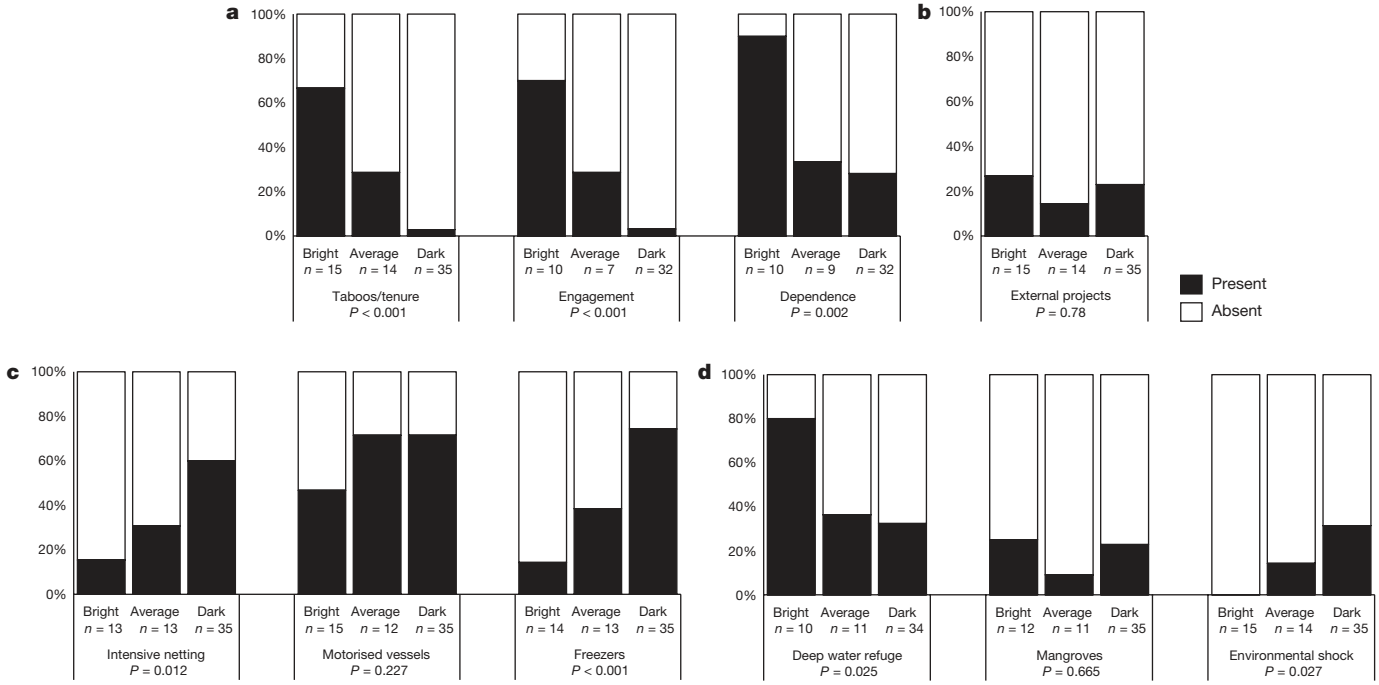

Figure 3 | Differences in key social and environmental conditions between bright spots, dark spots, and 'average' sites. a, Social and institutional conditions; **b**, external- or donor-driven projects; **c**, technologies; **d**, environmental conditions. *P* values are determined using Fisher's exact test. Intensive netting includes beach seine nets, surround gill nets, and muro-ami.

gravity[17] (Methods), more so than local or national population pressure, management, environmental conditions, or national socioeconomic context, had the strongest relationship with reef fish biomass (Fig. 1). Specifically, we found that reef fish biomass decreased as the size and accessibility of markets increased (Extended Data Fig. 1b). Somewhat counter-intuitively, fish biomass was higher in places with high local human population growth rates, probably reflecting human migration to areas of better environmental quality[18]—a phenomenon that could result in increased degradation at these sites over time. We found a strong positive, but less certain relationship (that is, a high standardized effect size, but only >75% of the posterior distribution above zero) with the Human Development Index, meaning that reefs tended to be in better condition in wealthier nations/states (Fig. 1c). Our analysis also confirmed the role that marine reserves can play in sustaining biomass on coral reefs, but only when compliance is high (Fig. 1b), reinforcing the importance of fostering compliance for reserves to be successful.

Next, we identified 15 bright spots and 35 dark spots among the world's coral reefs, defined as sites with biomass levels more than two standard deviations higher or lower than expectations from our global model, respectively (Fig. 2; Methods; Extended Data Table 5). Rather than simply identifying places in the best or worst condition, our bright spots approach reveals the places that most strongly defy expectations. Using them to inform the conservation discourse will certainly challenge established ideas of where and how conservation efforts should be focused. For example, remote places far from human impacts are conventionally considered near-pristine areas of high conservation value[6], yet most of the bright spots we identified occur in fished, populated areas (Extended Data Table 5), some with biomass values below the global average. Alternatively, some remote places such as parts of the northwest Hawaiian Islands underperform (that is, were identified as dark spots).

Detailed analysis of why bright spots can evade the fate of similar areas facing equivalent stresses will require a new research agenda gathering detailed site-level information on social and institutional conditions, technological innovations, external influences, and ecological processes[19] that are simply not available in a global-scale analysis. As a hypothesis-generating exploration to begin uncovering why bright and dark spots may diverge from expectations, we surveyed data providers who sampled the sites and other experts with first-hand knowledge about the presence or absence of ten key social and environmental conditions at the 15 bright spots, 35 dark spots, and 14 average sites with biomass values closest to model expectations (see Methods and Supplementary Information for details). Our initial exploration revealed that bright spots were more likely to have high levels of local engagement in the management process, high dependence on coastal resources, and the presence of sociocultural governance institutions such as customary tenure or taboos (Fig. 3; Methods). For example, in one bright spot, Karkar Island, Papua New Guinea, resource use is restricted through an adaptive rotational harvest system based on ecological feedbacks, marine tenure that allows for the exclusion of fishers from outside the local village, and initiation rights that limit individuals' entry into certain fisheries[20]. Bright spots were also generally proximate to deep water, which may help provide a refuge from disturbance for corals and fish[21] (Fig. 3; Extended Data Fig. 4). Conversely, dark spots were distinguished by having fishing technologies allowing for more intensive exploitation, such as fish freezers and potentially destructive netting, as well as a recent history of environmental shocks (for example, coral bleaching or cyclone; Fig. 3). The latter is particularly worrisome in the context of climate change, which is likely to lead to increased coral bleaching and more intense cyclones[22].

Our global analyses highlight two novel opportunities to inform coral reef governance. The first is to use bright spots as agents of change to expand the conservation discourse from the current focus on protecting places under minimal threat[8], towards harnessing lessons from places that have successfully confronted numerous or severe stressors. Our bright spots approach can be used to inform the types of investments and governance structures that may help to create more sustainable pathways for impacted coral reefs. Specifically, our initial investigation highlights how investments that strengthen fisheries governance, particularly issues such as participation and property rights, could help communities to innovate in ways that allow them to defy expectations. Conversely, the more typical efforts to provide capture and storage infrastructure, particularly where there are environmental shocks and local-scale governance is weak, may lead to

social–ecological traps[23] that reinforce resource degradation beyond expectations. Effectively harnessing the potential to learn from both bright and dark spots will require scientists to increase research efforts in these places, NGOs to catalyse lessons from other areas, donors to start investing in novel solutions, and policy makers to ensure that governance structures foster flexible learning and experimentation. Indeed, bright spots may have much to offer in terms of how to creatively confront drivers of change and prioritize conservation actions. Likewise, dark spots can help identify development strategies to avoid. Critically, the bright spots we identified span the development spectrum from low to high income (for example, Solomon Islands and territories of the USA, respectively; Fig. 2), showing that lessons about effective reef management can emerge from diverse places.

A second opportunity stems from a renewed focus on managing the socioeconomic drivers that shape reef conditions. Many social drivers are amenable to governance interventions, and our comprehensive analysis (Fig. 1) suggests that an increased policy focus on social drivers such as markets and development could result in improvements to reef fish biomass. For example, given the important influence of markets in our analysis, reef managers, donor organizations, conservation groups, and coastal communities could improve sustainability by developing interventions that dampen the negative influence of markets on reef systems. A portfolio of market interventions, including eco-labelling and sustainable harvesting certifications, fisheries improvement projects, and value chain interventions have been developed within large-scale industrial fisheries to condition access to markets based on sustainable harvesting[24,25]. Although there is considerable scope for adapting these interventions to artisanal coral reef fisheries in both local and regional markets, effectively dampening the negative influence of markets may also require developing novel interventions that address the range of ways in which markets can lead to overexploitation. Existing research suggests that markets create incentives for overexploitation not only by affecting price and price variability for reef products[26], but also by influencing people's behaviour[27,28], including their willingness to cooperate in the collective management of natural resources[29].

The long-term viability of coral reefs will ultimately depend on international action to reduce carbon emissions[22]. However, fisheries remain a pervasive source of reef degradation, and effective local-level fisheries governance is crucial to sustaining ecological processes that give reefs the best chance of coping with global environmental change[30]. Seeking out and learning from bright spots is a novel approach to conservation that may offer insights into confronting the complex governance problems facing coupled human–natural systems such as coral reefs.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Supplementary Information is available in the online version of the paper.

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Author Information This is the Social-Ecological Research Frontiers (SERF) working group contribution no. 11. Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to J.E.C. (Joshua.cinner@jcu.edu.au).

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METHODS

No statistical methods were used to predetermine sample size.

Scales of data. Our data were organized at three spatial scales:

(i) Reef ($n = 2{,}514$). The smallest scale, which had an average of 2.4 surveys/transects.

(ii) Site (a cluster of reefs; $n = 918$). We clustered reefs together that were within 4 km of each other, and used the centroid of these clusters to estimate site-level social and site-level environmental covariates (Extended Data Table 1). To make these clusters, we first estimated the linear distance between all reefs, then used a hierarchical analysis with the complete-linkage clustering technique based on the maximum distance between reefs. We set the cut-off at 4 km to select mutually exclusive sites where reefs cannot be more distant than 4 km. The choice of 4 km was informed by a 3-year study of the spatial movement patterns of artisanal coral reef fishers, corresponding to the highest density of fishing activities on reefs based on GPS-derived effort density maps of artisanal coral reef fishing activities[31]. This clustering analysis was carried out using the R functions hclust and cutree, resulting in an average of 2.7 reefs per site.

(iii) Nation/state (nation, state, or territory; $n = 46$). A larger scale in our analysis was nation/state, which are jurisdictions that generally correspond to individual nations (but could also include states, territories, overseas regions, or extremely remote areas within a state such as the northwest Hawaiian Islands; Extended Data Table 2), within which sites and reefs were nested for analysis.

Estimating biomass. Reef fish biomass can reflect a broad selection of reef fish functioning and benthic conditions[12,32–34], and is a key metric of resource availability for reef fisheries. Reef fish biomass estimates were based on instantaneous visual counts from 6,088 surveys collected from 2,514 reefs. All surveys used standard belt-transects, distance sampling, or point-counts, and were conducted between 2004 and 2013. Where data from multiple years were available from a single reef, we included only data from the year closest to 2010. Within each survey area, reef associated fishes were identified to species level, abundance counted, and total length (TL) estimated, with the exception of one data provider who measured biomass at the family level. To make estimates of biomass from these transect-level data comparable among studies, we:

(iv) Retained families that were consistently studied and were above a minimum size cut-off. Thus, we retained counts of >10-cm diurnally active, non-cryptic reef fish that are resident on the reef (20 families, 774 species), excluding sharks and semi-pelagic species. We also excluded three groups of fishes that are strongly associated with coral habitat conditions and are rarely targets for fisheries (Anthiinae, Chaetodontidae, and Cirrhitidae). Families included are: Acanthuridae, Balistidae, Diodontidae, Ephippidae, Haemulidae, Kyphosidae, Labridae, Lethrinidae, Lutjanidae, Monacanthidae, Mullidae, Nemipteridae, Pinguipedidae, Pomacanthidae, Serranidae, Siganidae, Sparidae, Synodontidae, Tetraodontidae and Zanclidae. We calculated the total biomass of fish on each reef using standard published species-level length–weight relationship parameters or those available on FishBase[35]. When length–weight relationship parameters were not available for a species, we used the parameters for a closely related species or genus.

(v) Directly accounted for depth and habitat as covariates in the model (see Environmental conditions section below).

(vi) Accounted for any potential bias among data providers (capturing information on both inter-observer differences, and census methods) by including each data provider as a random effect in our model.

Biomass means, medians, and standard deviations were calculated at the reef-scale. All reported log values are the natural log.

Social drivers

Local population growth. We created a 100 km buffer around each site and used this to calculate human population within the buffer in 2000 and 2010 based on the Socioeconomic Data and Application Centre (SEDAC) gridded population of the world database[36]. Population growth was the proportional difference between the population in 2000 and 2010. We chose a 100 km buffer as a reasonable range at which many key human impacts from population (for example, land-use and nutrients) might affect reefs[37].

Management. For each site, we determined if it was unfished, that is, whether it fell within the borders of a no-take marine reserve (we asked data providers to further classify whether the reserve had high or low levels of compliance); restricted—whether there were active restrictions on gears (for example, bans on the use of nets, spear guns, or traps) or fishing effort (which could have included areas inside marine parks that were not necessarily no take); or fished, that is, regularly fished without effective restrictions. To determine these classifications, we used the expert opinion of the data providers, and triangulated this with a global database of marine reserve boundaries[38].

Gravity. We adapted the economic geography concept of 'gravity'[17,39–41], also called interactance[42], to examine potential interactions between reefs and: (i) major urban centres/markets (defined as provincial capital cities, major population centres, landmark cities, national capitals, and ports); and (ii) the nearest human settlements. This application of the gravity concept infers that potential interactions increase with population size, but decay exponentially with the effective distance between two points. Thus, we gathered data on both population estimates and a surrogate for distance: travel time.

Population estimations. We gathered population estimates for: (i) the nearest major markets (which includes national capitals, provincial capitals, major population centres, ports, and landmark cities) using the World Cities base map from ESRI; and (ii) the nearest human settlement within a 500 km radius using LandScan 2011 database. The different data sets were required because the latter is available in raster format while the former is available as point data. We chose a 500 km radius from the nearest settlement as the maximum distance any non-market fishing activities for fresh reef fish are likely to occur.

Travel time calculation. Travel time was computed using a cost–distance algorithm that computes the least 'cost' (in minutes) of travelling between two locations on a regular raster grid. In our case, the two locations were either the centroid of the site (that is, reef cluster) and the nearest settlement, or the centroid of the site and the major market. The cost (that is, time) of travelling between the two locations was determined by using a raster grid of land cover and road networks with the cells containing values that represent the time required to travel across them[43]:

- Tree cover, broadleaved, deciduous and evergreen, closed; regularly flooded tree cover, shrub, or herbaceous cover (fresh, saline, & brackish water) = speed of 1 km h^{-1}
- Tree cover, broadleaved, deciduous, open (open = 15–40% tree cover) = speed of 1.25 km h^{-1}
- Tree cover, needle-leaved, deciduous and evergreen, mixed leaf type; shrub cover, closed-open, deciduous and evergreen; herbaceous cover, closed-open; cultivated and managed areas; mosaic: cropland/tree cover/other natural vegetation, cropland/shrub or grass cover = speed of 1.5 km h^{-1}
- Mosaic: tree cover/other natural vegetation; tree cover, burnt = speed of 1.25 km h^{-1}
- Sparse herbaceous or sparse shrub cover = speed of 2.5 km h^{-1}
- Water = speed of 20 km h^{-1}
- Roads = speed of 60 km h^{-1}
- Track = speed of 30 km h^{-1}
- Artificial surfaces and associated areas = speed of 30 km h^{-1}
- Missing values = speed of 1.4 km h^{-1}

We termed this raster grid a friction-surface (with the time required to travel across different types of surfaces analogous to different levels of friction). To develop the friction-surface, we used global data sets of road networks, land cover, and shorelines:

- Road network data was extracted from the Vector Map Level 0 (VMap0) from the National Imagery and Mapping Agency's (NIMA) Digital Chart of the World (DCW). We converted vector data from VMap0 to 1 km resolution raster.
- Land cover data were extracted from the Global Land Cover 2000 (ref. 44).
- To define the shorelines, we used the GSHHS (Global Self-consistent, Hierarchical, High-resolution Shoreline) database version 2.2.2.

These three friction components (road networks, land cover, and water bodies) were combined into a single friction surface with a Behrmann map projection. We calculated our cost-distance models in R[45] using the accCost function of the gdistance package. The function uses Dijkstra's algorithm to calculate least-cost distance between two cells on the grid and the associated distance taking into account obstacles and the local friction of the landscape[46]. Travel time estimates over a particular surface could be affected by the infrastructure (for example, road quality) and types of technology used (for example, types of boats). These types of data were not available at a global scale but could be important modifications in more localized studies.

Gravity computation. To compute the gravity to the nearest market, we calculated the population of the nearest major market and divided that by the squared travel time between the market and the site. Although other exponents can be used[47], we used the squared distance (or in our case, travel time), which is relatively common in geography and economics. This decay function could be influenced by local considerations, such as infrastructure quality (for example, roads), the types of transport technology (that is, vessels being used), and fuel prices, which were not

available in a comparable format for this global analysis, but could be important considerations in more localized adaptations of this study.

To determine the gravity of the nearest settlement, we located the nearest populated pixel within 500 km, determined the population of that pixel, and divided that by the squared travel time between that cell and the reef site.

As is standard practice in many agricultural economics studies[48], an assumption in our study is that the nearest major capital or landmark city represents a market. Ideally we would have used a global database of all local and regional markets for coral reef fish, but this type of database is not available at a global scale. As a sensitivity analysis to help justify our assumption that capital and landmark cities were a reasonable proxy for reef fish markets, we tested a series of candidate models that predicted biomass based on: (1) cumulative gravity of all cities within 500 km; (2) gravity of the nearest city; (3) travel time to the nearest city; (4) population of the nearest city; (5) gravity to the nearest human population above 40 people km^{-2} (assumed to be a small peri-urban area and potential local market); (6) the travel time between the reef and a small peri-urban area; (7) the population size of the small peri-urban population; (8) gravity to the nearest human population above 75 people km^{-2} (assumed to be a large peri-urban area and potential market); (9) the travel time between the reef and this large peri-urban population; (10) the population size of this large peri-urban population; and (11) the total population size within a 500 km radius. Model selection revealed that the best two models were gravity of the nearest city and gravity of all cities within 500 km (with a 3 AIC value difference between them; Extended Data Table 3). Importantly, when looking at the individual components of gravity models, the travel time components all had a much lower AIC value than the population components, which is broadly consistent with previous systematic review studies[49]. Similarly, travel time to the nearest city had a lower AIC score than any aspect of either the peri-urban or urban measures. This suggests our use of capital and landmark cities is likely to better capture exploitation drivers from markets rather than simple population pressures. This may be because market dynamics are difficult to capture by population threshold estimates; for example some small provincial capitals where fish markets are located have very low population densities, while some larger population centres may not have a market. Downscaled regional or local analyses could attempt to use more detailed knowledge about fish markets, but we used the best proxy available at a global scale.

Human Development Index (HDI). HDI is a summary measure of human development encompassing: a long and healthy life, being knowledgeable, and having a decent standard of living. In cases where HDI values were not available specific to the State (for example, Florida and Hawaii), we used the national (for example, USA) HDI value.

Population size. For each nation/state, we determined the size of the human population. Data were derived mainly from census reports, the CIA fact book, and Wikipedia.

Tourism. We examined tourist arrivals relative to the nation/state population size (above). Tourism arrivals were gathered primarily from the World Tourism Organization's Compendium of Tourism Statistics.

National reef fish landings. Catch data were obtained from the Sea Around Us Project (SAUP) catch database (http://www.seaaroundus.org), except for Florida, which was not reported separately in the database. We identified 200 reef fish species and taxon groups in the SAUP catch database[50]. Note that reef-associated pelagics such as scombrids and carangids normally form part of reef fish catches. However, we chose not to include these species because they are also targeted and caught in large amounts by large-scale, non-reef operations.

Voice and accountability. This metric, from the World Bank survey on governance, reflects the perceptions of the extent to which a country's citizens are able to participate in selecting their government, as well as freedom of expression, freedom of association, and a free media. In cases where governance values were not available specific to the nation/state (for example, Florida and Hawaii), we used national (for example, USA) values.

Environmental drivers

Depth. The depth of reef surveys were grouped into the following categories: <4 m, 4–10 m, >10 m to account for broad differences in reef fish community structure attributable to a number of inter-linked depth-related factors. Categories were necessary to standardise methods used by data providers and were determined by pre-existing categories used by several data providers.

Habitat. We included the following habitat categories:

(i) Slope. The reef slope habitat is typically on the ocean side of a reef, where the reef slopes down into deeper water.

(ii) Crest. The reef crest habitat is the section that joins a reef slope to the reef flat. The zone is typified by high wave energy (that is, where the waves break). It is also typified by a change in the angle of the reef from an inclined slope to a horizontal reef flat.

(iii) Flat. The reef flat habitat is typically horizontal and extends back from the reef crest for 10's to 100's of metres;

(iv) Lagoon/back reef. Lagoon reef habitats are where the continuous reef flat breaks up into more patchy reef environments sheltered from wave energy. These habitats can be behind barrier/fringing reefs or within atolls. Back reef habitats are similar broken habitats where the wave energy does not typically reach the reefs and thus forms a less continuous 'lagoon style' reef habitat. Due to minimal representation among our sample, we excluded other less prevalent habitat types, such as channels and banks. To verify the sites' habitat information, we used the Millennium Coral Reef Mapping Project (MCRMP) hierarchical data[51], Google Earth, and site depth information.

Productivity. We examined ocean productivity for each of our sites in mg of C per m^2 per day (http://www.science.oregonstate.edu/ocean.productivity/). Using the monthly data for years 2005 to 2010 (in hdf format), we imported and converted those data into ArcGIS. We then calculated yearly average and finally an average for all these years. We used a 100 km buffer around each of our sites and examined the average productivity within that radius. Note that ocean productivity estimates are less accurate for near-shore environments, but we used the best available data.

Analyses. We first looked for collinearity among our covariates using bivariate correlations and variance inflation factor estimates (Extended Data Fig. 2 and Extended Data Table 4). This led to the exclusion of several covariates (not described above): (i) geographic basin (tropical Atlantic, western Indo-Pacific, central Indo-Pacific, or eastern Indo-Pacific); (ii) gross domestic product (purchasing power parity); (iii) rule of law (World Bank governance index); (iv) control of corruption (World Bank governance index); and (v) sedimentation. Additionally, we removed an index of climate stress, developed by Maina *et al.*[52], which incorporated 11 different environmental conditions, such as the mean and variability of sea surface temperature due to repeated lack of convergence for this parameter in the model, likely indicative of unidentified multicollinearity. All other covariates had correlation coefficients 0.7 or less and variance inflation factor scores less than 5 (indicating multicollinearity was not a serious concern). Care must be taken in causal attribution of covariates that were significant in our model, but demonstrated collinearity with candidate covariates that were removed during the aforementioned process. Importantly, the covariate that exhibited the largest effect size in our model, market gravity, was not strongly collinear with other candidate covariates.

To quantify the multi-scale social, environmental, and economic factors affecting reef fish biomass we adopted a Bayesian hierarchical modelling approach that explicitly recognized the three scales of spatial organization: reef (j), site (k), and nation/state (s).

In adopting the Bayesian approach we developed two models for inference: a null model, consisting only of the hierarchical units of observation (that is, intercepts-only) and a full model that included all of our covariates (drivers) of interest. Covariates were entered into the model at the relevant scale, leading to a hierarchical model whereby lower-level intercepts (averages) were placed in the context of higher-level covariates in which they were nested. We used the null model as a baseline against which we could ensure that our full model performed better than a model with no covariate information. We did not remove 'non-significant' covariates from the model because each covariate was carefully considered for inclusion and could therefore reasonably be considered as having an effect, even if small or uncertain; removing factors from the model is equivalent to fixing parameter estimates at exactly zero—a highly-subjective modelling decision after covariates have already been selected as potentially important[53].

The full model assumed the observed, reef-scale observations of fish biomass (y_{ijks}) were modelled using a non-central t distribution, allowing for fatter tails than typical log-normal models of reef fish biomass[32]. We chose the non-central t after having initially used a log-normal model because our model diagnostics suggested that several model parameters had not converged. We ran a supplementary analysis to support our use of the non-central t distribution with 3.5 degrees of freedom (see Supplementary Information). Therefore our model was:

$$\log[y_{ijks}] \sim \text{non-central } t(\mu_{ijks}, \tau_{\text{reef}}, 3.5)$$

$$\mu_{ijks} = \beta_{0jks} + \beta_{\text{reef}}\boldsymbol{X}_{\text{reef}}$$

$$\tau_{\text{reef}} \sim \text{U}(0,100)^{-2}$$

with $\boldsymbol{X}_{\text{reef}}$ representing the matrix of observed reef-scale covariates and β_{reef} array of estimated reef-scale parameters. The τ_{reef} (and all subsequent τ values) were assumed common across observations in the final model and were minimally

informative[53]. Using a similar structure, the reef-scale intercepts (β_{0jks}) were structured as a function of site-scale covariates ($\boldsymbol{X}_{\text{sit}}$):

$$\beta_{0jks} \sim \text{N}(\mu_{jks}, \tau_{\text{sit}})$$

$$\mu_{jks} = \gamma_{0ks} + \gamma_{\text{sit}}\boldsymbol{X}_{\text{sit}}$$

$$\tau_{\text{sit}} \sim \text{U}(0,100)^{-2}$$

with γ_{sit} representing an array of site-scale parameters. Building upon the hierarchy, the site-scale intercepts (γ_{0ks}) were structured as a function of state-scale covariates ($\boldsymbol{X}_{\text{sta}}$):

$$\gamma_{0ks} \sim \text{N}(\mu_{ks}, \tau_{\text{sta}})$$

$$\mu_{ks} = \gamma_0 + \gamma_{\text{sta}}\boldsymbol{X}_{\text{sta}}$$

$$\tau_{\text{sta}} \sim \text{U}(0,100)^{-2}$$

Finally, at the top scale of the analysis we allowed for a global (overall) estimate of average log-biomass (γ_0):

$$\gamma_0 \sim \text{N}(0.0,1000)$$

The relationships between fish biomass and reef, site, and state-scale drivers was carried out using the PyMC package[54] for the Python programming language, using a Metropolis-Hastings (MH) sampler run for 10^6 iterations, with a 900,000 iteration burn-in thinned by 10, leaving 10,000 samples in the posterior distribution of each parameter; these long burn-in times are often required with a complex model using the MH algorithm. Convergence was monitored by examining posterior chains and distributions for stability and by running multiple chains from different starting points and checking for convergence using Gelman–Rubin statistics[55] for parameters across multiple chains; all were at or close to 1, indicating good convergence of parameters across multiple chains.

Overall model fit. We conducted posterior predictive checks for goodness of fit (GoF) using Bayesian *P* values[43] (BpV), whereby fit was assessed by the discrepancy between observed or simulated data and their expected values. To do this we simulated new data (y_i^{new}) by sampling from the joint posterior of our model (θ) and calculated the Freeman–Tukey measure of discrepancy for the observed (y_i^{obs}) or simulated data, given their expected values (μ_i):

$$D(y|\theta) = \sum_i (\sqrt{y_i} - \sqrt{y_i})^2$$

yielding two arrays of median discrepancies $D(y^{\text{obs}}/\theta)$ and $D(y^{\text{new}}/\theta)$ that were then used to calculate a BpV for our model by recording the proportion of times $D(y^{\text{obs}}/\theta)$ was greater than $D(y^{\text{new}}/\theta)$ (Extended Data Fig. 3a). A BpV above 0.975 or under 0.025 provides substantial evidence for lack of model fit. Evaluated by the deviance information criterion (DIC), the full model greatly outperformed a null model that included no covariates ($\Delta\text{DIC} = 472$).

To examine homoscedasticity, we checked residuals against fitted values. We also checked the residuals against all covariates included in the model, and several covariates that were not included in the model (primarily due to collinearity), including: (i) Atoll, a binary metric of whether the reef was on an atoll or not; (ii) control of corruption, perceptions of the extent to which public power is exercised for private gain, including both petty and grand forms of corruption, as well as 'capture' of the state by elites and private interests, derived from the World Bank survey on governance; (iii) geographic basin, whether the site was in the tropical Atlantic, western Indo-Pacific, central Indo-Pacific, or eastern Indo-Pacific; (iv) connectivity, we examined three measures based on the area of coral reef within a 30 km, 100 km, and 600 km radius of the site; (v) sedimentation; (vi) coral cover (which was only available for a subset of the sites); (vii) climate stress[52]; and (viii) census method. The model residuals showed no patterns with these eight additional covariates, suggesting they would not explain additional information in our model.

Bright and dark spot estimates. Because the performance of site scale locations are of substantial interest in uncovering novel solutions for reef conservation, we defined bright and dark spots at the site scale. To this end, we defined bright (or dark) spots as locations where expected site-scale intercepts (γ_{0ks}) differed by more than two standard deviations from their nation/state-scale expected value (μ_{ks}), given all the covariates present in the full hierarchical model:

$$\text{SS}_{\text{spot}} = |(\mu_{ks} - \gamma_{0ks})| > 2[\text{s.d.}(\mu_{ks} - \gamma_{0ks})]$$

This, in effect, probabilistically identified the most deviant sites, given the model, while shrinking sites towards their group-level means, thereby allowing us to overcome potential bias due to low and varying sample sizes that can lead to extreme values from chance alone. After an initial log-normal model formulation, where we were not confident in model convergence, we employed a non-central *t* distribution at the observation scale, which facilitated model convergence and dampened any effects of potentially extreme reef-scale observations on the bright and dark spot estimates. Further, we did not consider a site a bright or dark spot if the group-level (that is, nation/state) mean included fewer than five sites.

Analysing conditions at bright spots. For our preliminary exploration into why bright and dark spots may diverge from expectations, we surveyed data providers and other experts about key social, institutional, and environmental conditions at the 15 bright spots, 35 dark spots, and 14 sites that performed most closely to model specifications. Specifically, we developed an online survey (SI) using Survey Monkey (http://www.surveymonkey.com) software, which we asked data providers who sampled those sites to complete with input from local experts, where necessary. Data providers generally filled in the survey in consultation with nationally based field team members who had detailed local knowledge of the socioeconomic and environmental conditions at each of the sites. Research on bright spots in agricultural development[19] highlights several types of social and environmental conditions that may lead to bright spots, which we adapted and developed proxies for as the basis of our survey into why our bright and dark spots may diverge from expectations. These include:

(i) Social and institutional conditions. We examined the presence of customary management institutions such as taboos and marine tenure institutions, whether there was substantial engagement by local people in management (specifically defined as there being active engagement by local people in reef management decisions; token involvement and consultation were not considered substantial engagement), and whether there were high levels of dependence on marine resources (specifically, whether a majority of local residents depend on reef fish as a primary source of food or income). All social and institutional conditions were converted to presence/absence data. Dependence on resources and engagement were limited to sites that had adjacent human populations. All other conditions were recorded regardless of whether there is an adjacent community.

(ii) Technological use/innovation. We examined the presence of motorized vessels, intensive capture equipment (such as beach seine nets, surround gill nets, and muro-ami nets), and storage capacity (that is, freezers).

(iii) External influences (such as donor-driven projects). We examined the presence of NGOs, fishery development projects, development initiatives (such as alternative livelihoods), and fisheries improvement projects. All external influences were recorded as present/absent then summarized into a single index of whether external projects were occurring at the site.

(iv) Environmental/ecological processes (for example, recruitment and connectivity). We examined whether sites were within 5 km of mangroves and deep-water refuges, and whether there had been any major environmental disturbances such as coral bleaching, tsunami, and cyclones within the past 5 years. All environmental conditions were recorded as present/absent.

As an exploratory analysis of associations between these conditions and whether sites diverged more or less from expectations, we used two complementary approaches. The link between the presence/absence of the aforementioned conditions and whether a site was bright, average, or dark was assessed using a Fisher's exact test. Then we tested whether the mean deviation in fish biomass from expected was similar between sites with presence or absence of the mechanisms in question (that is, the presence or absence of marine tenure/taboos) using an ANOVA assuming unequal variance. The two tests yielded similar results, but provide slightly different ways to conceptualize the issue, the former is correlative while the latter explains deviation from expectations based on conditions, so we provide both (Fig. 3 and Extended Data Fig. 4). It is important to note that some of these social and environmental conditions were significantly associated (that is, Fisher's exact probabilities <0.05), and further research is required to uncover how these and other conditions may make sites bright or dark.

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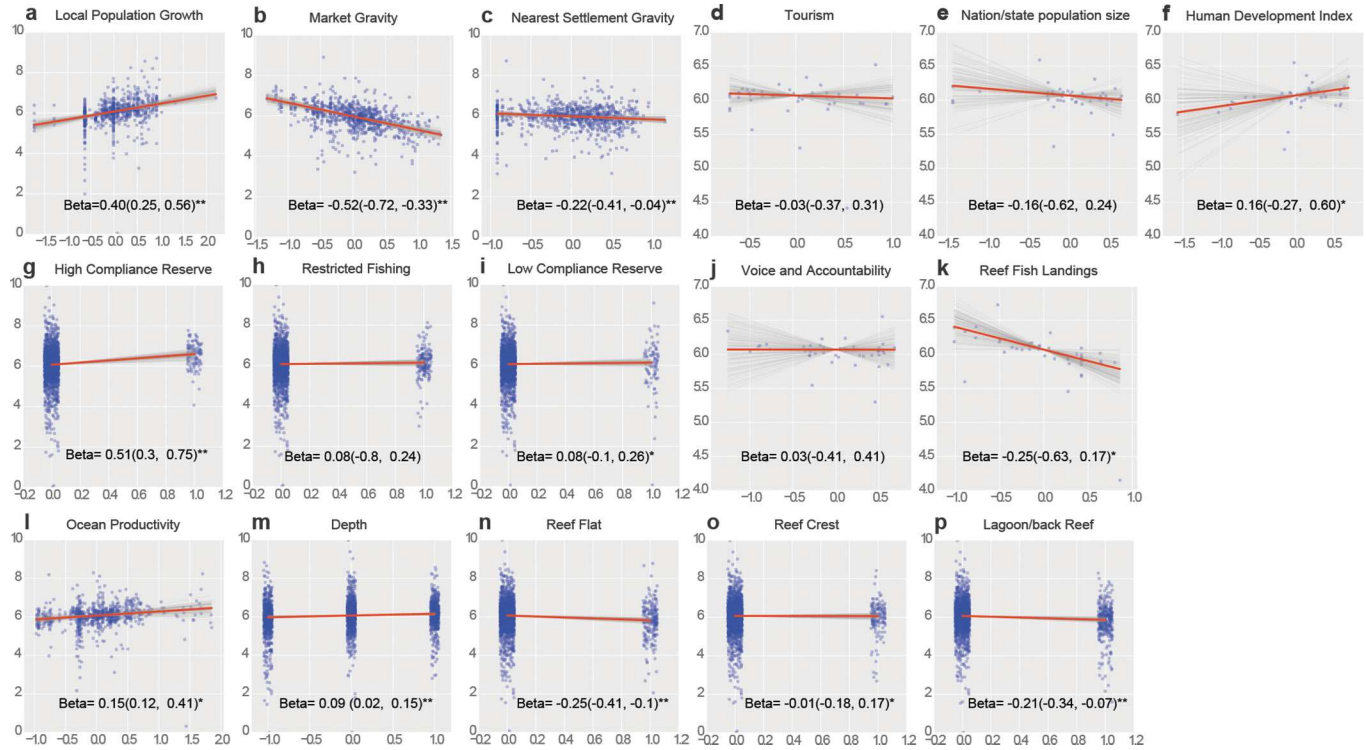
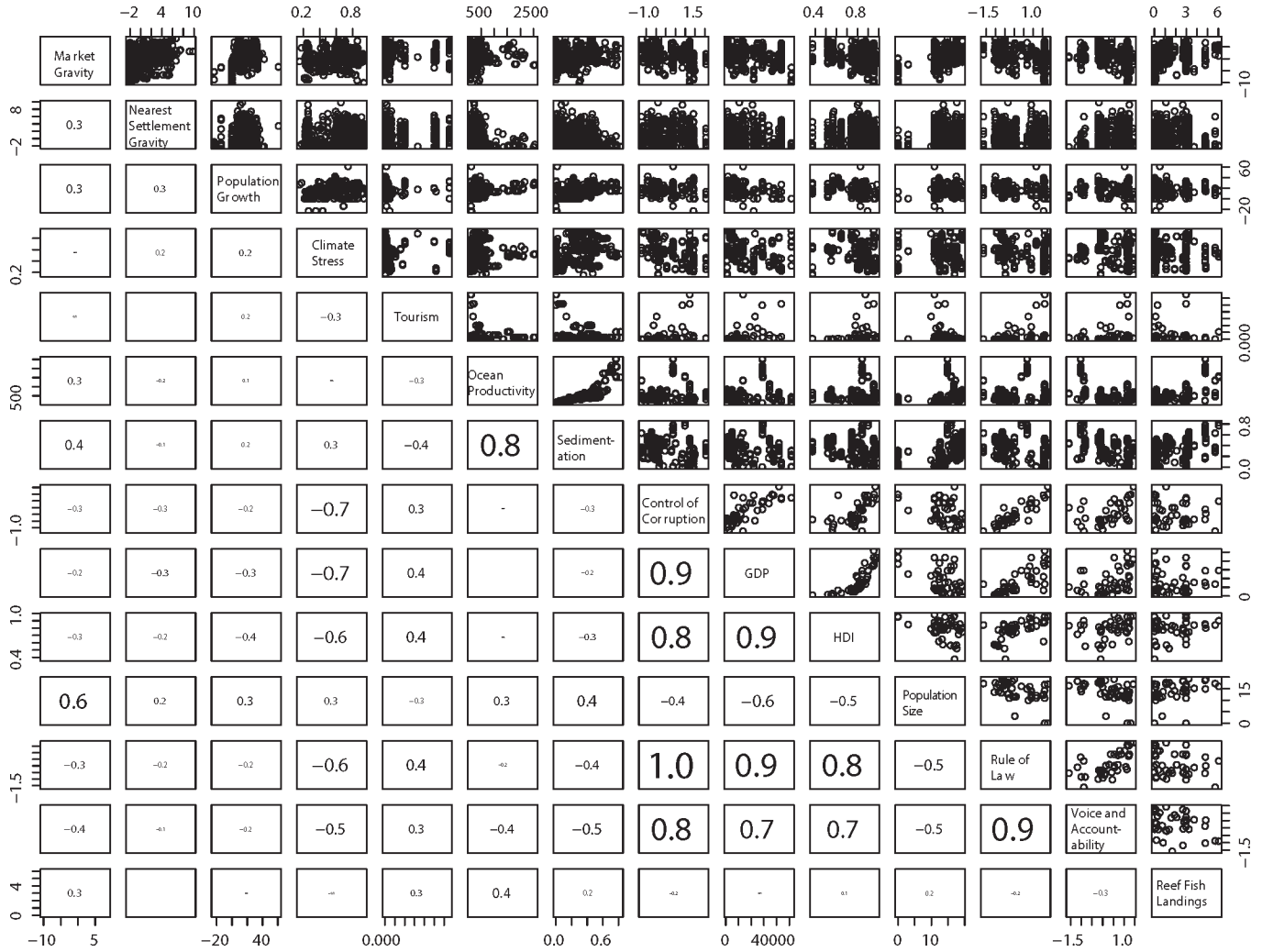
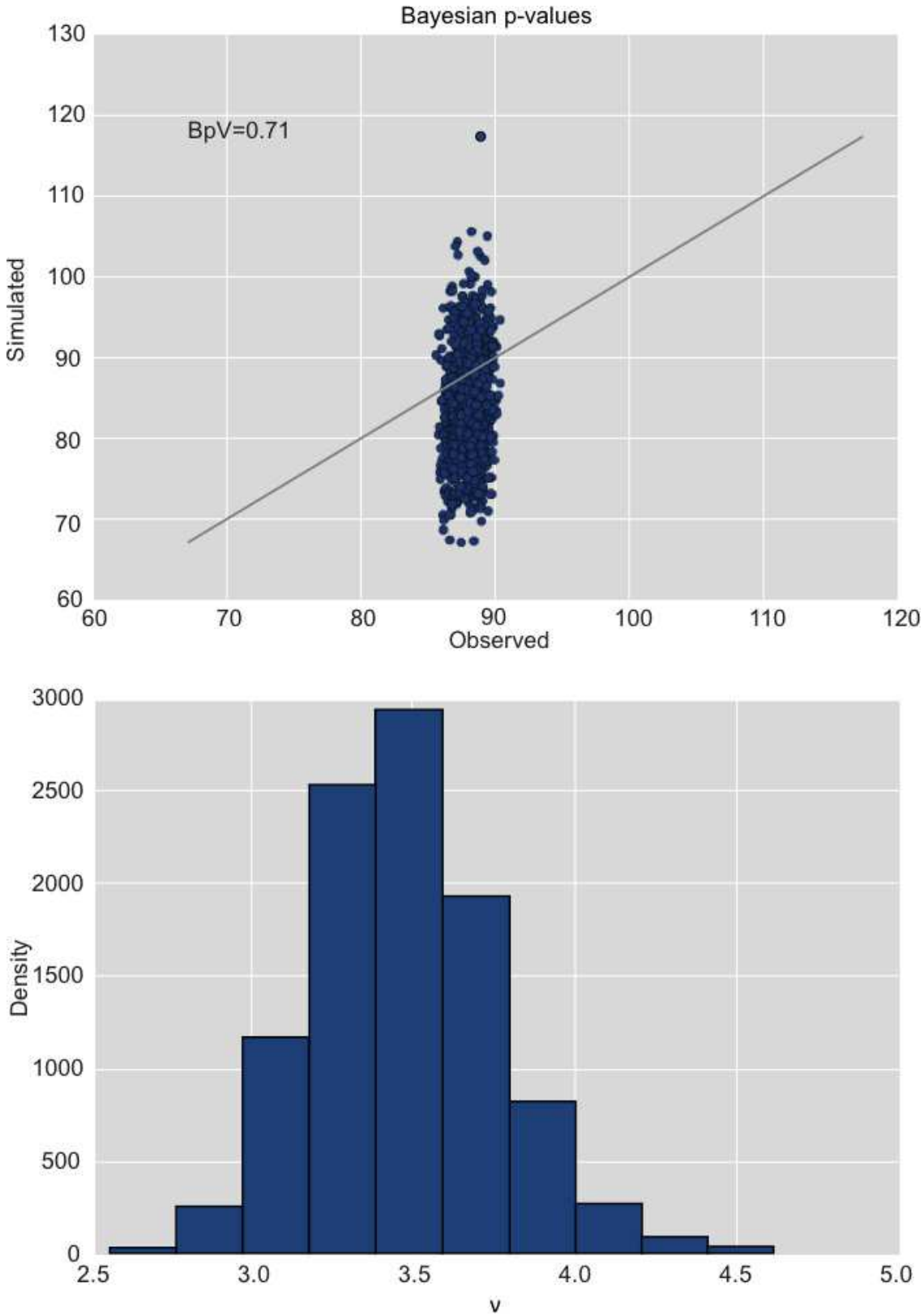


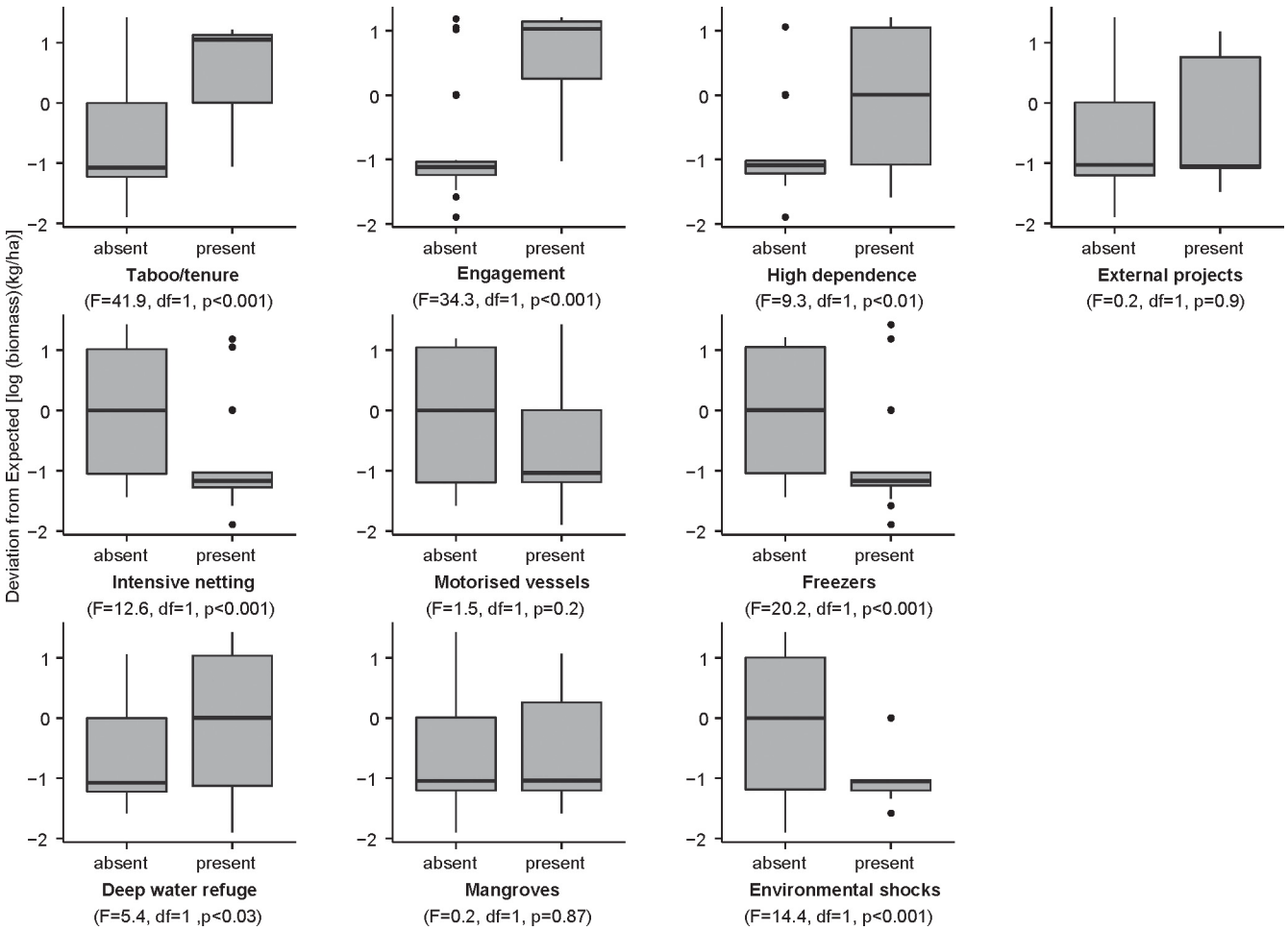
Extended Data Figure 1 | Marginal relationships between reef fish biomass and social drivers. a, Local population growth; **b**, market gravity; **c**, nearest settlement gravity; **d**, tourism; **e**, nation/state population size; **f**, Human Development Index; **g**, high compliance marine reserve (0 is fished baseline); **h**, restricted fishing (0 is fished baseline); **i**, low-compliance marine reserve (0 is fished baseline); **j**, voice and accountability; **k**, reef fish landings; **l**, ocean productivity; **m**, depth (−1 = 0–4 m, 0 = 4–10 m, 1 = >10 m); **n**, reef flat (0 is reef slope baseline); **o**, reef crest flat (0 is reef slope baseline); **p**, lagoon/back reef flat (0 is reef slope baseline). All variables displayed on the *x* axis are standardized. Red lines are the marginal trend line for each parameter as estimated by the full model. Grey lines are 100 simulations of the marginal trend line sampled from the posterior distributions of the intercept and parameter slope, analogous to conventional confidence intervals. Two asterisks indicate that 95% of the posterior density is in either a positive or negative direction (Fig. 1b–d); a single asterisk indicates that 75% of the posterior density is in either a positive or negative direction.



Extended Data Figure 2 | Correlation plot of candidate continuous covariates before accounting for collinearity (Extended Data Table 4). Collinearity between continuous and categorical covariates (including biogeographic region, habitat, protection status, and depth) were analysed using box plots.



Extended Data Figure 3 | Model fit statistics. Top, Bayesian *P* values (BpV) for the full model indicating goodness of fit, based on posterior discrepancy. Points are Freeman–Tukey differences between observed and expected values, and simulated and expected values within the MCMC scheme ($n = 10{,}000$). Plot shows no evidence for lack of fit between the model and the data. Bottom, Posterior distribution for the degrees of freedom parameter (ν) in our supplementary analysis of candidate distributions. The highest posterior density of 3.46, with 97.5% of the total posterior density below 4 provides strong evidence in favour of a non-central *t* distribution relative to a normal distribution and supports the use of 3.5 for ν.



Extended Data Figure 4 | Box plot of deviation from expected as a function of the presence or absence of key social and environmental conditions expected to produce bright spots. Boxes range from the first to third quartile and whiskers extend to the highest value that is within 1.5× the inter-quartile range (that is, distance between the first and third quartiles). Data beyond the end of the whiskers are outliers, which are plotted as points.

Extended Data Table 1 | Summary of social and environmental covariates

Covariate	Description	Scale	Key data sources
Local population growth	Difference in local human population (i.e. 100km buffer around our sites) between 2000-2010	Site	Socioeconomic Data and Application Centre (SEDAC) gridded population of the work database[36]
'Gravity' of major markets within 500km	The population of the major market divided by the squared travel time between the reef sites and the market. This value was summed for all major markets within 500km of the site.	Site	Human population size, land cover, road networks, coastlines
'Gravity' of the closest human settlement	The population of the nearest human settlement divided by the squared travel time between the reef site and the settlement.	Site	Human population size, land cover, road networks, coastlines
Protection status	Whether the reef is openly fished, restricted (e.g. effective gear bans or effort restrictions), or unfished	Reef	Expert opinion, global map of marine protected areas.
Human Development index	A summary measure of human development encompassing: a long and healthy life, being knowledgeable and have a decent standard of living. We used linear and quadratic functions for HDI.	Nation/state	United Nations Development Programme
Population Size	Total population size of the jurisdiction	Nation/ state	World Bank, census estimates, Wikipedia
Tourism	Proportion of tourist visitors to residents	Nation/ state	World Tourism Organization's Compendium of Tourism Statistics, census estimates
Voice and accountability	Perceptions of the extent to which a country's citizens are able to participate in selecting their government.	Nation/ state	World Bank
Fish landings	Landings of reef fish (tons) per Km^2 of reef	Nation/ state	Teh et al.[50]
Productivity	The average (2005-2010) ocean productivity in mg C / m2 / day	Site	http://www.science.oregonstate.edu/ocean.productivity/
Habitat	Whether the reef is a slop, crest, flat, or back reef/lagoon	Reef	Primary data
Depth	Depth of the ecological survey (<4m, 4.1-10m, >10m)	Reef	Primary data

Further details can be found in the Methods. The smallest scale is the individual reef. Sites consist of clusters of reefs within 4 km of each other. Nations/states generally correspond to countries, but can also include or territories or states, particularly when geographically isolated (for example, Hawaii). Refs 36 and 50 are cited in this table.

Extended Data Table 2 | List of nations/states covered in study and their respective average biomass (kg ha^{-1} ± standard error)

Nation/states	Average biomass	(± SE)
American Samoa	235.93	(± 17.75)
Australia	735.01	(± 136.85)
Belize	981.16	(± 65.32)
Brazil	663.35	(± 115.17)
British Indian Ocean Territory (Chagos)	2975.58	(± 603.99)
Cayman Islands	464.09	(± 25.41)
Colombia	846.07	(± 162.49)
Commonwealth of the Northern Mariana Islands	505.54	(± 99.3)
Comoros Islands	305.62	(± 38.73)
Cuba	2107.37	(± 466.34)
Egypt	552.73	(± 70.18)
Farquhar	2665.48	(± 492.62)
Federated States of Micronesia	377.90	NA (n=1)
Fiji	1464.54	(± 144.39)
Florida	1661.35	(± 198.42)
French Polynesia	1077.20	(± 101.4)
Guam	118.98	(± 16.81)
Hawaii	380.45	(± 25.11)
Indonesia	275.76	(± 19.89)
Israel	445.16	(± 105.13)
Jamaica	275.77	(± 50.75)
Kenya	335.25	(± 65.81)
Kiribati	1219.93	(± 93.2)
Madagascar	409.48	(± 46.1)
Maldives	688.64	(± 97.07)
Marshall Islands	707.72	(± 174.38)
Mauritius	166.93	(± 73.7)
Mayotte	631.43	(± 68.25)
Mexico	1930.81	(± 737.09)
Mozambique	461.01	(± 60.14)
Netherlands Antilles	428.01	(± 53.99)
New Caledonia	1460.27	(± 143.18)
NW Hawaiian Islands	729.71	(± 46.33)
Oman	282.79	(± 70.22)
Palau	3212.26	(± 332.02)
Panama	373.78	(± 85.41)
Papua New Guinea	566.70	(± 31.76)
Philippines	202.62	NA (n=1)
Pacific Remote Island Areas (PRIA), USA	641.47	(± 79.25)
Reunion	172.32	(± 30.67)
Seychelles	446.99	(± 46.6)
Solomon Islands	1280.30	(± 216.74)
Tanzania	346.29	(± 41.51)
Tonga	1149.97	(± 151.27)
United Arab Emirates	81.35	(± 28.66)
Venezuela	1472.39	(± 496.95)

In most cases, nation/state refers to an individual country, but can also include states (for example, Hawaii or Florida), territories (for example, British Indian Ocean Territory), or other jurisdictions. We treated the northwestern Hawaiian islands and Farquhar as separate 'nation/states' from Hawaii and the Seychelles, respectively, because they are extremely isolated and have little or no human population. In practical terms, this meant different values for a few nation/state scale indicators that ended up having relatively small effect sizes (Fig. 1b): population, tourism visitations, and in the case of the northwestern Hawaiian islands, fish landings.

Extended Data Table 3 | Model selection of potential gravity indicators and components

Model	Covariates	AIC	Delta AIC
M2	Gravity of nearest city	2666.4	0
M1	Gravity of all cities in 500km	2669.5	3.1
M3	Travel time to nearest city	2700.0	33.6
M5	Gravity of nearest small peri-urban area (40 people/km2)	2703.9	37.5
M11	Total Population in 500km radius	2712.0	45.6
M9	Travel time to the nearest large peri-urban area (75 people/km2)	2712.1	45.7
M6	Travel time to nearest small peri-urban area (40 people/km2)	2713.8	47.4
M8	Gravity to the nearest large peri-urban area (75 people/km2)	2722.9	56.5
M7	Population of nearest small peri-urban area (40 people/km2)	2792.7	126.3
M4	Population of the nearest city	2812.8	146.5
M10	Population of the nearest large peri-urban area (75 people/km2)	2822.2	155.8
M0	Intercept only	2827.7	161.27

Extended Data Table 4 | Variance inflation factor (VIF) scores for continuous data before and after removing variables due to collinearity

Covariate	starting VIF	ending VIF
Market gravity (log)	1.9	1.5
Nearest settlement gravity	1.4	1.3
Population growth	1.4	1.3
Climate stress	2.7	X
Ocean productivity	6.5	2.2
Sedimentation	6.0	X
Tourism	2.5	2.0
Control Corruption	10.5	X
GDP	8.2	X
HDI	5.5	3.3
Population size	1.9	1.8
Reef fish landings	3.1	2.2
Rule of Law	33.8	x
Voice and Accountability	3.2	3.2

X = covariate removed.

Extended Data Table 5 | List of bright and dark spot locations, population status, and protection status

Bright or Dark	Nation/State	Location	Populated	Protection
Bright	British Indian Ocean Territory	Chagos	Unpopulated	Unfished (high compliance)
	Commonwealth of the Northern Mariana Islands	Agrihan	Unpopulated	Fished
		Guguan	Unpopulated	Fished
	Indonesia	Raja Ampat 1	Populated	Restricted
		Raja Ampat 2	Populated	Restricted
		Kalimantan	Populated	Restricted
	Kiribati	Tabueran 1	Populated	Fished
		Tabueran 2	Populated	Fished
	Papua New Guinea	Karkar	Populated	Restricted
	PRIA	Baker	Unpopulated	Restricted
		Jarvis Island	Unpopulated	Restricted
	Solomon Islands	Choiseul	Populated	Fished
		Isabel	Populated	Fished
		Makira	Populated	Fished
		New Georgia	Populated	Fished
Dark	Australia	Lord Howe	Populated	Unfished (high compliance)
	Hawaii	Hawaii	Populated	Fished
		Kauai 1	Populated	Fished
		Kauai 2	Populated	Fished
		Lanai	Populated	Fished
		Maui 1	Populated	Fished
		Maui 2	Populated	Fished
		Molokai	Populated	Fished
		Oahu 1	Populated	Fished
		Oahu 2	Populated	Fished
		Oahu 3	Populated	Fished
		Oahu 4	Populated	Fished
		Oahu 5	Populated	Fished
		Oahu 6	Populated	Fished
	Indonesia	Karimunjawa 1	Populated	Fished
		Karimunjawa 2	Populated	Unfished (low compliance)
		Karimunjawa 3	Populated	Unfished (low compliance)
		Pulau Aceh	Populated	Fished
	Jamaica	Montego Bay 1	Populated	Unfished (low compliance)
		Montego Bay 2	Populated	Fished
		Rio Bueno	Populated	Fished
	Kenya	Diani	Populated	Fished
	Madagascar	Toliara	Populated	Fished
	Mauritius	Anse Raie	Populated	Fished
		Grand Sable	Populated	Fished
	NW Hawaii	Lisianski	Unpopulated	Unfished (high compliance)
		Pearl & Hermes 1	Unpopulated	Unfished (high compliance)
		Pearl & Hermes 2	Unpopulated	Unfished (high compliance)
	Reunion	Reunion	Populated	Fished
	Seychelles	Bel Ombre	Populated	Restricted
	Tanzania	Bongoyo	Populated	Unfished (high compliance)
		Chapwani	Populated	Fished
		Mtwara	Populated	Fished
		Stone Town, Zanzibar	Populated	Fished
	Venezuela	Chuspa	Populated	Fished

Abstract: Coral reefs have the greatest biodiversity of any ecosystem on the planet and support ecosystem goods and services to million people who depend directly on them for food, economic income, coastal protection and cultural values. Ecosystem accessibility, through road networks, is the main driver of their conditions, with the most accessible ecosystems being most at risk of resource depletion. To date, measuring accessibility to humans was strictly limited to examining the linear distance which ignores ragged coastlines and road networks that can affect the time required to reach fishing grounds. This thesis presents a double challenge: *(i)* developing new metrics of accessibility that account for seascape heterogeneity to better assess human impacts on coral reefs; (ii) evaluating the importance of coral reef accessibility, in interactions with their management, to explain variations of fish biomass. First, I developed novel metrics of reef proximity to human populations and markets based on the friction distance which is related to transport surfaces (paved road, dirt road, water) influencing the effective reach of human settlements. Travel time was used to build the gravity index, defined as human population divided by the squared travel time, to assess the level of human pressure on any reef of the world. I found that both travel time and gravity are strong predictors of fish biomass globally. Second, three applications using these new metrics highlighted that *(i)* gravity identified critical ecological trade-offs in conservation since reserves placed with moderate-to-high impacts may provide substantial conservation gains for fish biomass while reserve locations with low human impacts were more likely to support higher-order predation, *(ii)* using a study case in Northwest Madagascar, I illustrated how market proximity can affect fishermen communities and, ultimately, trigger changes in marine resources exploitation, and *(iii)* I implemented a new Community-Wide Scan (CWS) approach to identify fish species that significantly contribute to the biomass and coral cover on Indo-Pacific reefs and which provided tractable conservation targets. Within the context of global changes and biodiversity loss, the thesis challenges the sustainable and efficient management of coral reef socio-ecological systems with accessibility being the cornerstone.
Key words: fish community, fish biomass, ecosystem functioning, ecosystem services, human pressure, accessibility, gravity, Marine Protected Areas, coral reefs, socio-ecological systems, conservation.

Résumé : Les récifs coralliens hébergent la plus grande biodiversité sur Terre et fournissent la nourriture, le revenu économique, la protection côtière et les valeurs culturelles pour des millions de personnes. L'accessibilité des écosystèmes via les réseaux routiers est un déterminant majeur de leurs conditions, les écosystèmes les plus accessibles étant les plus menacées. Longtemps, l'estimation de l'accessibilité par l'Homme s'est limitée à l'utilisation de la distance linéaire qui ignore l'irrégularité des côtes maritimes et les réseaux routiers, facteurs influençant le temps nécessaire pour atteindre les lieux de pêche. Cette thèse présente un double enjeu : *(i)* développer des indices d'accessibilité intégrant l'hétérogénéité du milieu marin pour quantifier les impacts humains sur les récifs ; *(ii)* évaluer l'importance de ces nouveaux indices, en interaction avec les mesures de protection, pour expliquer les variations de la biomasse de poissons. Dans un premier temps, j'ai caractérisé la proximité des hommes aux récifs, en tenant compte des surfaces rencontrées (routes, chemin, eau) qui influencent le temps de trajet jusqu'aux récifs. Le temps de trajet a permis de calculer un indice de gravité, défini comme la population humaine divisée par le temps de trajet au carré, pour évaluer le niveau de pression humaine de n'importe quel récif au monde. J'ai trouvé que le temps de trajet et la gravité sont des déterminants majeurs de la biomasse de poissons à l'échelle globale. Dans un second temps, trois applications utilisant ces nouveaux indices ont permis de montrer que *(i)* la gravité permet de révéler l'efficacité des actions de conservation : les réserves placées là où les impacts humains sont modérés à forts fournissent des gains de conservation élevés pour la biomasse de poissons, mais elles sont peu susceptibles de protéger les prédateurs supérieurs, qui sont uniquement présent dans les réserves soumises à de faibles impacts humains ; *(ii)* en utilisant un cas d'étude réalisé dans le Nord-Ouest de Madagascar, j'ai illustré comment la proximité du marché peut affecter les communautés de pêcheurs et, finalement, engendrer des changements dans l'exploitation des ressources marines ; *(iii)* j'ai développé une nouvelle approche, le Community-Wide Scan (CWS), pour identifier les espèces de poissons qui contribuent de manière significative à la biomasse et à la couverture corallienne des récifs de l'Indopacifique, celles-ci pouvant constituer des espèces cibles à protéger. Dans le contexte de changements globaux et de perte de biodiversité, la mesure d'accessibilité constitue un outil puissant et permet de relancer le défi de gestion durable et efficace des socio-écosystèmes coralliens.
Mots clés : communauté de poissons, biomasse de poissons, fonctionnement des écosystèmes, services écosystémiques, pression anthropique, accessibilité, gravité, Aires Marines Protégées, récifs coralliens, socio-écosystèmes, conservation.
