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

Thesis submitted by
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Statement of the contribution

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My PhD is integrated into the *Cinner Research Group* led by Prof Joshua Cinner, which allowed me to use one of the largest sets of reef data available that compiles coral reef conditions and socioeconomic drivers from more than 2,500 reefs worldwide and collected by >30 data providers. This dataset was used in Chapters 4 and 5.
I developed some metrics related to accessibility of reefs by human populations that were the basement of two publications (Cinner *et al.* 2016, 2018) to which I have been involved in (second author in Cinner *et al.* 2018). These two publications led by Prof Joshua Cinner are part of the contribution of this thesis and will be presented in Chapter 4.
For Chapter 5, I was responsible for project design, analysis and interpretation of data. My co-authors provided intellectual guidance and editorial assistance.

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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. I found that travel time is a strong predictor of fish biomass. Second, using a downscaling of the travel time approach I illustrated how market proximity can affect the behavior 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. Third, travel time was used to build a human gravity index, defined as human population divided by the squared travel time, to better assess the level of human pressure on any reef of the world. Then, 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. 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

Coral reefs are among the richest ecosystems on Earth. While covering less than 1 per cent of the ocean floor (Spalding *et al.* 2001), 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). Millions of people in coastal areas depend directly on the ecosystem goods and services provided by coral reefs which sustain from artisanal subsistence fisheries, commercial fisheries, aquaculture, live reef-fish for food industry, recreational fishing and aesthetic and spiritual values (Teh *et al.* 2013; Cinner 2014). Coral reefs do not support only livelihood of people but they also offer coastal protection, jobs, medicines, recreational and touristic opportunities (Ferrario *et al.* 2014). Coral reefs are among the richest ecosystems on earth (Fisher *et al.* 2015) and provide valuable and vital ecosystem services estimated on average at $350,000/ha/year (de Groot *et al.* 2012). Coral-dominated reefs have higher productivity and when well-managed, coral reefs 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). Thus, fish are socially and ecologically important and the challenge of maintaining both food supply and fish biodiversity is one of the most challenging but also one of the most urgent challenge that scientists and managers are facing today.

1.1. Research context

1.1.1. Importance of fish biodiversity on coral reefs

1.1.1.1. Linking biodiversity and 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 highlight 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 1.1 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 1.1 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.

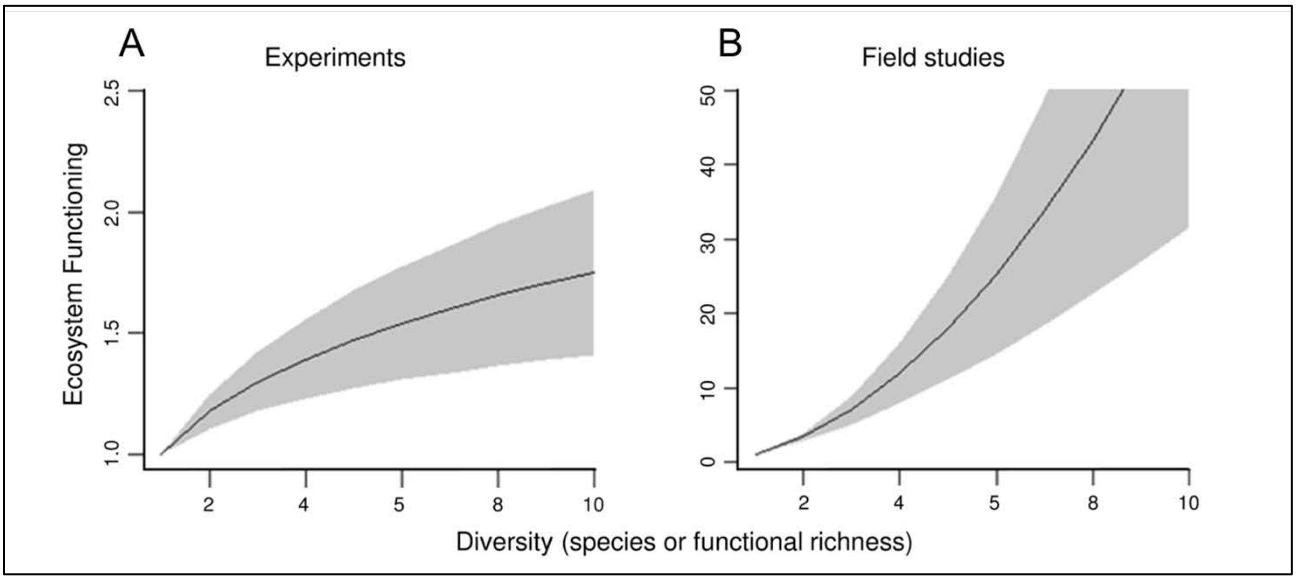

Figure 1.1 I *Experimental (A) and natural (B) ecosystems relationships between biodiversity and ecosystem functioning* (Mora *et al.* 2014).

1.1.1.2. Understanding the multiple facets of fish biodiversity

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, levels of redundancy are high as functions are packed in a few functional entities while 38% of the functions are represented by only one species and thus, are highly vulnerable. 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).

1.1.2. Coral reefs in the Anthropocene

1.1.2.1. 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 animal protein consumed by human populations in coastal regions or small islands (Moffitt & Cajas-Cano 2014) (Kawarazuka & Béné 2011; Teh *et al.* 2013; Charlton *et al.* 2016) and also provide critical nutrients essential to human nutrition (Béné *et al.* 2016; Golden *et al.* 2016; Thilsted *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).

1.1.2.2. 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 pyramids 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 pyramids 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 kilometre is enough to make bigger parrotfishes (*Bolbometopon muricatum, Chlorurus sp.*) locally extinct (Figure 1.2).

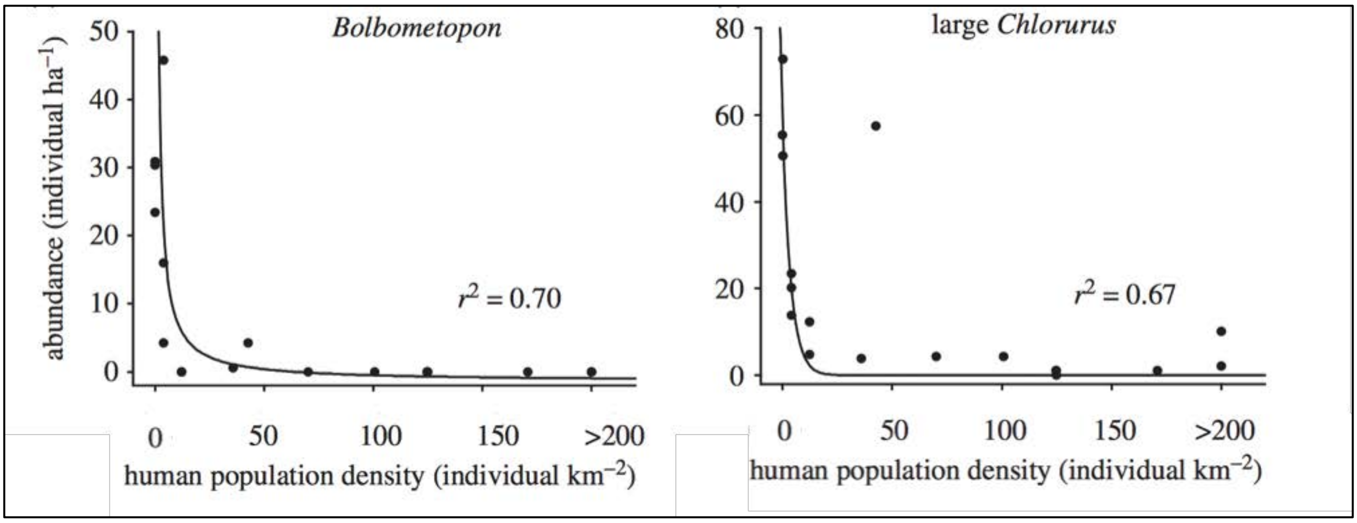

Figure 1.2 I ***Relationships between human density (inhabitants per km2) and the abundance of Green humphead parrotfishes (Bolbometopon) and large Chlorurus parrotfishes*** *(Bellwood et al. 2012).*

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. This results in heavier 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.

1.1.2.3. Complex population-environment dynamics in small-scale fisheries

Relationships between population growth and the environment are intensively debated in social science with two main opposing views from Thomas Malthus and Ester Boserup. Thomas Malthus promoted the idea that 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). Ester Boserup published her theory known as the ‘necessity is the mother of invention’ in the year 1965 and thus, challenged the Malthusian theory. Her theory admits that the combination of population growth and natural resource scarcity will inspire innovation to increase food production (Boserup 1965).
Applied to fisheries, Malthus’s theory predicts that the causes of overfishing are driven by “too many fishers chasing too few fish” (Pauly 1990) with fishing effort growing proportionately to human population growth. Regions in the world characterized by positive population growth, high level of poverty and strong dependence on marine resources fall within the context of ‘Malthusian overfishing’.

The relationships between population dynamics and fishery resources are more complex than the concept of Malthusian overfishing implies and while there is compelling evidence that human population growth can impact natural resources around the world (Vitousek *et al.* 1997; McKee *et al.* 2004; Johnson *et al.* 2017), it is not accurate to consider that global or local population growth is the only driver affecting natural resources (Allison 2001; Robbins 2011). Indeed 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). Also, 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).

From a management perspective, the Malthusian theory postulates that policy interventions that reduce fisher access, the number of fishers, or the human population may be needed (Pauly 1990; Roberts 1995) while the Boserupian theory predicts that environmental scarcity leads to creativity, innovation and policy that conserves natural resources (Boserup 1965). Fisheries management relies on a better understanding of all the factors affecting the coral reef socio-ecological systems to provide effective and equitable actions without blaming local fishermen (Finkbeiner *et al.* 2017).

1.1.2.4. Importance of markets: the location theory

Earth’s ecosystems are under increasing pressure as globalization connects the world (Liu *et al.* 2013). Markets create links between local activities and economic centers through trade and have become one of the most important factors driving human activities 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). Von Thunen's Theory of Agricultural Location describes the influence of the 'transport rate' on the location of agricultural activities in a region. His theory has long been one of basic concerns in economic geography and states that agricultural goods are produced at increasing distances from the market based on how expensive they are to transport (Von Thünen 1966). Goods that are cheap to transport will be produced relatively farther from the market than goods that are expensive to transport. His theory also points out that it exists a distance beyond which no agricultural production takes place.

This theory might hold true for small-scale fisheries with transportation costs to reach both fishing grounds and markets being critical. As many reefs are located in developing countries (Mora *et al.* 2011), these costs are particularly relevant since scarce road network and poor conditions roads will limit transportation. Thus, coral reefs might show great variability in their degree of accessibility since *(i)* reefs are located on varied coastal and oceanic places with different levels of infrastructure development (roads, markets); and *(ii)* fishing communities can be located far from markets and thus face even greater transportation costs. This theory has never been applied to coral reef socio-ecological systems while it seems promising to better explain how human activities affect reefs.

1.1.2.5. 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). If the social, institutional, and environmental conditions that support the success of management to achieve ecological benefits are well studied (Dulvy *et al.* 2004; Mora *et al.* 2011; Williams *et al.* 2015b; Bozec *et al.* 2016b; Cinner *et al.* 2016), it remains to be explored how conservation benefits of the different management actions (fishing restriction or marine reserve) can be maximized (Devillers *et al.* 2015; Pressey *et al.* 2015). To date, the intensity of human impacts in the surrounding seascape might influence the effectiveness of management to achieve conservation gains (Devillers *et al.* 2015; Pressey *et al.* 2015), while these effects have never been quantified.

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 affects the ability of MPAs to achieve conservation objectives.

1.2. Better understanding the variations of fish biomass on coral reefs

1.2.1. The importance of fish biomass

Coral reefs host no less than 6,000 fish species which represent the major group of vertebrates (Kulbicki *et al.* 2013). Fish play key roles in marine ecosystems functioning and ensure key ecological processes. They maintain coral reef in a state of coral dominance with herbivorous fish playing a key role in exerting a top-down control of algae and regulating coral-algae competition (Mumby *et al.* 2006; Hughes *et al.* 2007). They also regulate trophic structure and thus influence the stability, resilience, and food web dynamics of aquatic ecosystems but also participate to nutrients cycling and control algae and macrophytes growth (Holmlund & Hammer 1999; Bascompte *et al.* 2005). Numerous studies have shown that fish biomass is a strong predictor of species richness and their ecological functions. One effective way to maintain fish species and their ecological roles is to prevent fish biomass from falling below a critical threshold (McClanahan & Jadot 2017).

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). Beyond protein supply, fish also provide critical nutrients essential to human nutrition, including iron, zinc, vitamin A, vitamin B12, omega-3 and omega-6 fatty acids, and others (Béné *et al.* 2016; Golden *et al.* 2016; Thilsted *et al.* 2016) and is associated with a wide range of health benefits (Mozaffarian & Rimm 2006; Black *et al.* 2013; Lund 2013).

Fish biomass is a primary driver of coral reef ecosystem services and has high importance for the ecological processes and food and nutrition security. However, two questions remain unresolved to better explain variations of fish biomass on coral reefs:

(i) Are many complementary species or only a subset of 'key species' are necessary?

(ii) How can we improve our understanding of how people affect reefs by accounting for the degree of accessibility to reefs by human populations?

1.2.2. Identifying key fish species for coral reef functioning

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 fish communities 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 (Tilman *et al.* 1996; Tilman 1997; McCann 2000; Loreau *et al.* 2001; Tilman *et al.* 2001). 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.

1.2.3. 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.

1.2.4. 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.

1.3. 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 a heterogeneous 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 1.3):

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

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

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

RQ 4. Which and how many species are necessary to maintain fish biomass on coral reefs beyond environmental and anthropogenic conditions?

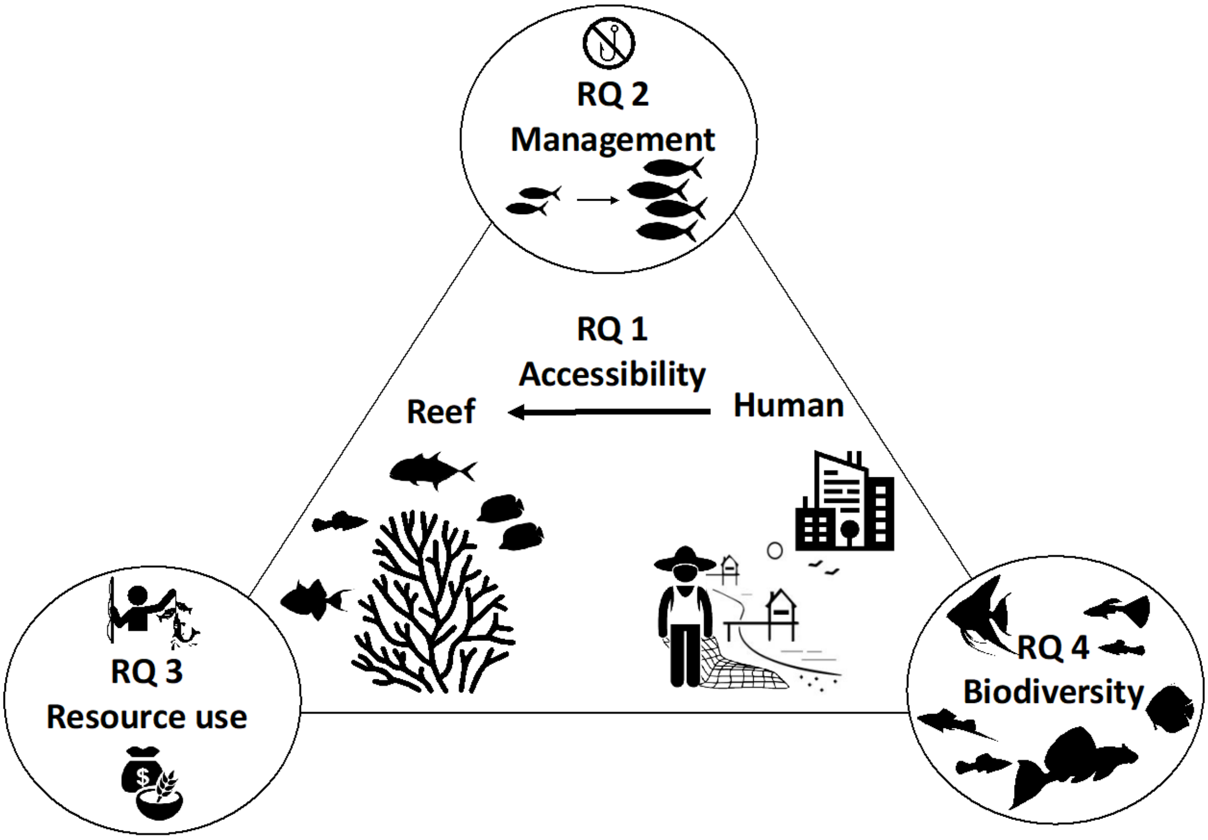

Figure 1.3 | Key aims of the thesis through 4 distinct research questions (RQ 1-4).

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

In this general introduction **(Chapter 1)**, I first provide the methodological and theoretical basis of my PhD. **Chapter 2** 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. **Chapter 3** 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**. Chapter 4** describes how to combine travel time and human population into an integrative metric of human impacts called 'gravity'. It also explores how the intensity of human gravity affects the effectiveness of management in tropical reefs. **Chapter 5** exposes the framework I developed to define which species are necessary to maintain fish communities and their associated services beyond environmental and anthropogenic conditions.

Lastly, **Chapter 6** consists on a synthetic analysis presenting the main conclusions and limitations of the thesis. It also provides perspectives and future applications.

2. 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.*

2.1. 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.

2.1.1. Theory on accessibility

Accessibility refers to transport geography which aims to quantify and qualify "the mobility of people, freight and information and its spatial organization considering attributes and constraints related to the origin, destination, extent, nature and purpose of movements" (Rodrigue *et al.* 2016). Our ability to move or transport goods is refereed as 'transportation' in geography and is shaped by a wide range of human and physical constraints such as distance, time, administrative boundaries and topography. Under these constraints, a friction of distance is conferred to any movement. In other words, any movement can be converted in time or in money (Rodrigue *et al.* 2016). Transportation is vital for economic and social activities and thus is an important component of human societies (Edwards 1992). Also, transportation relies on four essential components which are modes (vehicles), infrastructures (routes), networks (organization) and flows (movement) (Rodrigue *et al.* 2016).

In my thesis, I have focused on the accessibility of coral reefs defined as the time for human populations to reach the reefs. Since reefs are located on varied coastal and oceanic places with different levels of infrastructure development (road networks, markets), I have investigated how infrastructures can affect accessibility. The goal of this first chapter was to determine how far coral reefs were from human populations.

2.1.2. Travel time calculation

2.1.2.1. 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 include road and rail networks, navigable rivers and shipping lanes. Environmental factors such as land cover and slope can also affect travel speeds off the transport network. Political factors such as national or international boundaries and border crossings can alter transportation and provide 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.

2.1.2.2. 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).

2.1.2.3. 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 2.1).

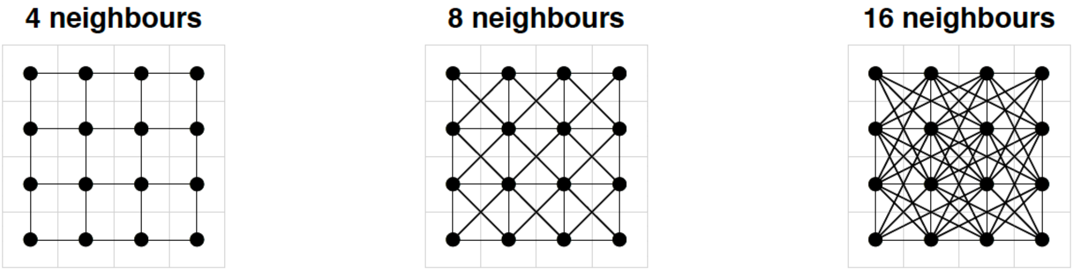


Figure 2.1 | The three ways to describe connectivity between cells within grids. *Cells can be connected (i) orthogonally to their four immediate neighbors, which is called the von Neumann neighborhood (left panel), (ii) with their eight orthogonal and diagonal nearest neighbors, the Moore neighborhood. 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 and half of the cell 2 (Figure 2.2). 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.

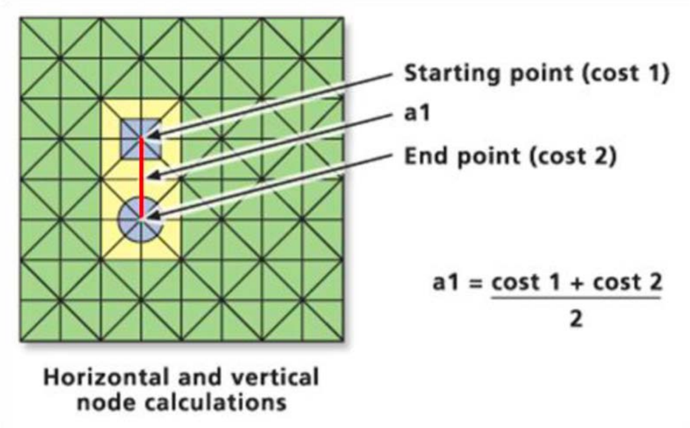


__Figure 2.2 | The accumulative perpendicular cost between 2 cells__ with a length of 1 represents the mean of the costs of the two cells (source: ArcGIS Resources).

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 2.3) depends on the square root of two times the square cells length and the mean of the costs of the cells 1 and 2.

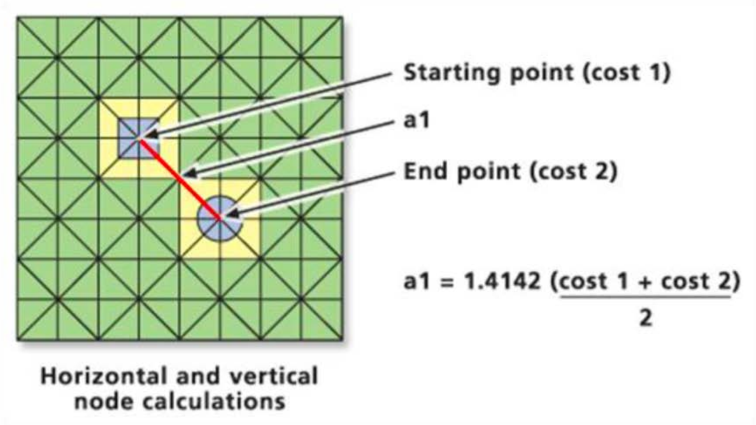


Figure 2.3 | The accumulative diagonal cost between 2 cells *with a length of 1 represents the mean of the costs of the two cells multiplied by the square root of 2 or approximately 1.4 (source: ArcGIS Resources).*

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.

2.1.2.4. 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).

2.1.2.5. 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

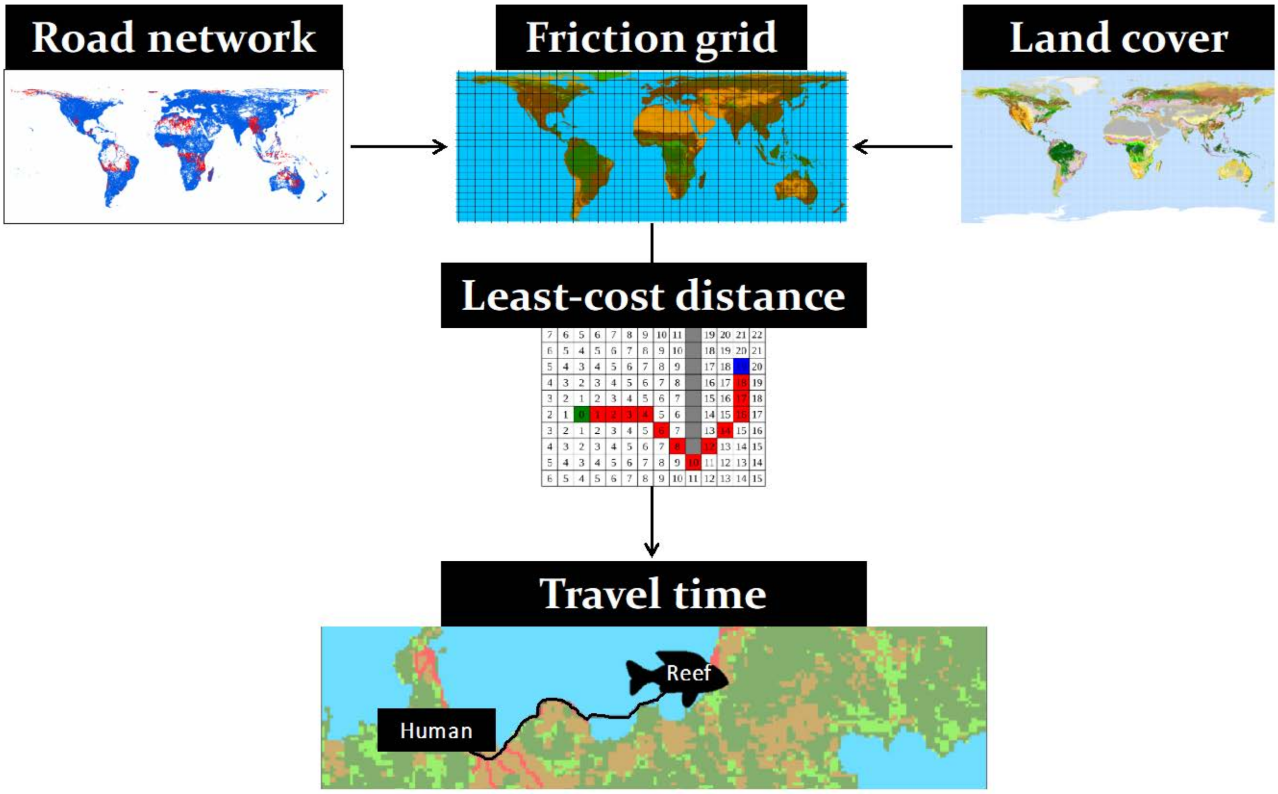
Markets have become one of the most important factors driving human activities which in turn, profoundly shape the exploitation of both terrestrial and marine natural resources (Laurance *et al.* 2009; Dobson *et al.* 2010; Mora *et al.* 2011; Ahmed *et al.* 2014; Barber *et al.* 2014; Alamgir *et al.* 2017) while it has been shown that even low human settlement or population densities can deplete resources on close reefs and have great impacts on fish abundance (Bellwood *et al.* 2012). For these reasons, two human settlements were considered as having strong influence on coral reefs thus, the nearest major market and the nearest human settlement were defined as destination points.

Following standard convention in agricultural economics (Von Thünen 1966), the nearest city was defined as the market. I built the list of major markets using the World Cities map layer given by Esri^{TM} (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^{TM} 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.

2.1.2.6. 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



7	6	5	6	7	8	9	10	11		19	20	21	22
6	5	4	5	6	7	8	9	10		18	19	20	21
5	4	3	4	5	6	7	8	9		17	18	19	20
4	3	2	3	4	5	6	7	8		16	17	18	19
3	2	1	2	3	4	5	6	7		15	16	17	18
2	1	0	1	2	3	4	5	6		14	15	16	17
3	2	1	2	3	4	5	6	7		13	14	15	16
4	3	2	3	4	5	6	7	8		12	13	14	15
5	4	3	4	5	6	7	8	9	10	11	12	13	14
6	5	4	5	6	7	8	9	10	11	12	13	14	15

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).

2.1.3. 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 2.4). 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 the 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).

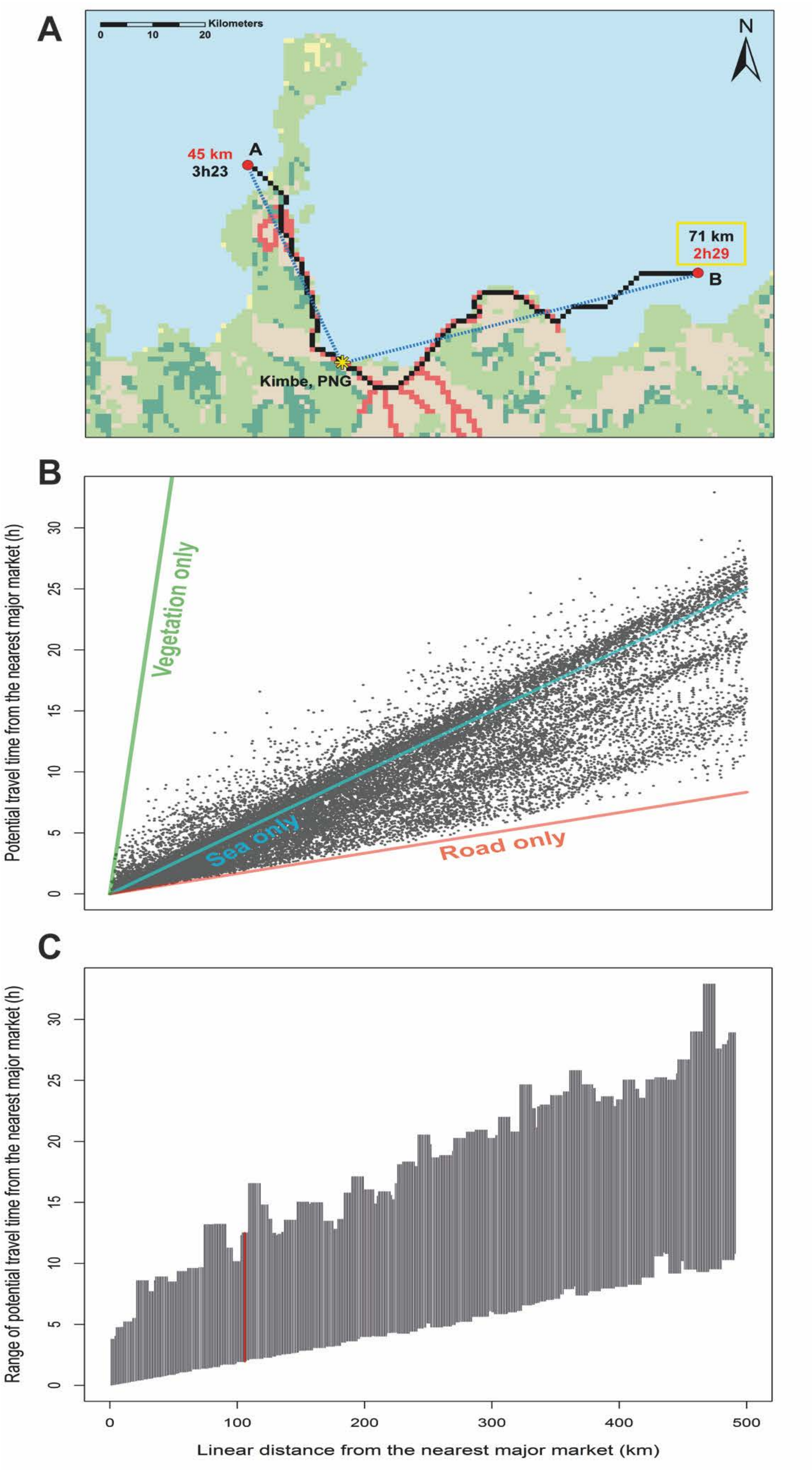

A
Kilometers
0
10
20
N
45 km
3h23
A
71 km
2h29
B
Kimbe, PNG
B
Potential travel time from the nearest major market (h)
0
5
10
15
20
25
30
Vegetation only
Sea only
Road only
C
Range of potential travel time from the nearest major market (h)
0
5
10
15
20
25
30
0
100
200
300
400
500
Linear distance from the nearest major market (km)

Figure 2.4 | 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 2.4B). 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 2.4C). 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 2.4C) 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 2.4 B). 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.

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

2.1.4.1. 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 2.5 A) to quantify the relative influences of environment, habitat, and human impact on fish biomass (Table III, Figure III).

2.1.4.2. 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 (Kulbicki 1997; Kulbicki 2006; Andréfouët & Wantiez 2010; Wantiez 2010; D'Agata *et al.* 2014). 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. Transects were performed on both the reef flat and slope for each reef, 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). Chondrichthyes (rays and sharks) were excluded from the main species list because their abundance is poorly assessed with UVC. The dataset comprises 352 species belonging to 33 different families.

The biomass of individual fishes was estimated using the allometric length-weight relationship: $W = aTL^b$, 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.

2.1.4.3. 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.

2.1.4.4. 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.

2.1.4.5. 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 (%) is calculated as the proportion of each variable which was selected to split the data among all the trees, weighted by the squared improvement to the model as a result of each split, and finally averaged over all trees. Highest contributions are attributed to the most important variables contributing to the model.

2.1.5. 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 2.1).

Table 2.1 | 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 2.5 B). 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 2.1), 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 2.5 C). Low biomass values (<100 kg.ha^{-1}) are mostly found when travel time is lower than 10h (Figure 3.5C). All remote reefs (Figure 2.5 A) 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.* 2011a; MacNeil *et al.* 2015).

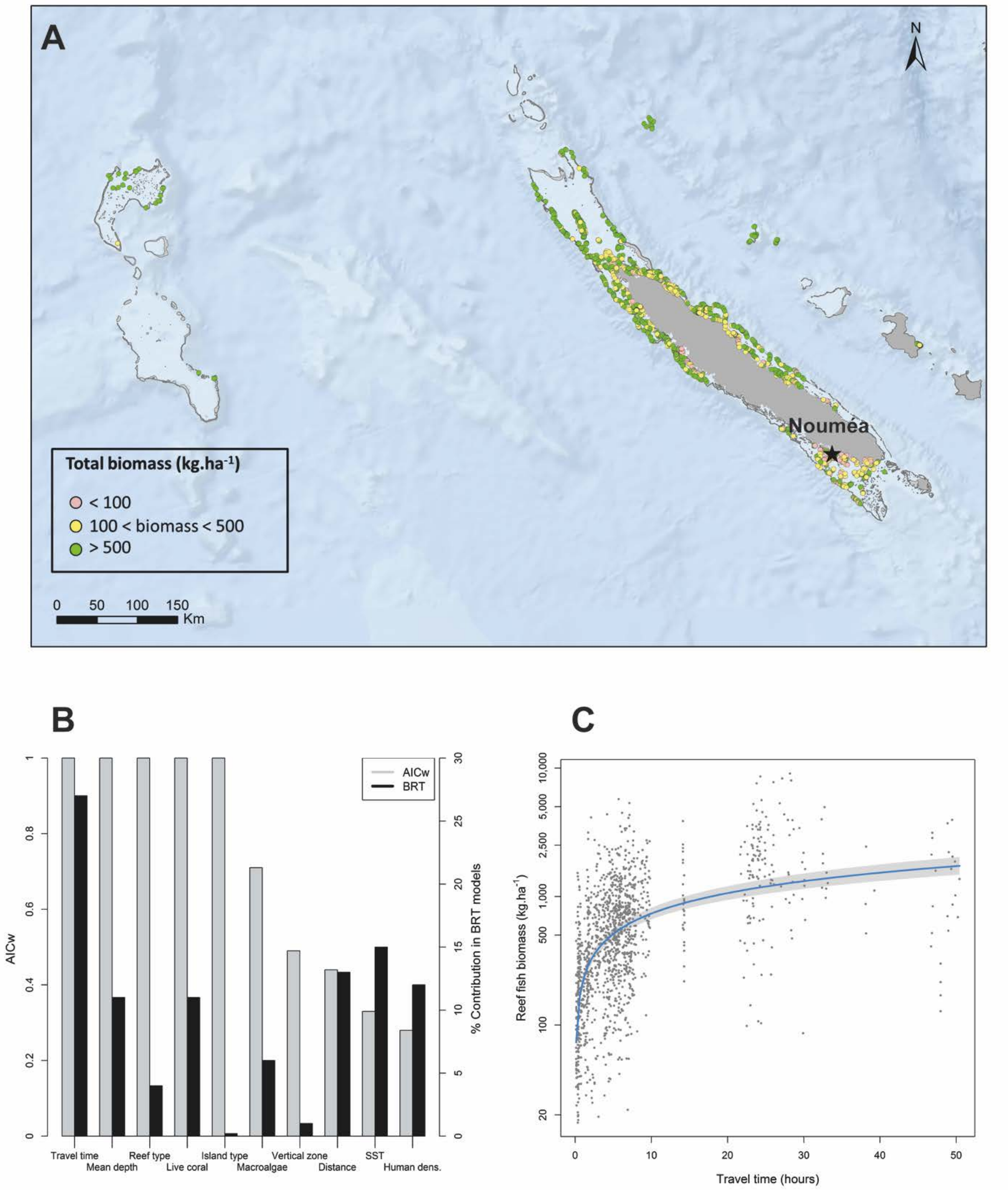


Figure 2.5 | Potential travel time as the main driver of fish biomass. *Fish biomass estimates from 1,357 Underwater Visual Census (UVC) surveys performed across coral reefs of New Caledonia (a). The relative influences of predictor variables (environment, habitat and human impact) are assessed using 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.

2.1.6. 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 2.6). 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 2.6 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 2.6 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 the initial exploration of travel time.

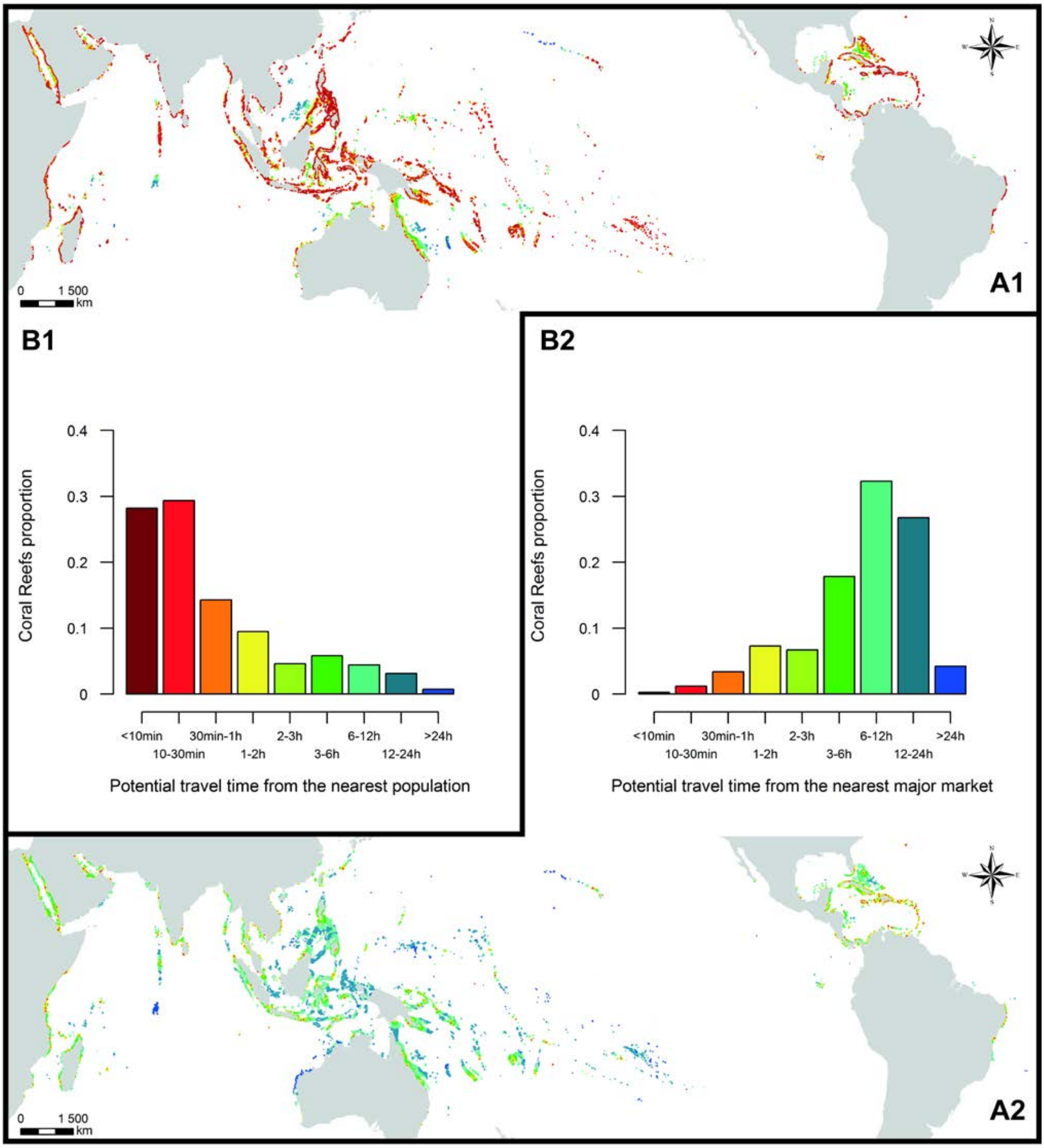


Figure 2.6 | Accessibility of any coral reef from people (nearest market and nearest human settlement) around the world. *Global coral reefs are extremely close to people (A1 & B1); 58% of reefs located at < 30 min travelling from the nearest human settlement while 25% of reefs are located at < 4 h from 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.*

2.1.7. 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 showed 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, my global assessment of coral reefs accessibility presents two major limitations:

(i) The travel time framework as previously described 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, travel time can be influenced by local considerations, such as infrastructure quality (road network) and the variability of available boat technology. This limitation will be discussed in **Chapter 3** which considers a study case in Northwest Madagascar and where travel time calculation integrates the local levels of infrastructure and technology.

(ii) Travel time from a given human settlement does not accurately reflect human impacts on reefs since two locations, one densely and one sparsely populated can have the same travel time from a specific reef but potential human pressure may be different. Thus, population size of human settlements also needs to be taken into account. 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 **Chapter 4** will propose one alternative to the first limitation by describing how to combine travel time and human population density into an integrative metric of human impact.

3. Market *vs* coastal communities: disentangling complex interactions in small-scale reef fisheries in Northwest Madagascar[2]

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

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[2] *Maire, E., D'agata, S., Cinner, J., Aliaume, C., Darling, E. & Mouillot, D. Ecology and Society (in prep)*

3.1. Introduction

Earth's ecosystems are 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 ecological conditions are still unclear. A parallel literature on the role of economic development and its impacts on the environment highlights three main mechanisms, which may also be relevant to changing market accessibility: *(i)* a scale effect, whereby human societies displace their local environmental footprint by harnessing resources from further afield (typically the scale effect indicates an increase in environmental stresses related to higher use of natural resources in poorer, less regulated or remote areas); *(ii)* a technique effect, whereby technologies used by humans change as societies become more developed, leading to differing levels of impact on the environment; and *(iii)* a composition effect, which suggests that the structure of the local economy changes with economic development to transition, for example from a natural-resource based economy (subsistence fishing) to a service-based economy (fishing trade) (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 how levels of development influence 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 influences local human communities and surrounding ecological conditions through those

three main effects together remains overlooked and could hide important social and economic dynamics at local scale, with significant consequences on ecosystem states.
Indeed, understanding how accessibility from human societies affects natural resources is a critical step toward long-term management of the ecosystems for which actions are needed to insure ecological and economic sustainability. As both market and nearest communities shape coastal resources at global scale (Cinner *et al.* 2016) 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.

Small-scale fisheries remain an essential source of food, employment and revenue for people around the world (Béné *et al.* 2007; Bell *et al.* 2009; Teh *et al.* 2013). Specifically, I focused on small-scale artisanal coral reef fisheries in Northwest Madagascar. I hypothesize that coral reefs resource conditions improve with decreasing accessibility to both markets and coastal communities, but this rate will depend on the type of fisheries management (see Methods). I also hypothesize that community-level characteristics of socioeconomic conditions or resource use (ex. primary occupation, livelihoods diversity, technology used etc.) may change with access to markets. Here, I investigated: *(i)* the relative effects of market access, fisheries management and key environmental variables on reef fish biomass in the northwest of Madagascar; and *(ii)* the influence of markets on socioeconomic characteristics on coastal communities through the scale, the composition, and the technique effects. I address these questions using ecological data collected in 31 reefs and social drivers collected at household-level in 10 coastal communities in Northwest Madagascar.

Context and study area

Despite its biological and cultural richness, Madagascar is one of the world's poorest developing countries, and local communities depend heavily on the exploitation of natural resources for subsistence and livelihoods (World Bank 2010; Conservation International 2015). The artisanal fishery is a significant economic sector comprised of multi-gear and multi-species fishing activities, where fishers access is from the shore or using wooden pirogue canoes (McKenna & Allen 2003; Doukakis *et al.* 2008; Davies *et al.* 2009). 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 (climate change and extreme weather events threaten agricultural productivity) 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.* 2011a; Obura 2012). The west coast of Madagascar is now considered as a high priority for increased management efforts as a potential 'climate refugia' in the Western Indian Ocean (McClanahan *et al.* 2011b; Beyer *et al.* 2018). Coral reef 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). In northwest Madagascar, there are currently two forms of marine resources management: *(i)* formal Marine Protected Areas (MPAs) mainly of IUCN categories V and VI managed by national or international associations or NGOs but with strong involvement of local communities and *(ii)* Locally Managed Marine Areas (LMMAs) managed by local communities based on social conventions known as "dinas" (Rakotoson & Tanner 2006) and aiming 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). Most of the MPAs and LMMAs contain *(i)* temporary fishing closure for octopus (particularly in the southwest and northeast), *(ii)* areas in which fishing is allowed using certain types of gears and for fishermen with fishing access only (restricted zones) and *(iii)* permanent reserves (no-take zones where fishing activities are prohibited). Beach seining, considered as a destructive fishing practice, has been historically prohibited along most coastal areas through dinas and is now nationally prohibited in Madagascar since 2018. Shark fishing and sea cucumber harvesting are regulated in the northwest while some pelagic fish are under seasonal closures (such as the Indian mackerel *Rastrelliger kanagurta*). Yet despite regulations, those practices, particularly beach seining are still happening in Madagascar particularly where no management structures are in place.

3.2. Methods

3.2.1. Study area

The study includes reefs along ~150 km of coastline from Nosy Iranja to Nosy Mitsio (Figure 3.1). The area is characterized 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 (despite legal regulations) (Doukakis *et al.* 2008; Davies *et al.* 2009; Jadot *et al.* 2015).

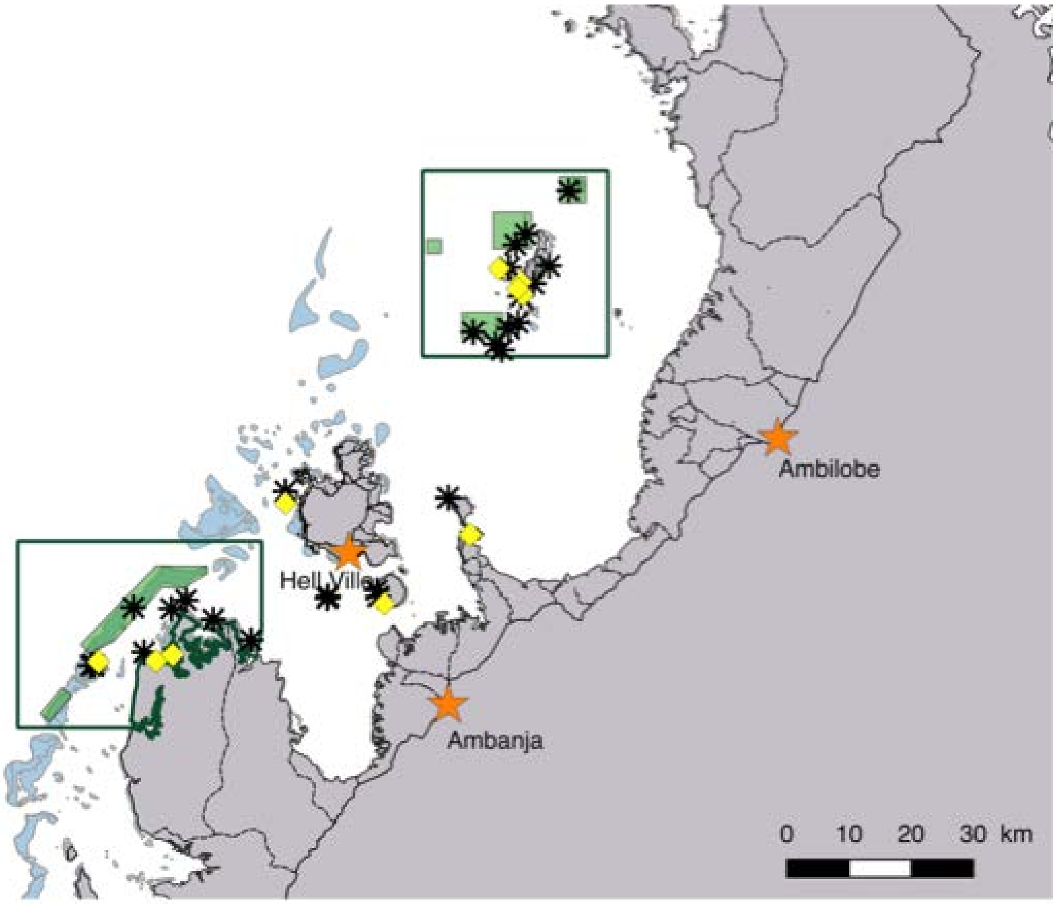


Figure 3.1 I Map of the Northwest Madagascar reefs. *Surveyed reefs (black asterisks) and coastal communities (yellow diamonds), local markets (orange stars), MPAs boundaries (green lines) with no-take zones (green polygons) and cartography of reefs (blue polygons) are represented.*

This area includes two MPAs (Ankarea and Ankivonjy) that are co-managed between local communities and the Wildlife Conservation Society (WCS) and officially established in April

2015. The two MPAs have designated access restriction strategies in which local fishermen within the MPA boundaries have exclusive access rights to fishing areas inside each MPA. The management plans for each MPA are based on the existing dinas in both areas, complemented by national policies on gear restrictions, including: *(i)* beach seines, *(ii)* nets with mesh size under 25mm, *(iii)* nets over 500m long and *(iv)* any fishing gear directly entering in contact with the bottom to avoid coral reefs destruction. Outside the MPAs, these rules do not apply. Because reefs in MPAs under restrictions still experience fishing activities, I only considered two different management categories as following: fished reefs (open access and restricted reefs) or unfished (low to high compliance reserves).

3.2.2. Ecological surveys

Data used in this analysis were collected on social and ecological study sites. Social sites consisted of 10 Malagasy coastal communities (Figure 3.1) 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 fished (open access and restricted reefs) and unfished (low to high compliance reserves) reefs to collect ecological data. In total, 31 ecological sites (hereafter "reefs") were surveyed between April and November 2016 with 16 fished reefs and 15 located in low to high compliance reserves where fishing activities were prohibited (Figure 3.1).

Reef fish survey 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.

I included 25 fish families which represent the main reef fish families in the study region (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). 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=aTLb, where parameters a and b are species-specific constants, TL is the individual total fork length in centimetres 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 this study, I 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.

To evaluate environmental conditions on each reef, 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, I calculated the average of monthly temperature and ocean primary productivity over the 5-years period.

Since these environmental and habitat conditions may have confounding effects, I performed a Principal Coordinates Analysis (PCoA using Gower's distance) using the common environmental predictors which describe similarities between the ecological sites including: depth, weekly average SST and net 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 (representing 74% of the total variance) as environmental covariates for further analysis.

3.2.3. Socioeconomic surveys

Socioeconomic variables

I 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 and 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 field campaigns in March-April 2016.

I also assessed the human population occurring within a 4km radius of each reef using the WorldPop dataset version 2.0 (Tatem 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). I set the cut-off at 4 km to reduce spatial overlap between reefs.

Social characteristics

Socio-economic surveys were conducted in 10 Malagasy coastal communities across three districts in Northwest Madagascar from November to December 2016 by trained and experienced Malagasy interviewers in local language (Figure 3.1; Table IV). For communities with less than 50 households, all households were surveyed. In larger communities, 50 households were randomly chosen when possible (Table IV). In total, 353 household surveys across the 10 communities. All survey activities were approved by the Wildlife Conservation Society (WCS) Institutional Review Board (IRB) and were part of the WCS global social-ecological systems approach (MACMON) for the monitoring of fisheries and the impact of conservation management interventions. Semi-structured 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, and household surveys lasted from 45 to 60 minutes. Additionally, key informant interviews were conducted with community leaders or particularly knowledgeable fishermen to better understand the characteristics of resource management and market connections for each community. All interviews were conducted by trained and experienced Malagasy interviewers in local languages.

I first identified the MACMON social indicators describing the actors involved in small-scale fisheries (number, socioeconomic attributes, norms, importance of resource, technology used) that could support the three mechanisms through which increasing market accessibility influences ecological conditions. I only considered those reported for all communities surveyed. Thus, I considered nine social indicators that I related to market proximity, by estimating for each community the mean value of these nine 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 3.1. Fishers represented households who participated in some fishing activity and targeted mainly coral reef fishes (excluding households who targeted only sharks). Finally, I was only able to consider social indicator describing whether coastal communities might be affected by market proximity through the technique and the composition effect (Table 3.1).

Table 3.1 I Description of the 9 social indicators estimated from household surveys for each community.

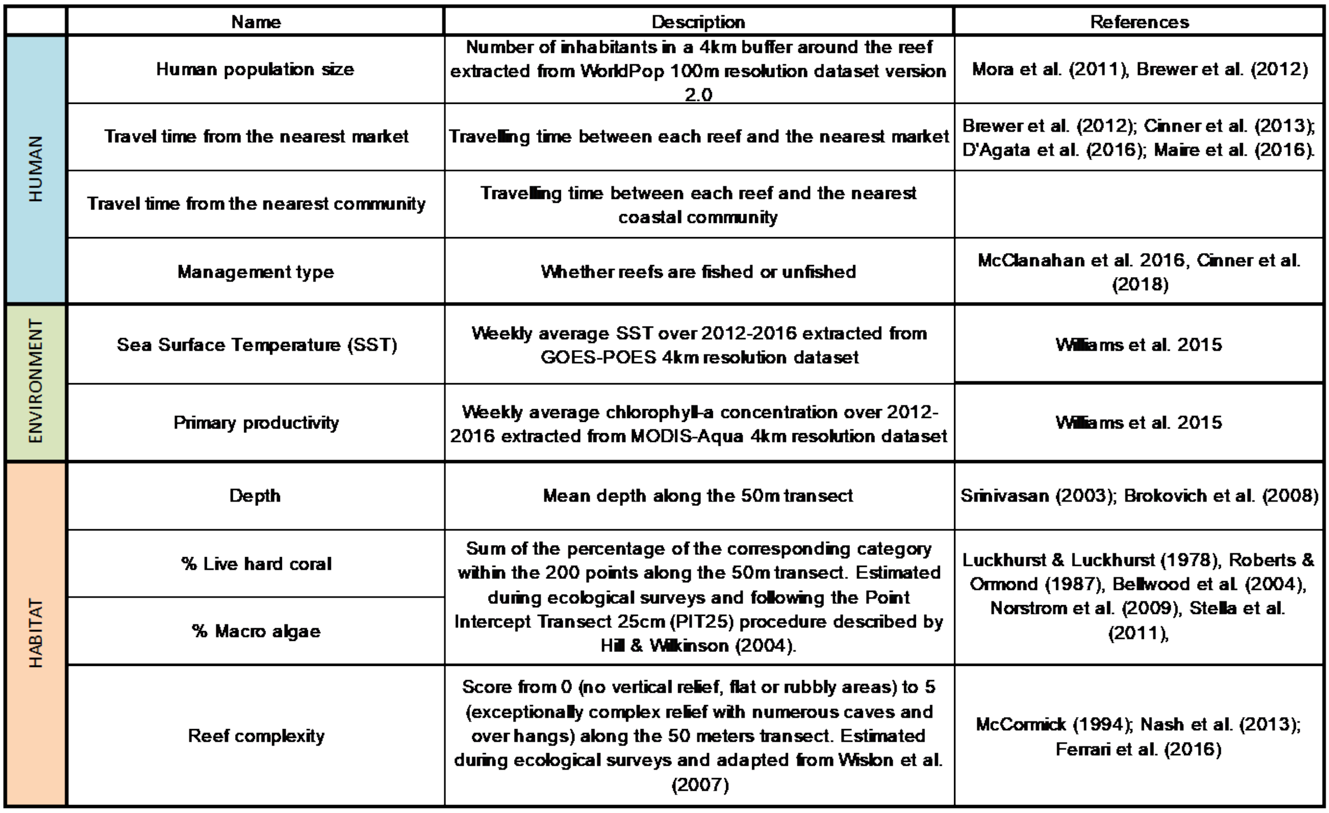
Market mechanism	Indicator	Description	Survey method	Sample size	Type of data	Mean	Range
Composition effect	Fishing activity	the proportion of households who ranked fishing as primary activity	All households surveys	354	Quantitative	46	25 - 67
	Farming activity	the proportion of households who ranked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

3.2.4. Data analysis

I 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 fishing households 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 are located in MPAs), management was included as a supplemental variable in the PCA. I checked the loadings of variables to identify which variables have the largest effect on each component and the score of each coastal community to quantify how communities are described by components.

The human and environmental variables considered in the model are described in Table 3.2. To explore how proximity to markets and communities affects the reef conditions beyond ecological and human population size effects, I built generalized additive models (GAMs) considering the two environmental covariates provided by PCoA (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 a 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. I 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). I also considered interactions between management and market or community. As all these models are nested, I performed a Likelihood Ratio Test (LRT) to determine which human variables significantly improved model fit (Wood 2006). I also assessed model fitting and parsimony by using AICc, Akaike Information Criterion corrected for small data samples (Hurvich & Tsai 1989).

Table 3.2 I 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)

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

3.3. Results

3.3.1. Influence of travel time and management on fish biomass

Among all the models tested, the best-fit model (LRT’s pvalue = 0.03 and lowest AICc = 18.6) explained up to 80% (adjusted R^2) of the variability observed in fish biomass (Tables 3.3 & 3.4).

Table 3.3 I 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 (M3C) 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 * Population	23.3	0.3
M3B	Env1 + Env2 + Population + Management + Market + Village	Management * Market	24.0	0.4
M3C	**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 3.4). 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). I found that population had a significant negative influence on fish biomass meaning that fish biomass decreases non-linearly as human population size increases, both on unfished and fished reefs at the same rate (Figure 3.2c) while biomass increases further away from market until reaching a maximum at approximately 6-7h from a market (Figure 3.2b, Table 3.4). In the same vein, fish biomass in fished reefs increased non-linearly with increasing travel time from the nearest community, with a sharp increase at approximately 1.5 hours (Figure 3.2 a). Conversely, fish biomass in unfished reefs showed no relationship with travel time from community (Figure 3.2 a, Table 3.4).

Table 3.4 I 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 community 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**

Overall, fished reefs at proximity of a market or communities presented lower levels of reef fish biomass than unfished reefs (Figure 3.2 b, c, d), demonstrating higher biomass in marine reserves that reached levels of reef fish biomass considered as resident biomass in the absence of fishing (median 1,235 kg.ha^{-1}) (Figure 3.2d). Fish biomass in fished reefs 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 community (Figure 3.2 a).

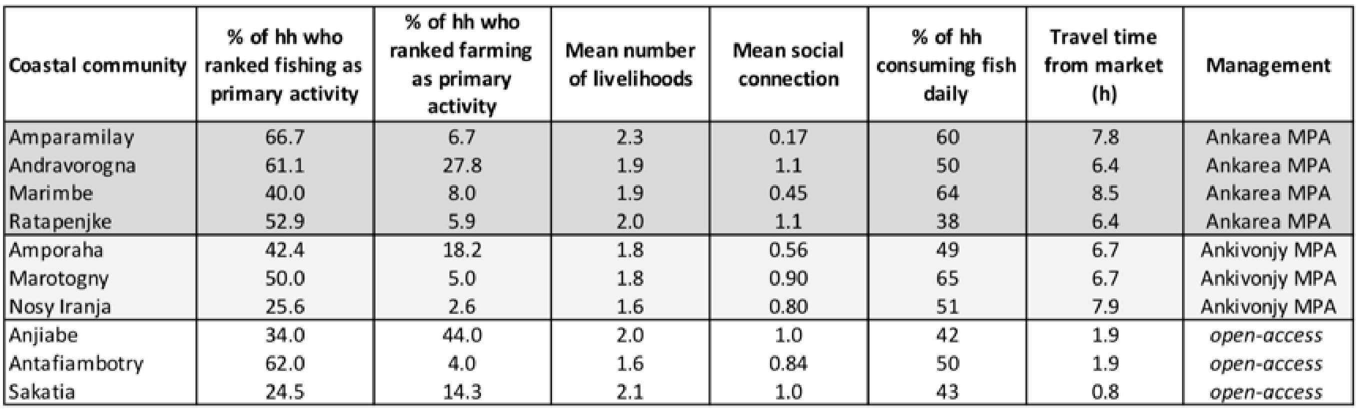
Figure 3.2 I Marginal effects of each socioeconomic covariate included in the fish biomass model while considering the other predictor variables are held constant. *Relationships between fish biomass and travel time from the nearest community (a), travel time from the nearest market (b), human population size (c) and management (d) for fished (green) and unfished reefs (orange).*

3.3.2. Effect of market proximity on local communities

I 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 3.5). In average, households had two activities (range at community level:

1.6 - 2.3; range of household responses: 1 - 4) and 51% of households consumed fish at least once a day (range at community level: 38 - 65%) (Table 3.5). Households were involved on average in only one community group (range at community level: 0.2 - 1.1; range of household responses: 0 - 4) (Table 3.5).

Table 3.5 I 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.*



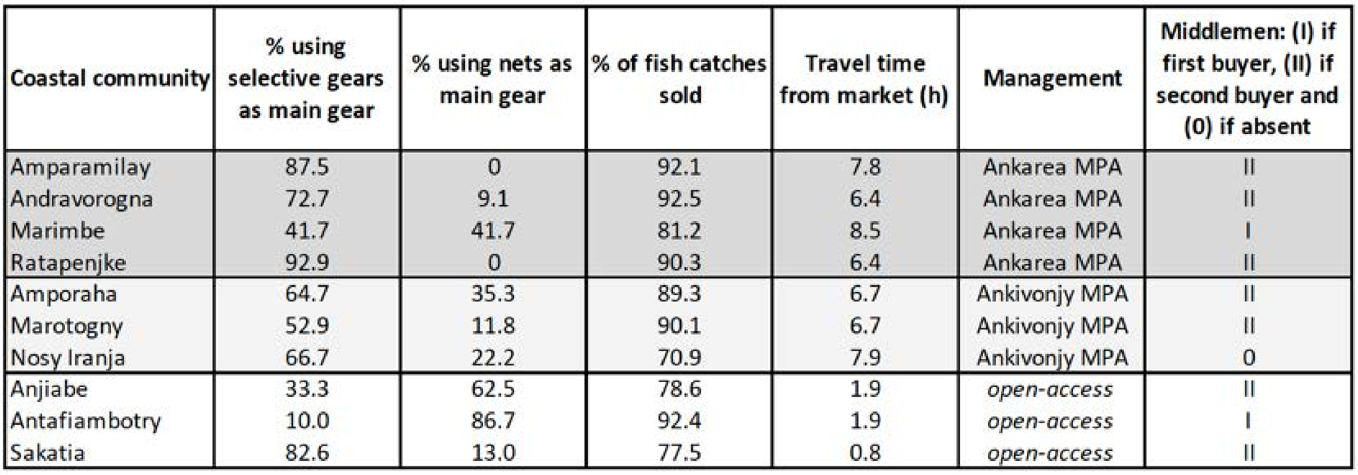
Coastal community	% of hh who ranked fishing as primary activity	% of hh who ranked farming as primary activity	Mean number of livelihoods	Mean social connection	% of hh consuming fish daily	Travel time from market (h)	Management
Amparamilay	66.7	6.7	2.3	0.17	60	7.8	Ankarea MPA
Andravorogna	61.1	27.8	1.9	1.1	50	6.4	Ankarea MPA
Marimbe	40.0	8.0	1.9	0.45	64	8.5	Ankarea MPA
Ratapenjke	52.9	5.9	2.0	1.1	38	6.4	Ankarea MPA
Amporaha	42.4	18.2	1.8	0.56	49	6.7	Ankivonjy MPA
Marotogny	50.0	5.0	1.8	0.90	65	6.7	Ankivonjy MPA
Nosy Iranja	25.6	2.6	1.6	0.80	51	7.9	Ankivonjy MPA
Anjiabe	34.0	44.0	2.0	1.0	42	1.9	*open-access*
Antafiambotry	62.0	4.0	1.6	0.84	50	1.9	*open-access*
Sakatia	24.5	14.3	2.1	1.0	43	0.8	*open-access*

I investigated whether proximity to market is related to communities' socioeconomic and resource use characteristics. Communities further away from market consumed more fish (ex. Marimbe) and were relatively more engaged in fishing as primary activity (ex. Amparamilay) compared to communities closer to market for which farming was the primary activity (ex. Anjiabe) (Figure 3.3 a, Table 3.5). Overall, communities further away from market were also less involved in community organizations (Figure 3.3 a, Table 3.5). There was no relationship between the number of livelihoods and remoteness to market (Figure 3.3a).

3.3.3. Effect of market proximity and management on fishing and selling practices

I highlighted a high heterogeneity in fishing practices since 10 to 93% of households (mean: 61%) used selective gears and 0 to 87% of households (mean: 28%) used nets as the main gear (Table 3.6).

Table 3.6 I 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	87.5	0	92.1	7.8	Ankarea MPA	II
Andravorogna	72.7	9.1	92.5	6.4	Ankarea MPA	II
Marimbe	41.7	41.7	81.2	8.5	Ankarea MPA	I
Ratapenjke	92.9	0	90.3	6.4	Ankarea MPA	II
Amporaha	64.7	35.3	89.3	6.7	Ankivonjy MPA	II
Marotogny	52.9	11.8	90.1	6.7	Ankivonjy MPA	II
Nosy Iranja	66.7	22.2	70.9	7.9	Ankivonjy MPA	0
Anjiabe	33.3	62.5	78.6	1.9	*open-access*	II
Antafiambotry	10.0	86.7	92.4	1.9	*open-access*	I
Sakatia	82.6	13.0	77.5	0.8	*open-access*	II

Communities far from market were located in MPAs and used more selective gears while nets are more common in communities closer to markets and outside of the two MPAs (Figure 3.3 b, Table 3.6). There was no clear relationship between the proportion of fish catch sold and accessibility to the market since overall, all communities sold a high proportion of their catch (median: 90%; range: 71 – 93%) (Table 3.6).

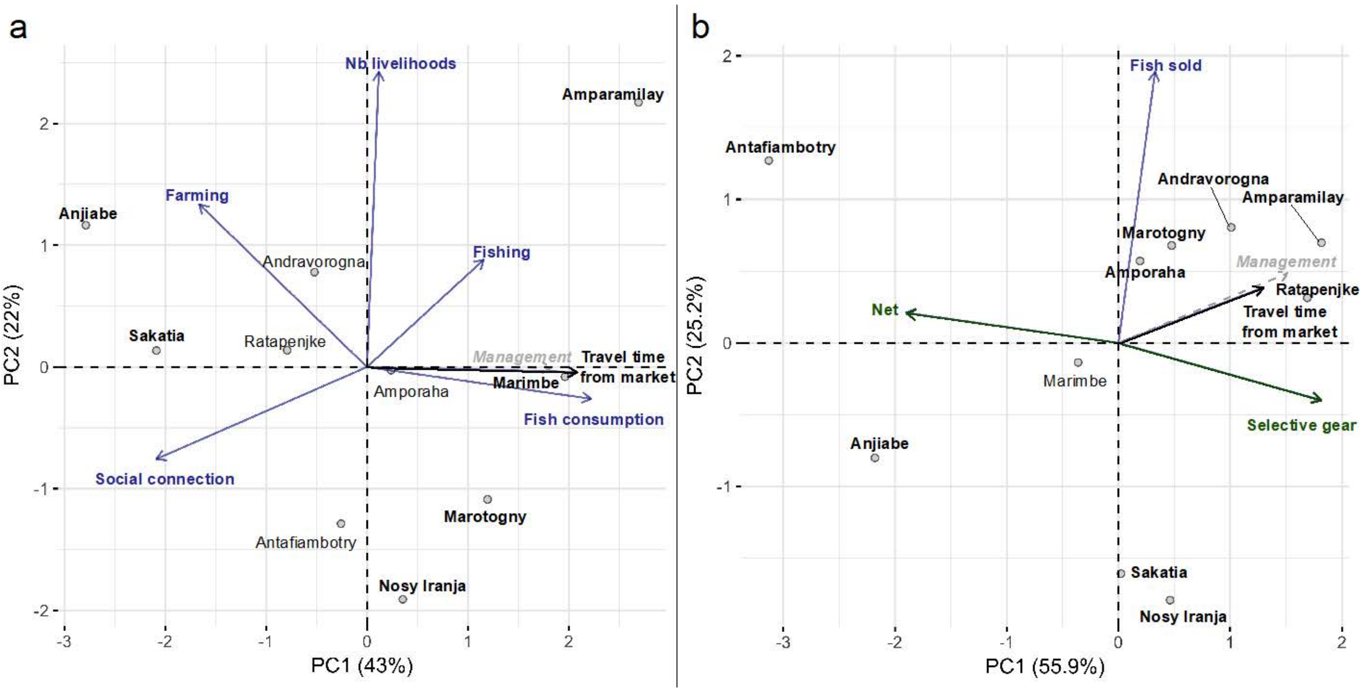


Figure 3.3 I Correlations between market access and social characteristics of local communities (a) and fishing households (b). *Five social indicators were assessed for each of the 10 coastal communities: the proportion of households who ranked fishing as primary activity (Fishing), the proportion of households who ranked farming as primary activity (Farming), the livelihoods diversity: the mean number of livelihood activities that households are involved in (Nb. Livelihoods), the mean number of community groups people are involved in (Social connection), the proportion of households consuming fish at least once a day (Fish consumption) that were related to market access (Travel time from market). For fishing households, only households engaged in fishing activities were considered and for each community: the proportion of fishing households who used as main gear nets (Net) or selective gears (Select. gear) respectively and the proportion of fish catches sold (Prop. fish sold) that were related to market access (Travel time from market) were assessed. Social indicators were associated with the composition (dark blue) or the technique (green) effect. As market accessibility and management actions had confounding effects in the study area (marine reserves are disproportionally located far from markets) one supplementary variable (Management) was included 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). All variables properly contributed to the two first components (PC1 & PC2) except the proportion of households who ranked fishing as primary activity (Fishing) (see Figures VI & VII).*

However, selling strategies tended to be affected by market proximity (Figure 3.4). I found that fishing households from distant communities (up to two hours from market) did not go to the nearby market to sell fish catches but sold preferentially to their own community or to middlemen who occasionally collected sea food products in those remote communities (Figure 3.4). Similarly, a proportion of fishing households sold their catch directly to market only if their community was located at less than two hours (Figure 3.4). Overall, middlemen's influence was widespread in the region since they collected seafood products from very close (at less than two hours) but also to more distant communities from markets (up to eight hours) (Figure 3.4, Table 3.6).

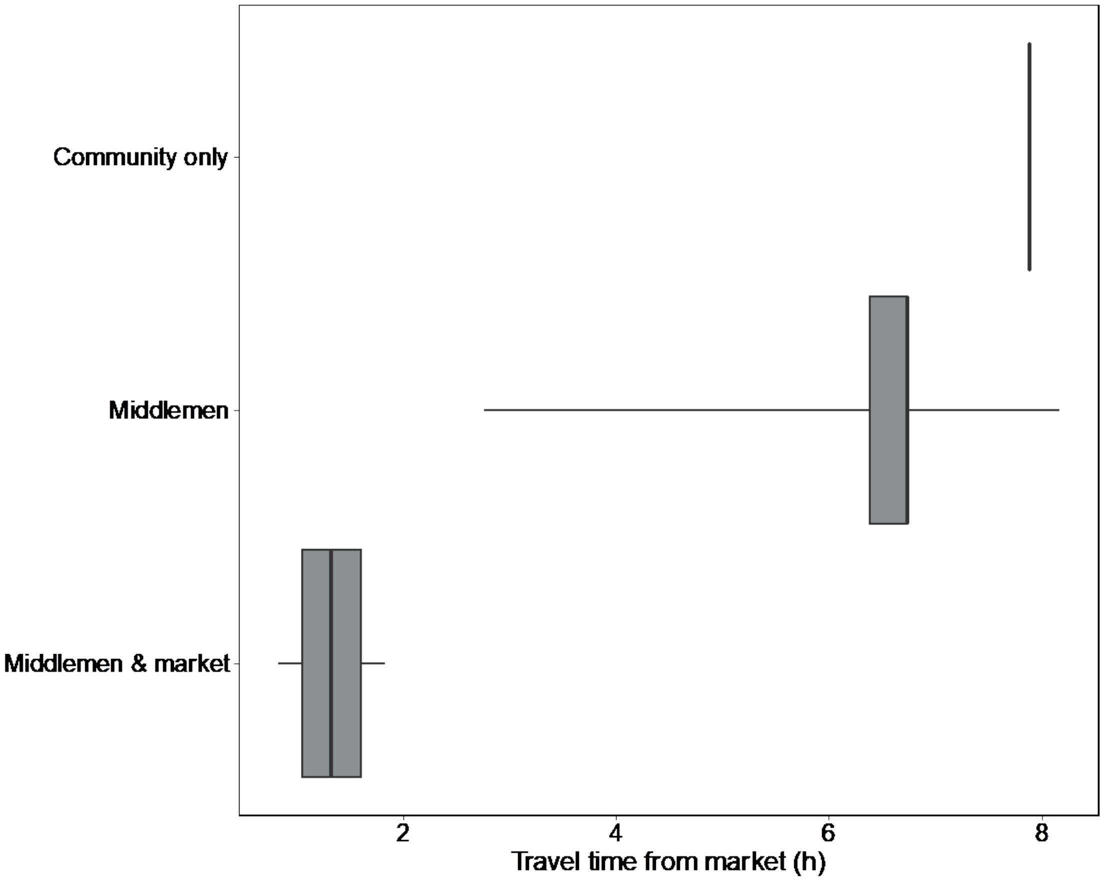


Figure 3.4 I Access to types of markets in remote and accessible communities. *When fish were sold, the preferred buyer was assessed for the 10 coastal communities surveyed included: own community, middlemen from another community or local market. At least part of fish catches was sold directly within 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.

3.4. Discussion

This 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, I 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, the study 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. This suggests that better quantifying effect of local market on household behaviors and practices could help our understanding of changes in natural resources exploitation, and ultimately support effective management of small-scale coral reef fisheries.

Redefining market effect on fishing communities to sustain social-ecological systems

Accessibility to markets can shape the composition and 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 and a higher consumption of fish (composition effect) (Figure 3.3 a). Given that small islands are less suitable for agricultural production and employment options are limited (Laroche & Ramananarivo 1995; Le Manach *et al.* 2012), this results in higher levels of dependence on seafood and exploitation of marine resources further away from markets while fishing was crucial for income generation in those remote communities. Decreased market accessibility has been found to be positively correlated with higher dependence on forest resources, where the most isolated households from the markets have the lowest incomes and higher dependence on non-timber forest products (Ghate *et al.* 2009). These results are consistent with previous studies in the terrestrial realm. It is thus essential to assess how strong dependence of local communities to marine resources influences the ecological state of surrounding reefs.

Second, market proximity can also influence the fishing techniques used by fishing households. Fishing practices are highly variable between households but I observed that gear selectivity increased as communities were located further away from markets (Figure 3.3 b). There is large amount of variation in how fishing gears differentially targeted the characteristic, proportion and number of species (Cinner *et al.* 2009b), some of them such as grazers and scrapers/excavators, identified as critical to the resilience of coral reefs (Bellwood *et al.* 2004; Mumby *et al.* 2006). Fishing gears can also provide detrimental damages on the environment (Link 2010). 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). Thus, there is an urgent need to identify environmental impacts of fishing gears used in northwest Madagascar to adapt selectively banning or restricting fishing and thus, promote the sustainability and the resilience of these small-scale fisheries.

Fishing communities in Madagascar and especially in remote areas, commonly use small dugout canoes fitting one to four persons that are unsafe for high sea fishing, de facto restricting fishing trips duration thus geographical influence on surrounding reefs. On the other hand, engine boats are seldom present and generally belong to rich owners hiring a team of fishermen having higher fishing efficacy. However, increased market demand and relatively higher economic development close to markets might lead fishermen to access more powerful and larger boats to expand their fishing grounds to more remote areas to maintain catch, as already demonstrated in Solomon Islands (Albert *et al.* 2015). Such changes are described through the scale effect and might explain that market influences fish biomass up to six hours (Figure 2) while I was not able to measure such changes in this study.

Unravelling human influence in coral reef fisheries in northwest Madagascar

Given that communities further away from markets had more households engaged in fishing and higher dependence on marine resources, I would expect lower biomass far from markets. Surprisingly, I found that fish biomass increased as reefs were further away from market in both fished and unfished reefs (Figure 3.2). 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 even on managed reefs. Beyond market proximity, I also found that travel time from community is a key driver of fish biomass interacting with management (Figure 3.2, Table 3.3). Local communities mainly influenced fish biomass at less than an hour and a half from the landing sites, with a decreasing influenced up to three hours while market influenced fish biomass up to six hours. Yet this is the first time that thresholds of influence are highlighted for both market and local communities using accessibility assessment.

Market proximity in Northwest Madagascar heavily affect the way coastal communities use marine resources and this finding is consistent with previous studies conducted at larger scales (i.e. national and global) highlighting that market integration is a major driver of decrease fish biomass through scales (Brewer *et al.* 2012; Cinner *et al.* 2013; D'Agata *et al.* 2016; Maire *et al.* 2016). 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 the most impoverished fishers are spurred to use destructive techniques (Cinner 2011). Innovation and technology are both driven by resource demand and at the same time, regulated by governance and managers. This suggests that better quantifying links between markets and fishing communities through household-level surveys should be a priority. Factors that influence household 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 the effect of markets on fish stocks and fishing communities. Yet the influence of market on coastal resources in more remote reefs might jeopardized remote communities’ well-being that are highly dependent on those resources for nutrition security and income generation. This suggests that better assessing links between markets and fishing communities is crucial to implement market-based actions that could help to regulate the effect of markets on fish stocks and fishing communities.

The importance of management to support remote communities

In addition, I thus tested the effect of management on the status of reef fish biomass in the northwest of Madagascar. The study highlighted that fish biomass was higher in permanent reserves (unfished reefs) despite the recent MPAs implementation (2015) with no effect of local communities on those unfished reefs. Previous studies in Madagascar have highlighted MPAs management effectiveness and positive impacts on fish stocks where higher fish density and biomass were found inside MPAs compared to fishing sites outside (Komeno & Randriamanantsoa 2013). Here it showed that MPAs in northwest Madagascar, through gear restrictions and higher compliance by local communities are effective tool to enhance fish biomass.

MPA compliance is relatively low in Madagascar due to limited enforcement (Rakotoson & Tanner 2006; McClanahan *et al.* 2014) which might explain that unfished areas are influenced by surrounding human populations at the same rate as fished areas. This finding is in accordance with a global scale study demonstrating that even if fish biomass was higher in marine reserves, it decreased along the increasing human gradient, highlighting the inevitable impact of surroundings seascapes on local resources, even in high compliance reserves (Cinner *et al.* 2018) . MPAs have been advocated as a powerful tool to conserve marine resources (Edgar *et al.* 2014; Sala *et al.* 2018) but with equivocal impacts on communities wellbeing living in those MPAs (Gurney *et al.* 2015; Gill *et al.* 2017). In this study area, there is a strong confounding effect between management and market accessibility since the two MPAs under study are located away from markets. This is consistent with previous studies showing that protected coral reefs around the world are disproportionally farther from -main cities and markets (Maire *et al.* 2016; Cinner *et al.* 2018) suggesting that conservation efforts, particularly through large MPAs, are targeting low-conflicts reefs to rapidly meet international conservation targets (O'Leary *et al.* 2018). Yet this study demonstrated that MPAs in remote locations can actually have positive effects on local communities highly dependent on those reefs by *(i)* legally protecting their resources and *(ii)* providing local communities with increasing support from external agencies such as non-governmental organizations through building capacity interventions, thus increasing their connectedness and agency (Gill *et al.* 2017). Yet I demonstrated that while bringing management and support to local communities is key to increase their resilience and protect their livelihoods, market influence is a severe threat for their local resources. Assessing and managing external pressures is thus crucial for consistent management actions at the seascapes level. This has even more resonance since marine protected areas are highly threatened by climate stress (Bruno *et al.* 2018).

Dealing with uncertainties in northwest Madagascar

Surprisingly, remote communities did not have more or less livelihoods compared to communities closer to markets, meaning that even though households were more engaged in fishing activities, it does not prevent them to be engaged in others activities such as farming (when possible) or tourism related, but at a lower rate. Indeed, fishing households in less developed communities might feel the need to supplement fishing as an adaptation strategy to natural hazard and environmental shocks, thus decreasing their inherent resilience; while communities in more developed communities might feel secure enough to engage into livelihood specialization (Cinner & Bodin 2010). While communities further away from market were more engaged in fisheries, and communities closer to market were more engaged in farming, demonstrating some degrees of specialization, the number of livelihoods remained in average identical along the accessibility gradient. Madagascar is one of the most impoverished country in the world and experienced several environmental and political crisis in the last decades (World Bank 2010; Conservation International 2015). This level of instability might explain why most households are engaged in a diverse portfolio of livelihoods at various degrees independently of their proximity to market, so households are able to spread risk across each of their livelihood sources (Allison & Ellis 2001; Badjeck *et al.* 2010; Forster *et al.* 2014). This strategy might increase their resilience to environmental and political shocks as both risk anticipation and coping strategies to environmental and political uncertainties (Allison & Ellis 2001; Goulden *et al.* 2013). This is further confirmed by the high proportion of catch sold across all communities which suggest the importance of fisheries-dependent cash-based economy for all communities. Fishers sold most of their catch independently of market accessibility whether to community members or middlemen when at more than two hours from a market, or directly to market for communities at proximity.

Finally, middlemen are essential intermediaries in coral reef fisheries who collect sea products directly from fishermen and provide links to markets (Crona *et al.* 2010; Brewer 2011). I found that middlemen are widespread in the study region (as in other countries, (Dacks *et al.* 2018).

By providing access to market, middlemen contribute to fishing income generation in remote communities whereas fishing households sold their catch directly closer to markets (Figures 3.3 & 3.4). Even if I observed that in some cases, fishers preferentially sell their catches to middlemen, it was not possible to measure whether demand from middlemen influence fishing practices or targeted fish species. Indeed, rights-based management actions are supposed to control harvesting pressure from 'outsiders' but this does not prevent rights holders from increasing 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).

Limitations of the study

While recent studies have suggested that higher catch in remote communities might be due to the presence of middlemen (Dacks *et al.* 2018), I could not unravel the direct effects of middlemen on coastal resources in this study. Also, there is a strong confounding effect between management actions and market accessibility since the two MPAs are located away from markets. While it was difficult to disentangle the relative effect of management and accessibility on communities' characteristics, it doesn't negate the importance of markets in shaping practices of local communities given management. Governance and rules highly influence fishing strategies in MPAs thanks to the management plans (which were preceded by the 'dinas', a set of social norms generally respected and agreed by the whole communities). Further work is therefore needed to assess fishing households' strategies with decrease market accessibility, particularly in developing countries.

3.5. Conclusion

Both local communities and market influenced fish biomass on fished and unfished reefs. 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 more significant effect than fishing communities even in managed reefs (permanent reserves). Community-based management with gear restrictions, limited access, marine protected areas, and rights-based fishing seem to be useful approaches to sustain fisheries resources and livelihoods of remote communities. 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 community) is thus a critical step toward long-term management of the coral reef fisheries.

4. The gravity of human settlements[3]

“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.

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[3] *Published as:*

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Cinner, J. E., Maire, E., Huchery, C., MacNeil, M. A., Graham, N. A. J., Mora, C., McClanahan, T. R. 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. The gravity concept

4.1.1. Theory on gravity

Sir Isaac Newton was a 17th-century astronomer who established the laws that govern the interactions of the Universe. One of the most famous, Newton's Law of Universal Gravitation law predicts that any two objects exert a gravitational force on each other and that this force depends on their masses and distance (Newton 1999). In other words, the bigger and closer objects are, the more they will be impacted by each other's gravity.

The gravity model uses the same law to describe relationships between places and instead of gravitational force, the degree of interaction between cities, or regions is considered. More specifically, the gravity predicts that interactions between two places (cities or regions) are positively related to their mass (i.e. people, information, commodities) 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. The concept of gravity has been used in economics and geography to describe economic interactions, migration patterns, and trade flows (Ravenstein 1889; Dodd 1950; Bergstrand 1985).

4.1.2. The gravity concept applied to coral reefs

Human pressure on coral reefs has been commonly expressed through the human population size within a spatial area around a given reef or the linear distance between a given reef and human settlements (Mora *et al.* 2006; Mora *et al.* 2011; Bellwood *et al.* 2012; Williams *et al.* 2015b). Very few variables combine these both aspects and the gravity concept can fill this gap. However, the initial law integrates the distance between places while travel time better represents the friction distance between places than linear distance (Chapter 2). 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/ hour^2 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^{TM} dataset where population density is positive, then, gravity of each populated pixel is summed.

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

4.1.3.1. 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. The current centerpiece of the Cinner Research Group is the “Bright Spots” project, which seeks to identify and learn from outliers, which in this case are reefs with more fish than expected, given the socioeconomic and environmental conditions they are exposed to.

The first paper developing the idea was published in *Nature* 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.

I also determined 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. While the squared ‘distance’ (here travel time) is relatively common in geography and economics, other exponents can be used (Black 1973). In the same vein, a 500-km radius from the reef was chosen as the maximum distance reef fishing activities are likely to occur (Cinner *et al.* 2016). Therefore, both aspects (exponent and radius) could influence the robustness of the gravity metric as previously described. Thus, a sensitivity analysis was performed to test 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) (Table 4.1). This analysis showed that the cumulative gravity calculated within a 500km-buffer and from the squared travel time provided the most parsimonious model of targeted fish biomass while the models controlled for environmental and socioeconomic conditions (Cinner *et al.* 2018).

Table 4.1 I Targeted biomass model comparisons using AIC, ΔAIC and conditional R^2 between different types of gravity considering 3 buffer sizes and 3 exponents. ΔAIC is calculated from the most parsimonious model (the lowest AIC) which is provided by the gravity within 500km-buffer and using squared travel time (Cinner *et al.* 2018).

Model	Sites with population within buffer (n=2233)	AIC	ΔAIC	Conditional R^2
50km-gravity				
Travel time	1682	7146	16	0.59
Travel time^2	1682	**7138**	8	0.60
Travel time^3	1682	**7138**	8	0.60
250km-gravity				
Travel time	1860	7153	23	0.59
Travel time^2	1860	**7135**	5	0.59
Travel time^3	1860	7140	10	0.60
500km-gravity				
Travel time	1937	7176	46	0.60
Travel time^2	1937	**7130**	0	0.59
Travel time^3	1937	7186	56	0.57

The study found that reef fish biomass decreased as the size and accessibility of markets increased (Figure 4.1).

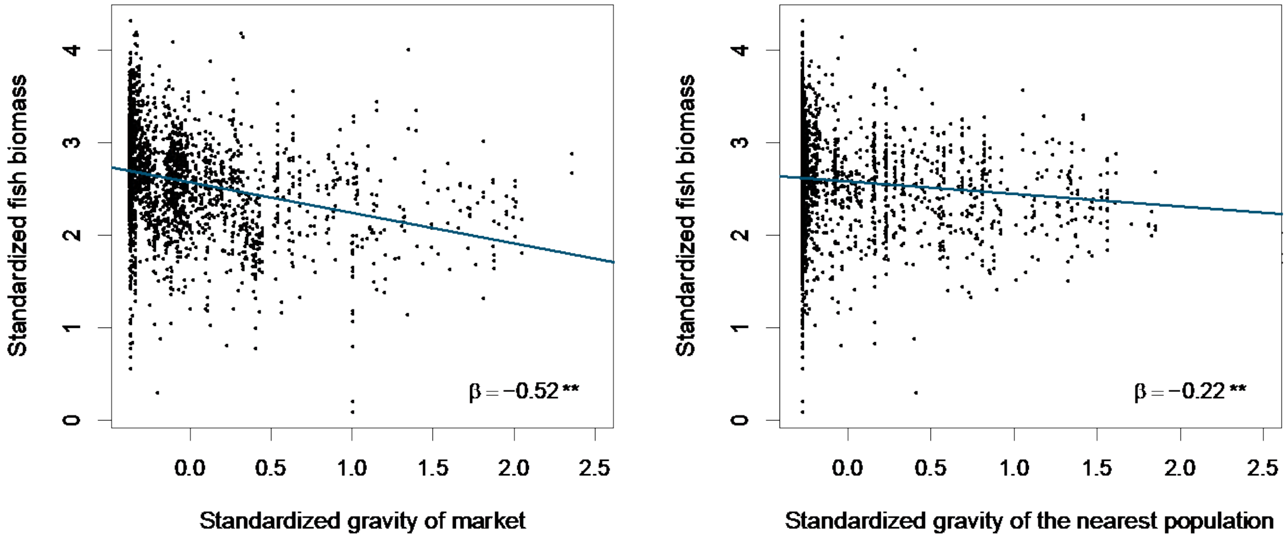


Figure 4.1 | Marginal relationships between reef fish biomass and gravity indices. *Standardized effect size of the gravity of market (left panel) and the gravity of the nearest human settlement (right panel). Parameter estimates (β) are Bayesian posterior.* (Cinner *et al.* 2016)

Specifically, the key finding from this 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 4.2).

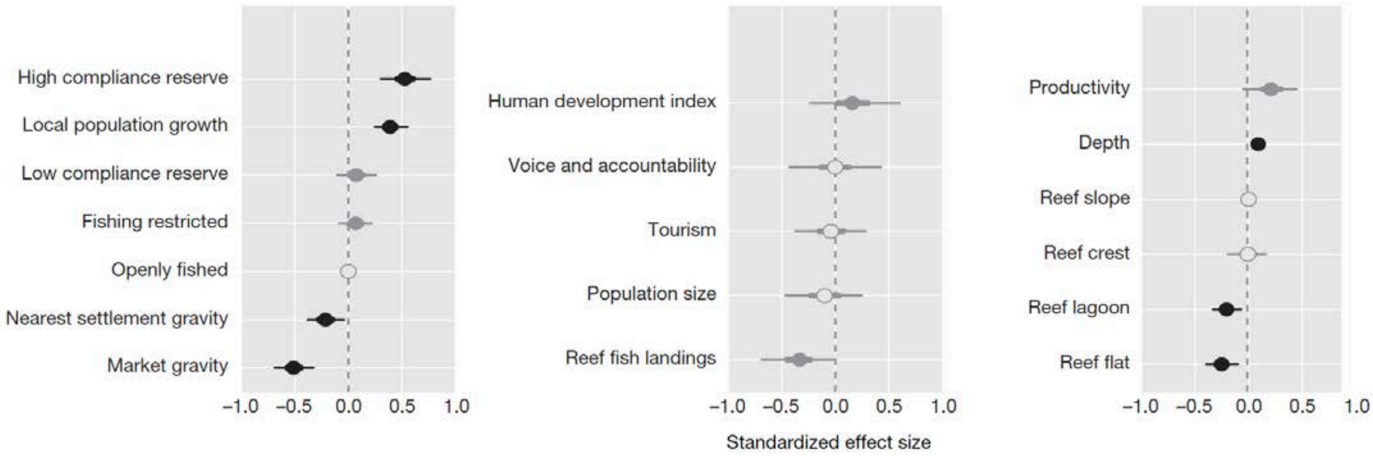
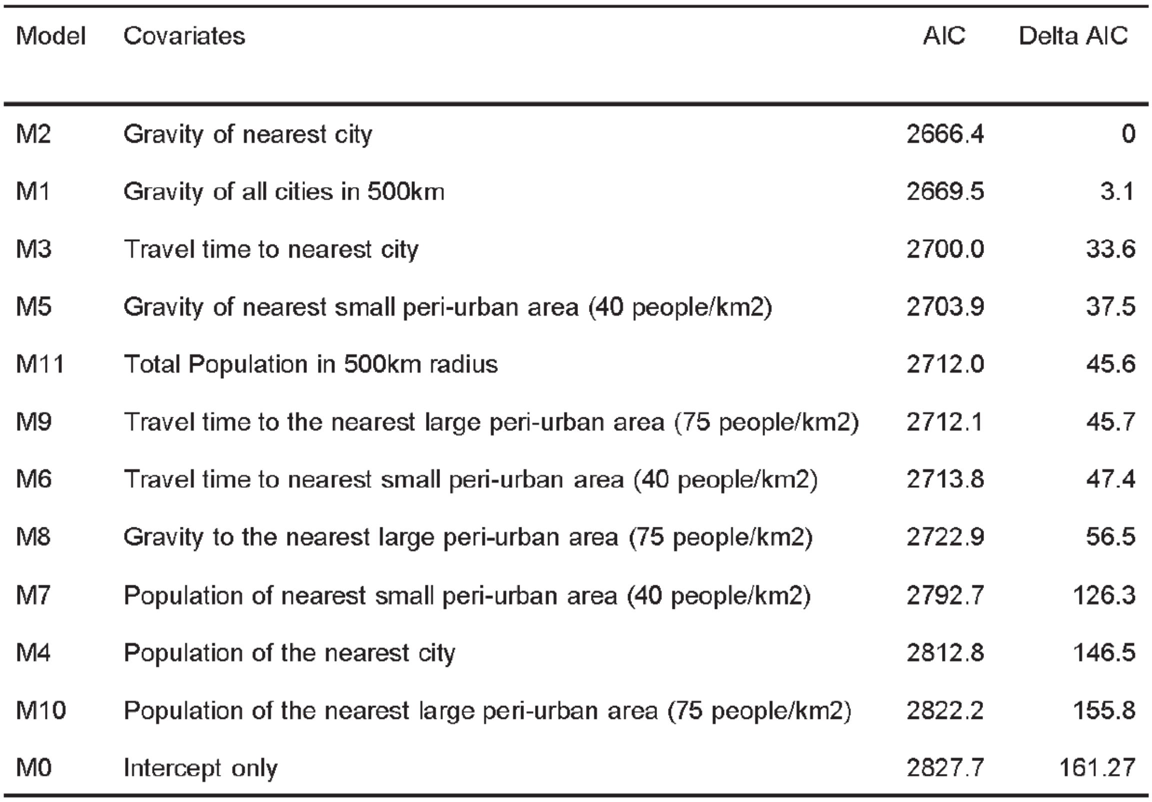


***Figure 4.2 | Drivers of reef fish biomass**. Standardized effect size of local scale social drivers, nation/state-scale social drivers, and environmental covariates, respectively. Parameter estimates are Bayesian posterior median values, 95% uncertainty intervals (UI; thin lines), and 50% UI (thick 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 4.2).

Table 4.2 | 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.

4.1.4. 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 4.3.

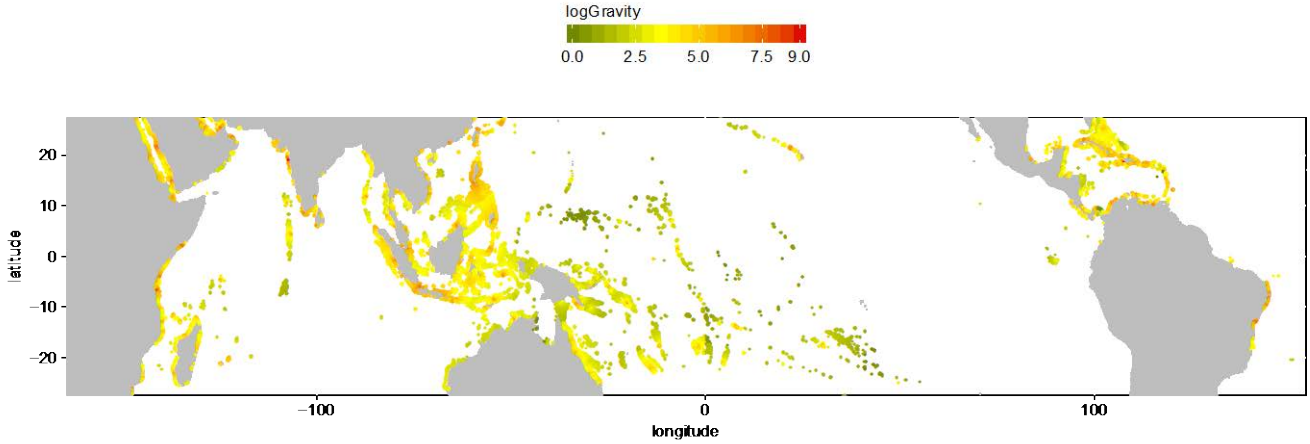


Figure 4.3 | Magnitude of gravity of market on the world's coral reefs.

The magnitude of gravity varies substantially among regions, with the central Indo-Pacific demonstrating lower gravity values (green points in Figure 4.3). 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 4.3). 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 4.3).

4.1.5. 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). However, there is compelling evidence that *(i)* 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) and *(ii)* proximity to major centers of population (cities or markets), is the strongest predictor of overfishing on coral reefs (Cinner & McClanahan 2006; Cinner *et al.* 2012; Cinner *et al.* 2013). By combining both crucial aspects of the human influence (population and accessibility) on natural environment, the gravity holds much promise in assessing human impacts in a more integrative way. Moreover, it has been proved that the gravity of human populations is the strongest predictor of fish biomass at the global scale (Cinner *et al.* 2016). Application of the gravity concept in coral reef socio-ecological systems could be helpful in examining other aspects that are influenced by human impacts. One key question is to define whether the intensity of human impacts can affect the management actions (fishery restriction or marine reserve). This specific point is addressed in the following part of Chapter 4.

4.2. Gravity of human impacts mediates coral reef conservation gains

4.2.1. 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). The 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.* 2011a; 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, it refers 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.* 2011a), 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.

4.2.2. Material and methods

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 were used to quantify how expected conservation gains in two key ecological outcomes are mediated by the intensity of human impact (expressed as the cumulative gravity of every human settlement within a 500-km buffer), namely: *(i)* targeted reef fish biomass (i.e. species generally caught in fisheries); and *(ii)* the presence of top predators (see details in *Appendices* and Table I). To quantify human impact at each site, we computed the cumulative gravity of every human settlement within a 500-km buffer which expressed potential human interactions with reefs as a function of how large and far away the surrounding human population is. At each site, the status of reef management was also determined and 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 *Appendices*). 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 were also calculated. It has been hypothesized that the ecological indicators considered (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, a general linear mixed model in R, using a log-normal distribution for biomass was developed. To quantify the relationships between gravity and presence/absence of top predators, a generalized linear mixed model with a binomial family and a logit link function was applied. For both models, reef cluster nested within nation/state was set 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). Social and environmental drivers, the sampling method and total sampling area, and an interaction between gravity and reserve age were included as covariates in the model.

Interactions between gravity and management were tested while AIC was used 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 the interaction with reserve age was chosen 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, the 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 Annexes, '*Global dataset on coral reefs used during the thesis' section*), 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 *Appendices*).

To examine the expected conservation gains of different management strategies: *(i)* the difference between the response of openly fished areas (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 were calculated. For ease of interpretation, conservation gains in kilograms per hectare (kg/ha; as opposed to log[kg/ha]) were plotted. 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.

4.2.3. Results

4.2.3.1. Gravity impacts on targeted fish biomass

This analysis reveals that human gravity was the strongest predictor of fish biomass (Figure 4.4 B, VI). Fish biomass consistently declined along a human gravity gradient, a trend particularly evident at the nation/state scale (Figure 4.4 C-E). However, this relationship can vary by management type (Figure 4.4, Figure VIII). Specifically, biomass in reserves demonstrated a flatter (but still negative) relationship with gravity compared with openly fished and restricted areas (Figure 4.4 B). Interestingly, this differential slope between reserves and fished areas (Figure 4.4 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 (Figure VIII).

Thus, given average reserve age in the sample considered (15.5 years), biomass in reserves did not decline as rapidly with gravity compared with fished and restricted areas (Figure 4.4 B). 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 4.4 B). At the reef site scale, there was considerable variability in reef fish biomass, particularly at low gravity (Figure 4.4 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 4.4 F-H). Importantly, there was never extremely high biomass encountered in high gravity locations. The estimate of fish biomass included key target species, including top-predators. As a supplemental analysis, target fish biomass with the biomass of top predators excluded was also examined, which displays a similar trend, but with lower fish biomass in reserves at low gravity compared to when top predators are included (Figure IX).

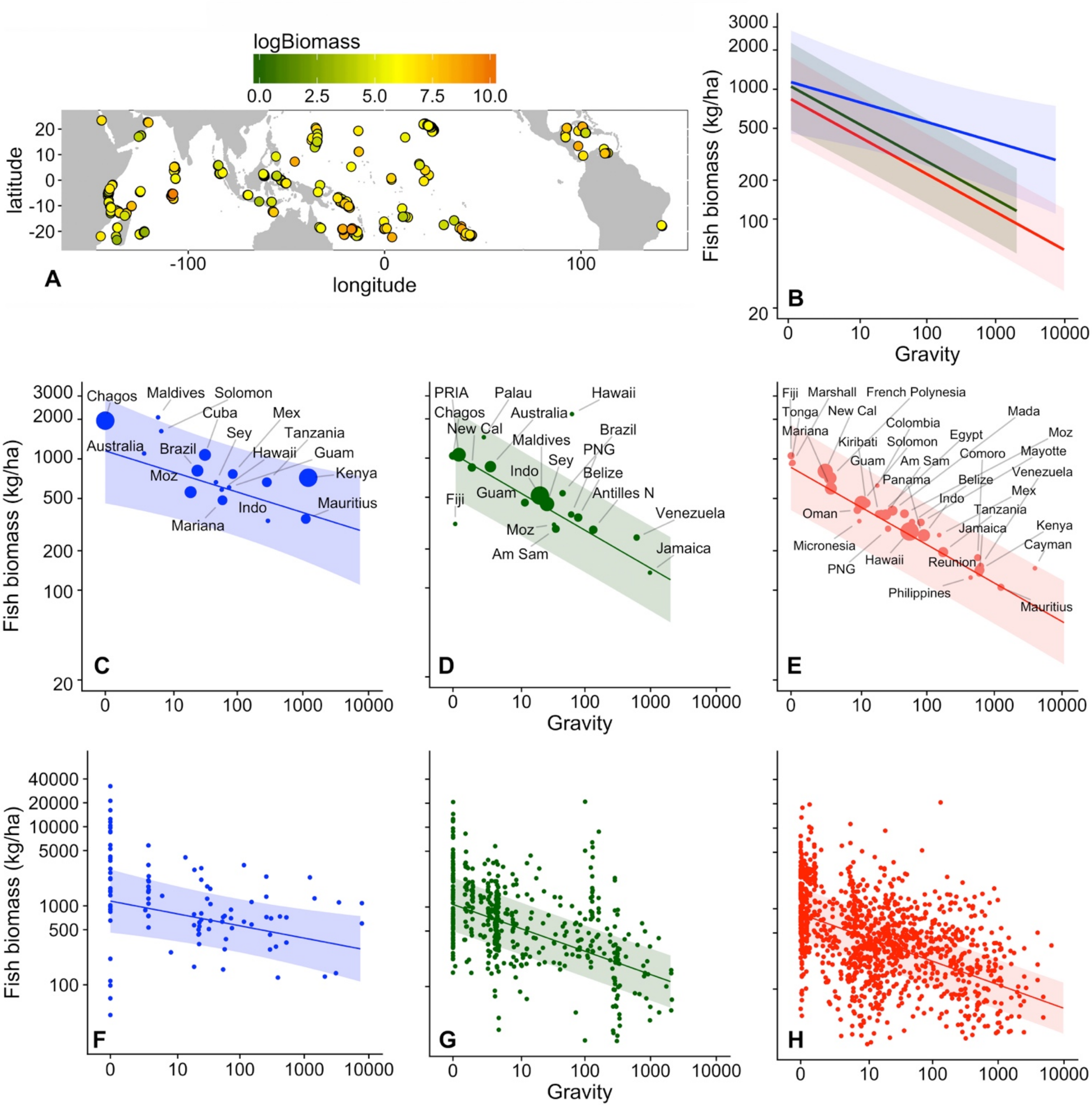


*Figure 4.4 | **Model-predicted relationships between human gravity and reef fish biomass under different types of fisheries management.** (A) Map of the study sites with color indicating the amount of fish biomass at each site. (B) Model-predicted relationships of how reef fish biomass declines as gravity 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 V). Nation/state name abbreviations for F-H are in Table V.

4.2.3.2. Gravity impacts on top predators

A key finding from this study is that top predators were encountered on only 28% of the reef sites considered, but as gravity increases, the probability of encountering top predator on tropical coral reefs dropped to almost zero (<0.005), regardless of management (Figure 4.5). 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 4.5, Figure VIII). 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 4.5, Figure VIII).

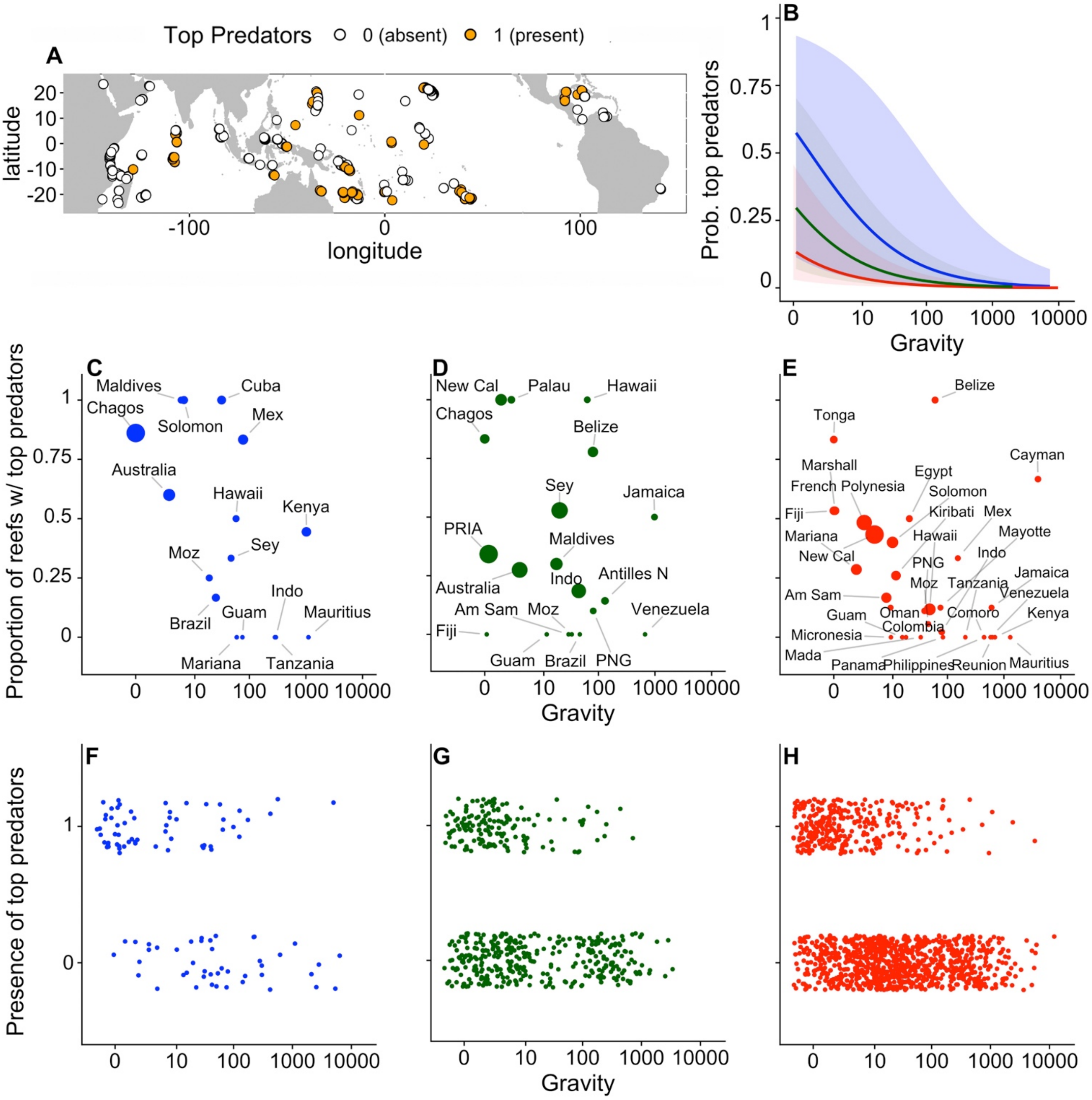


Figure 4.5 | Model-predicted relationships between human gravity and the probability of encountering top predators under different types of fisheries management. *(A) Map of the study sites indicating the presence of top predators. (B) Model-predicted relationships of how the probability of encountering 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 V). Nation/state name abbreviations for F–H in Table V.

4.2.3.3. Conservation benefits

The 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 the model (Figure VIII). Although absolute fish biomass and probability of top predators under all management categories declined with increasing gravity (Figure 4.4 B & 4.5 B), the maximum expected conservation gains (i.e. the difference between openly fished and managed) differed by management type along the gravity gradient (Figure 4.6).

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 4.6 A). 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 4.6 A). 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 4.6 A). Interestingly, the conservation gains for restricted fishing is highest in low gravity situations, but rapidly declines as human gravity increase (solid green line; Figure 4.6 A).

The 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 4.5). Yet, the expected conservation gains for top predators declines rapidly with gravity in both marine reserves and restricted areas (Figure 4.6 B).

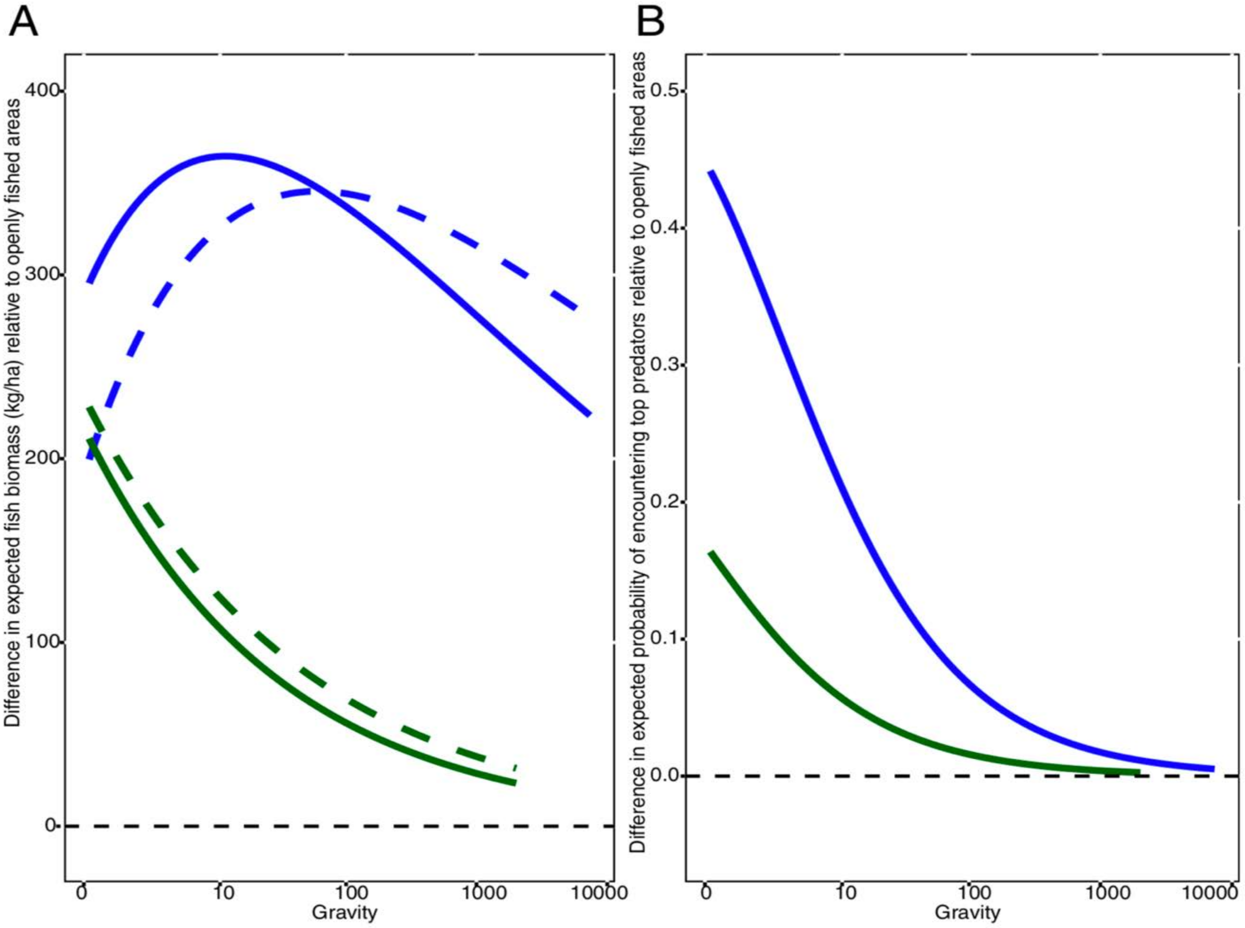


Figure 4.6 | The conservation gains (i.e. the difference between openly fished sites and managed areas) for high-compliance marine reserves (blue line) and restricted fishing (green line) *for (A) target fish biomass, and (B) the probability of encountering top predators change along a gradient of gravity.*

4.2.4. Discussion

4.2.4.1. Why was there a decline of ecological conditions indicators observed within marine reserves along a gravity gradient?

This study demonstrates the degree to which fish communities inside marine reserves can be affected by human impacts in the broader seascape (Figures 4.4 & 4.5). 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 4.4). 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 4.5 B). The 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 the sample possibly being too young, or too small to provide substantial conservation gains (Edgar *et al.* 2014; Krueck Nils *et al.* 2017).

A supplementary analysis was conducted to further examine this latter potential explanation. Because of collinearity, it was not possible to directly account for reserve size in the model, but a supplemental analysis was conducted where small (<28km2) and large reserves were separated (Figure X). It showed that the biomass and probability of encountering top predators was higher in large compared to small reserves, but surprisingly, a flatter slope for small compared to large reserves was found (Figure X). However, there were no large high compliance reserves in high gravity areas in the 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 the sample, it was not possible to distinguish the effects of reserve size from those of gravity, but this is an important area for future research.

Additionally, how the relationship between gravity and the ecological outcomes considered changed with reserve age was modelled, comparing outcomes using the average reserve age (15.5 years) to those from reserves nearly twice as old (29 years, which was the third quartile of the 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.

4.2.4.2. Successful conservation strategies

Although absolute fish biomass under all management categories declined with increasing gravity (Figure 4.4 B), the maximum expected conservation gains (i.e. the difference between openly fished and managed) differed by management type along the gravity gradient (Figure 4.6 A). Interestingly, the conservation gains for restricted fishing is highest in low gravity situations, but rapidly declines as human impacts increase (Campbell *et al.* 2018).

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 4.6 A). 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 4.6 A). The 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 the model (Figure VIII, Table VI). 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). The results make explicit the types of benefits – and the limitations- to placing reserves in high versus low human impact locations. The 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 4.6 A), yet they are unlikely to support key ecosystem functions like predation, even with high levels of compliance (Figure 4.6 B). This highlights the importance of having clear objectives for conservation initiatives and recognizing the tradeoffs involved (Beger *et al.* 2015; Boon & Beger 2016).

This analysis does not allow us to uncover the mechanisms behind why it might be observed 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 X), 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. Conservation gains can be produced by gear restrictions, though they are low relative to marine reserves (Figure 4.6). 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 .

As a supplemental analysis, the conservation gains for biomass of non-target species were examined (Figure VIII 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. Very different patterns for non-target species compared to target species were found, suggesting the relationship between target fish biomass and gravity (Figure VIII) is primarily driven by fishing pressure.

4.2.4.3. Securing the future of coral reefs

Overall, the 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.

4.2.5. Gravity future directions

The gravity index makes several key assumptions that could potentially be refined in further applications. First, the 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, the 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. The adaptation of gravity was designed to examine the observed conditions of reefs as a function of potential interactions with markets and local settlements, so the 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, the database considered here 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, a global dataset of gravity for every reef pixel globally was provided.

4.2.6. Conclusion

This study demonstrates 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, the study finds 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. 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'

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[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*

5.1. 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, I 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). Here, I 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, I 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. I 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.

5.2. Material and methods

5.2.1. General framework

The Community-Wide Scan (CWS) framework to identify species that are associated with higher levels of ecosystem services involves three steps (Figure 5.1): *(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 5.1).

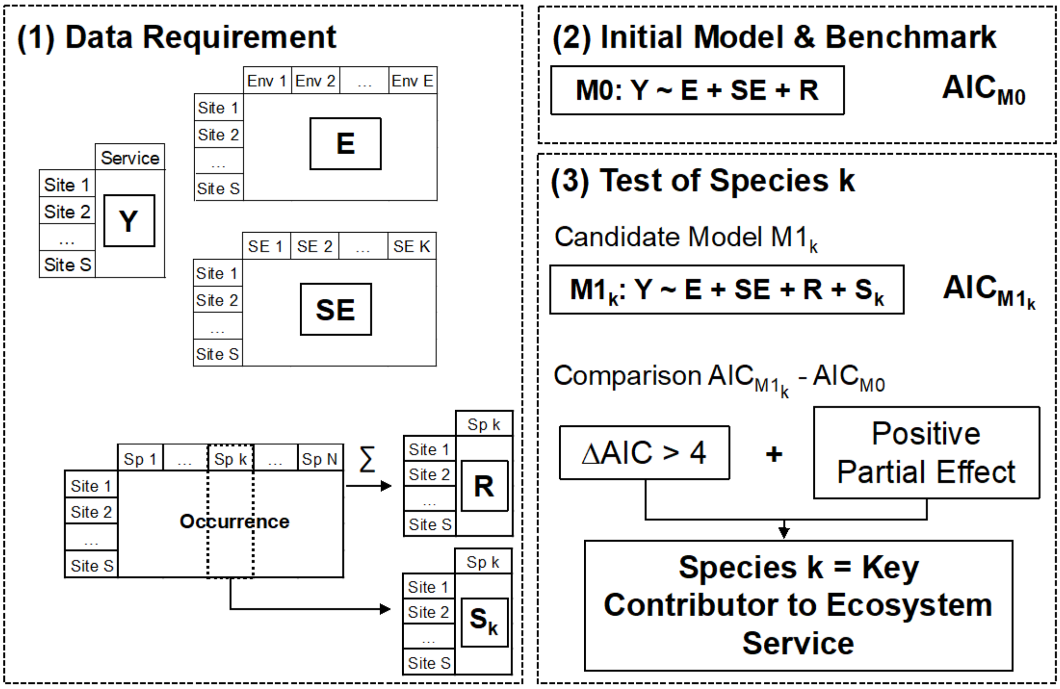

Figure 5.1 | Statistical framework to assess the significant potential contribution of species to ecosystem services beyond the effects of environmental and socioeconomic conditions and species richness.

Step 1: 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.

Step 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 Akaike Information Criterion (AIC_{M0}) as a reference for the next step.

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).

5.2.2. Coral reef data

Coral reef services. The proxies for coral reef services considered in the study 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). I 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 I 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}) I 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, I estimated the number of reefs where a given fish species was present. To avoid results only influenced by a few reefs I 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 I 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 I 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.

5.2.3. 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, I 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 this study (i.e. presence of at least 1 individual) but could be also determined using any relative abundance threshold (Figure 5.1 and Supplementary Material).

5.2.4. 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).

5.2.5. Statistical analyses.

I 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, I 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, I 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.

I 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 I compared modelled estimates of fish biomass and live coral between reefs while increasing the number of key species. I 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). I 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.

5.2.6. 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).

I 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 this case) functional space filled by key species, where axes are defined by species traits.

5.2.7. Fish phylogeny.

I 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.

5.3. Results

5.3.1. 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).

5.3.2. 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 5.2), 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, I 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 5.3).

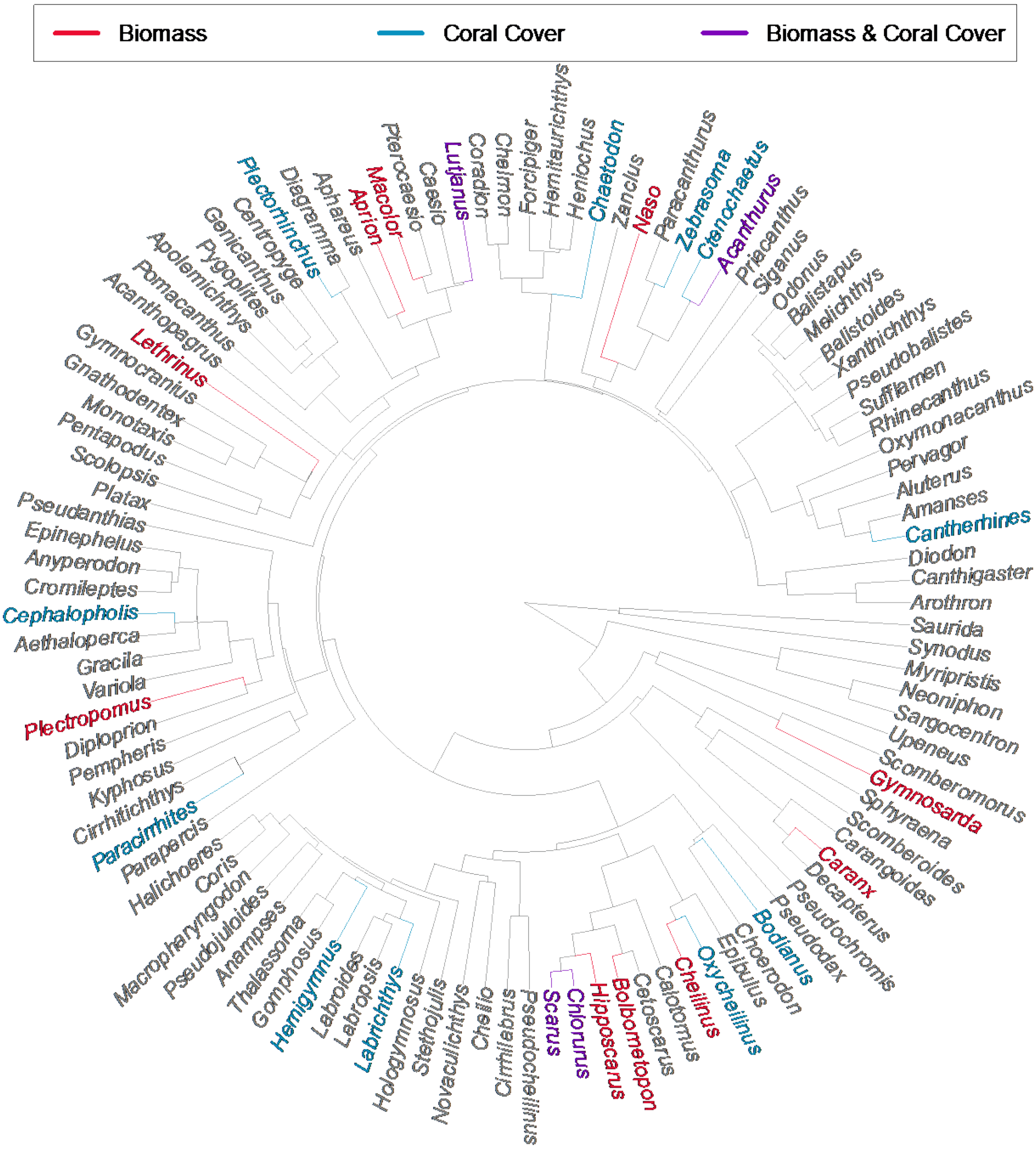

Figure 5.2 | Positions of key species for biomass (red), live coral cover (blue) or both of them (purple) represented as their corresponding fish genera in the Tree of Life of Coral Reef Fishes, adapted from Near et al. (2013). *The 26 key species for biomass represent 16 genera while the 28 key species for coral cover represent 15 genera with 4 common genera. Elagatis and Parupeneus genera are missing.*

5.3.3. Key species associated with live coral cover

I 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 5.2), 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, 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 5.3). 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).

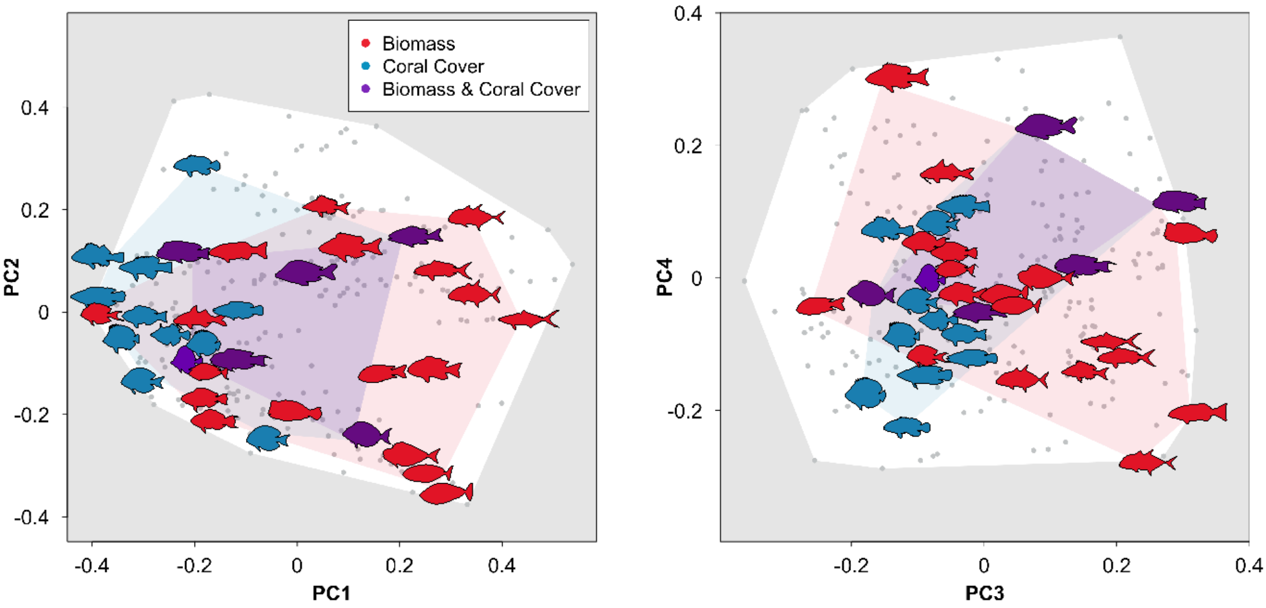

Figure 5.3 | Functional attributes of key fish species. *In total, 51 fish species which correspond to 35 out of 240 functional entities (15%) have been identified as strongly related to high biomass (18 red shapes), high live coral cover (11 blue shapes) or both of them (6 purple shapes). The positions 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.

5.3.4. 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 5.2, Table S6).

Only six functional entities were common and significantly associated with both biomass and live coral cover (Figure 5.3), namely small and medium herbivores, small planktivores, medium and large fishes targeting mobile invertebrates and meso-predators (Table S6).

5.3.5. 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 5.4). For clarity, I 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 5.4). 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).

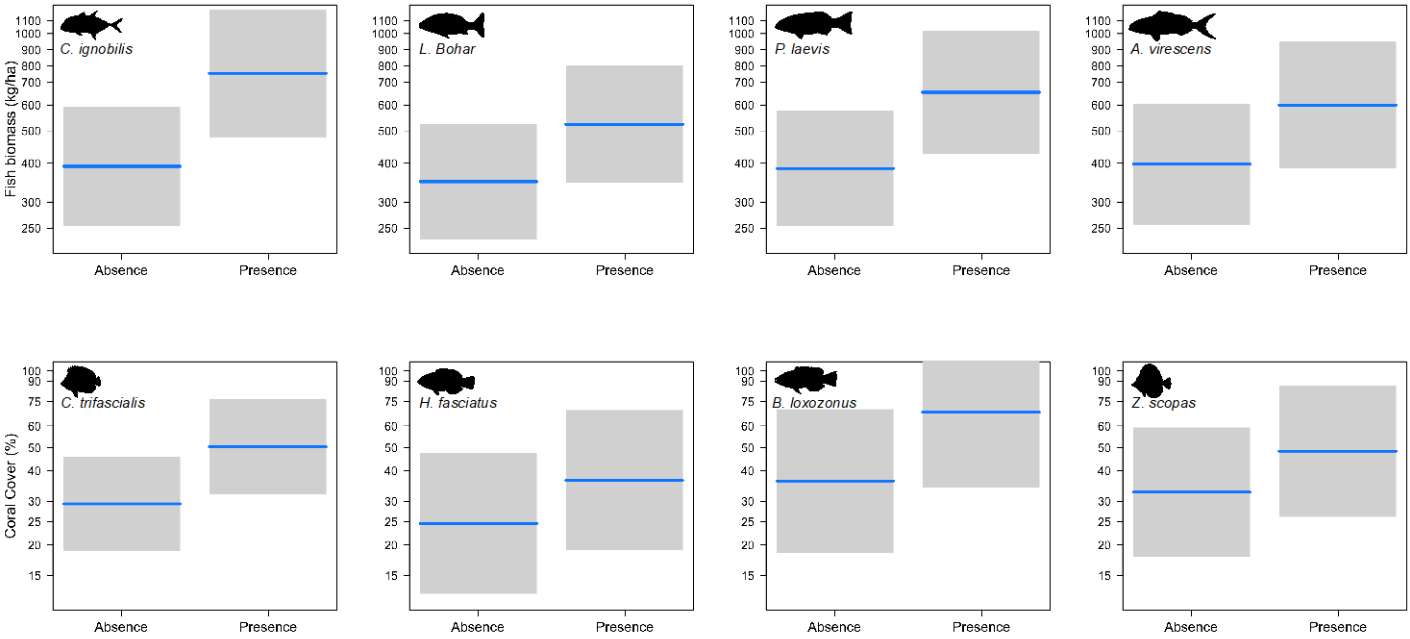

Figure 5.4 | Net effect of the 4 most significant (lowest AIC) key fish species when present for fish biomass (top) and live coral cover (bottom) *(among the 26 and 28 key species respectively) using a partial plot from the linear mixed models while the other variables are held constant. When present, 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 5.5).

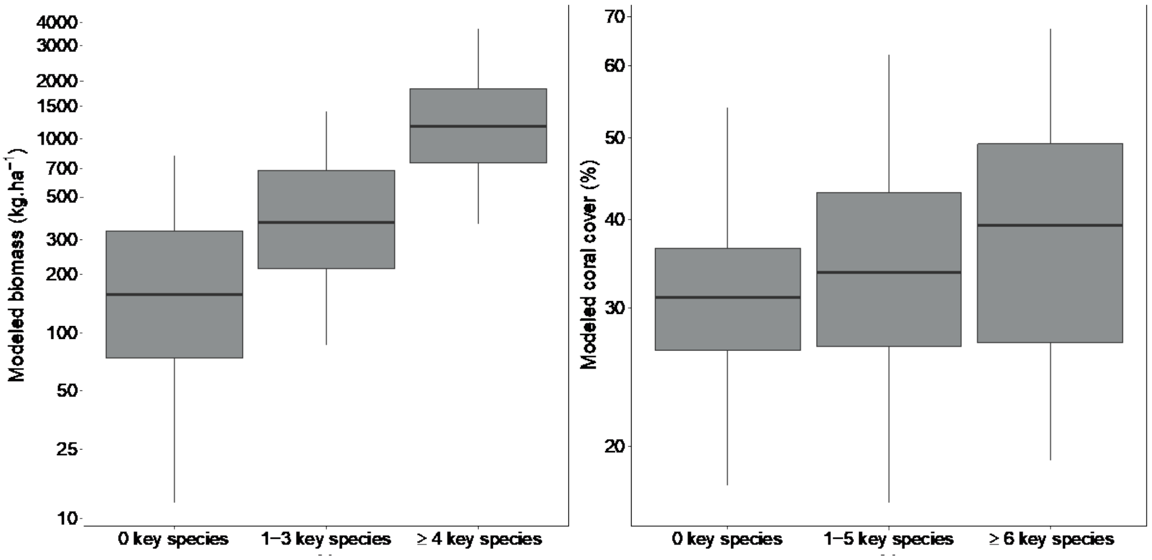

Figure 5.5 | The accumulation of key species co-occurring on coral reefs is positively related to fish biomass (left) and live coral cover (right). *To control for positive effect of species richness on ecosystem functioning, I compared modelled estimates of fish biomass and live coral between reefs 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.*

5.4. Discussion

5.4.1. 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, the results (Tables S2 & S3) were consistent 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, the 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, the study shows that predatory species like *Aprion, Caranx, Cephalopholis, Elagatis, Gymnosarda, Lethrinus, Lutjanus, Oxycheilinus,* and *Plectropomus* (Figure 5.4, 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.

5.4.2. 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 5.2, 5.3 & 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, the study shows 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. It suggests 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 5.5). Maintaining habitat heterogeneity and associated processes as well as high species diversity is thus a major component of management and conservation. 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 in an increasingly uncertain future (Webster *et al.* 2017).

5.4.3. 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 I 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, I 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 these findings. Finally, the response of coral communities to disturbances and their recovery trajectories remain poorly understood (Holbrook *et al.* 2016). Application of the CWS framework to time-series of reef monitoring could help in defining fish species that may be associated with different stages (newly established, recovering, resilient) of coral communities.

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.

5.5. 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. The present 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.

6. General discussion and perspectives

6.1. Achievement of objectives and thesis contributions

6.1.1. Identifying key species for reef functioning and services

Research Question 1. Which fish species contribute to maintain coral reef functioning and services?

To address Research Question 1, I developed a statistical framework, the 'Community-Wide Scan' (CWS) analogous to the genome-wide scan, to determine which species are necessary to maintain ecosystem functioning beyond environmental and anthropogenic conditions. 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).

The CWS has the potential to reveal unsuspected species that overcontribute to ecosystem functioning and its associated services and appears particularly useful in complex and biodiverse ecosystems 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). In **Chapter 5**, I applied this framework to identify key fish species that are significantly linked to the biomass and coral cover on Indo-Pacific reefs and I 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.

In some places the establishment of marine reserves is not practical and selectively banning or restricting fishing gears can be an effective tool to manage coral reefs (MacNeil *et al.* 2015; Campbell *et al.* 2018). Key species identified in **Chapter 5** could represent conservation targets and thus, encourage species-focused management strategies to maintain fish species considered as fish biomass and coral cover and provide higher level of ecosystem functioning. Such measures can be beneficial for both ecosystems and people.

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. Moreover, the framework I developed is not only limited to coral reef systems and can examine the complex relationships between biodiversity and ecosystem functioning for a wide range of ecosystems. It offers a new and flexible way to analyze the ongoing massive empirical data relating biodiversity to ecosystem functioning and services with the potential to guide management strategies as well as new experiments to decipher underlying ecological processes.

6.1.2. Redefining human impacts on coral reef systems

Research Question 2. How can we improve our understanding of how people affect reefs by accounting for the degree of accessibility to reefs by human populations?

To address Research Question 2, 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 2**). Accessibility is an 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). However, 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). Nonetheless, 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.

Specifically, even if only few studies have considered accessibility to characterise the condition of marine ecosystems, the thesis used local (**Chapter 3**), national (**Chapter 2**) and global studies (**Chapters 4 and 5**) and proved that accessibility is a key driver of resource exploitation on coral reefs. Accessibility through the travel time or the gravity metric provided a better comprehension of the drivers of fish biomass and the thesis has contributed to the emergence of potential solutions to sustain coral reefs as social-ecological systems by:

(i) Identifying ‘bright spots’ among coral reefs (Cinner *et al.* 2016) which are reefs with more fish than expected based on their exposure to pressures such as human population, poverty, and unfavourable environmental conditions. Bright spots are reefs that have more fish biomass than they should, given the pressures they face and are not necessarily pristine reefs. Thus, the bright spots offer a good opportunity to learn from their success and identify some conservations solutions that can be applied more broadly across the world’s coral reefs.

(ii) Proposing opportunities for conservation benefits given human pressure (low, moderate, high gravity) and ecological outcomes (targeted biomass or top predators). Even if the success of conservation is highly variable and depend on a wide range of social considerations (Bennett *et al.* 2017), the potential conservation benefits found in **Chapter 4** can help to guide the location and the type of future management actions according to the local human gravity and support to establish protection.

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 presents multiple applications.

6.1.3. Improving our ability to predict variations of fish biomass on coral reefs

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 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 (see Annexes, '*Global dataset on coral reefs used during the thesis' section*) 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 5**).

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 6.1), even if linear distance and travel time are highly correlated globally (**Chapter 2**). It means that locally or regionally (see Madagascar or New-Caledonia **Chapters 2 & 3**) 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 6.1). 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 6.1). Once again, the best improvement is related to the maximization of log-likelihood and thus, optimal values of the estimated coefficients.

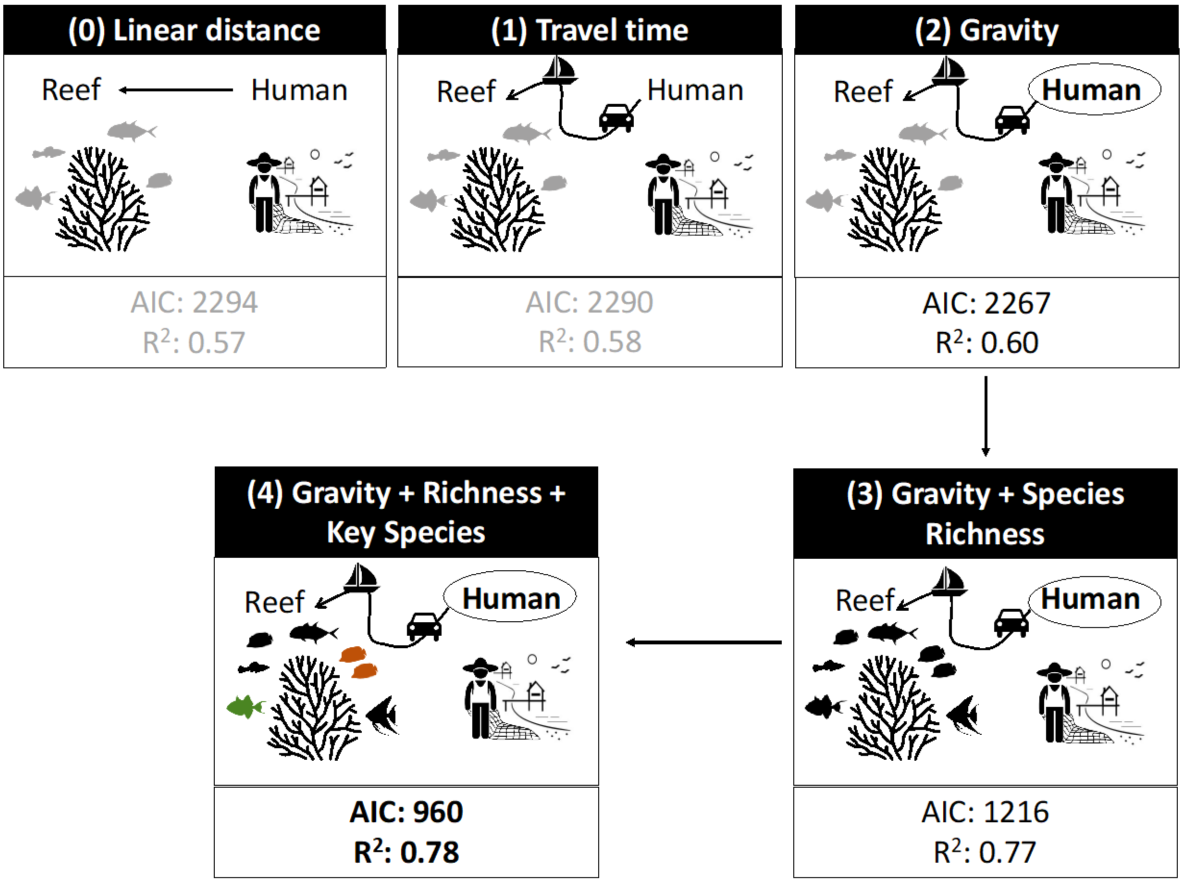

Figure 6.1 | Comparison of a series of models that predicted fish biomass *including different variables such as (0) linear distance from the nearest market, (1) travel time from the nearest market, (2) total gravity, (3) total gravity and species richness and (4) total gravity, species richness and 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.*

6.1.4. Open-source data

To facilitate applications related to coral reefs accessibility, potential travel time estimates (**Chapter 2**) 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 analyze 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).

6.2. Limits

Refining travel time in accordance with local infrastructures and technology

In the first assessment of travel time (**Chapter 2**), 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.

Also, only simple fishing trips to reach a given reef were considered while longer trips can be undertaken. In such cases, fish preservation and associated requirements are essential for the expansion of fisheries. When available, future studies should consider whether vessels are equipped with on board freezers, cold storage or any storage facility.

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 2**) 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 3**, 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 lead to even greater 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.

Human impact on fish communities

Reef fish biomass can reflect a broad selection of reef fish functioning and benthic condition (McClanahan *et al.* 2011a; 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 has also been shown that fish size, rather than biomass, can be a better predictor of the resilience and the recovery of life-history characteristics of fish communities (Houk *et al.* 2014; McClanahan & Graham 2015). However, more work is needed to determine how human impacts affect the composition and the length distribution of fish communities.

6.3. 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 2**), 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 predict 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

If travel time seems to be a good proxy of fishing pressure that reefs experience given their accessibility (**Chapters 2 and 3**), it does not translate how much fish is caught according to fishing technics and intensity. Sustaining fisheries requires accurate information about patterns of resource use and particularly fishing effort while in most coral reef fisheries, accurate information is not available or not assessed at very fine scale (Delaney *et al.* 2017). 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 by increasing people’s awareness of the importance of conservation, promoting conservation actions and supporting scientific projects.

7. References

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8. Appendices

8.1. Global dataset on coral reefs used during the thesis

My PhD is integrated into the *Cinner Research Group* led by Prof 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 (Chapters 4 and 5) 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.

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).

Reef Fish biomass

Reef fish biomass can reflect a broad selection of reef fish functioning and benthic condition (McClanahan *et al.* 2011a; 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 3), top predators presence (Chapter 3) and Indo-Pacific fish biomass (Chapter 5) 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 5) 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.

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.

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 net primary 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.

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 net primary 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)

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 3 or total biomass in Chapter 4), 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 3 & 4) 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.

8.2. Supplementary tables and figures (Roman numbering) for Chapters 2-4

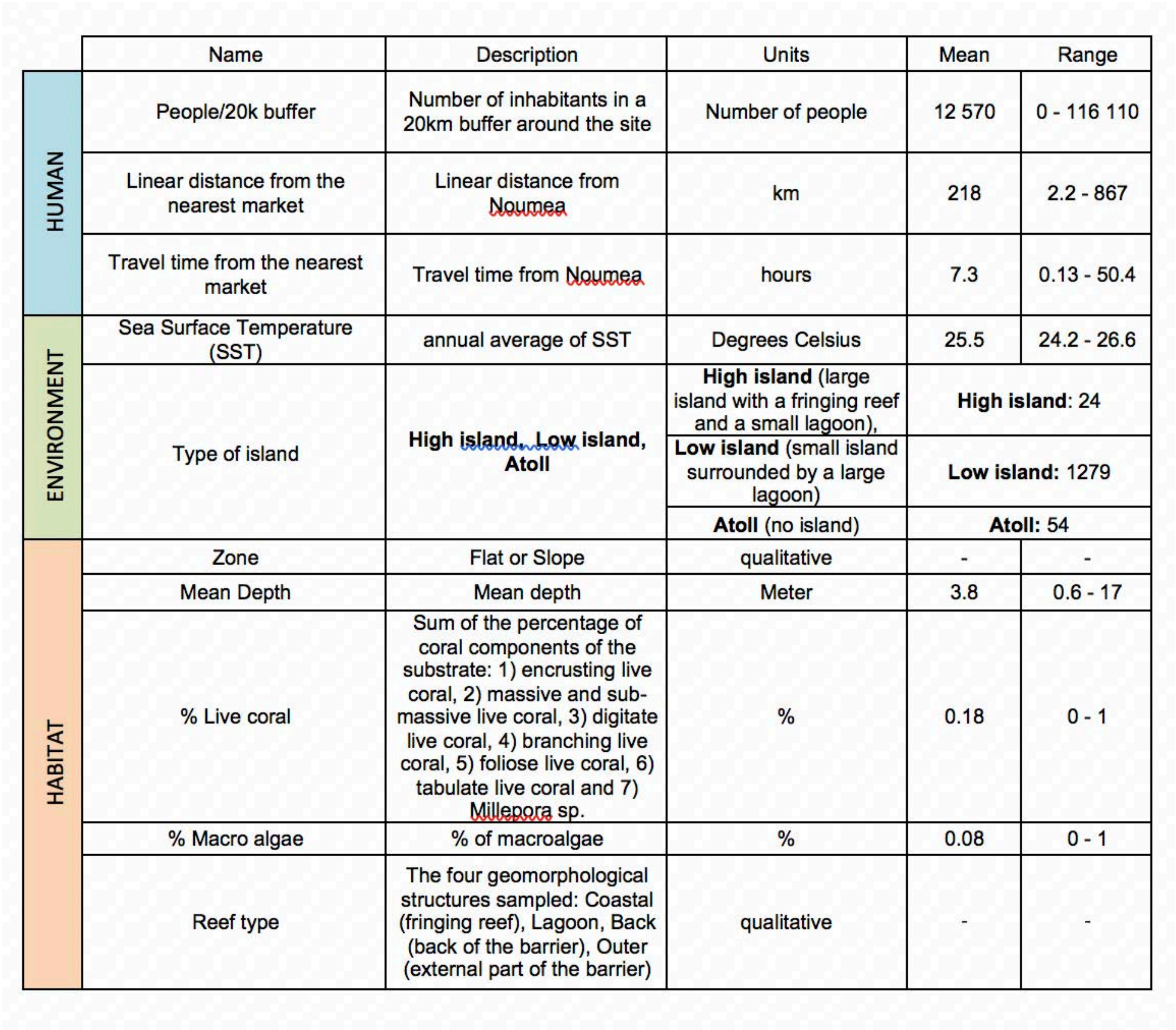
Table I | List of fish families recorded in the thesis, their common name, and whether they are commonly targeted in artisanal coral reef fisheries or considered at top predators. Due to varying tastes, values, and preferences, not all families listed as target species will necessarily be targeted in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



	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	-	-

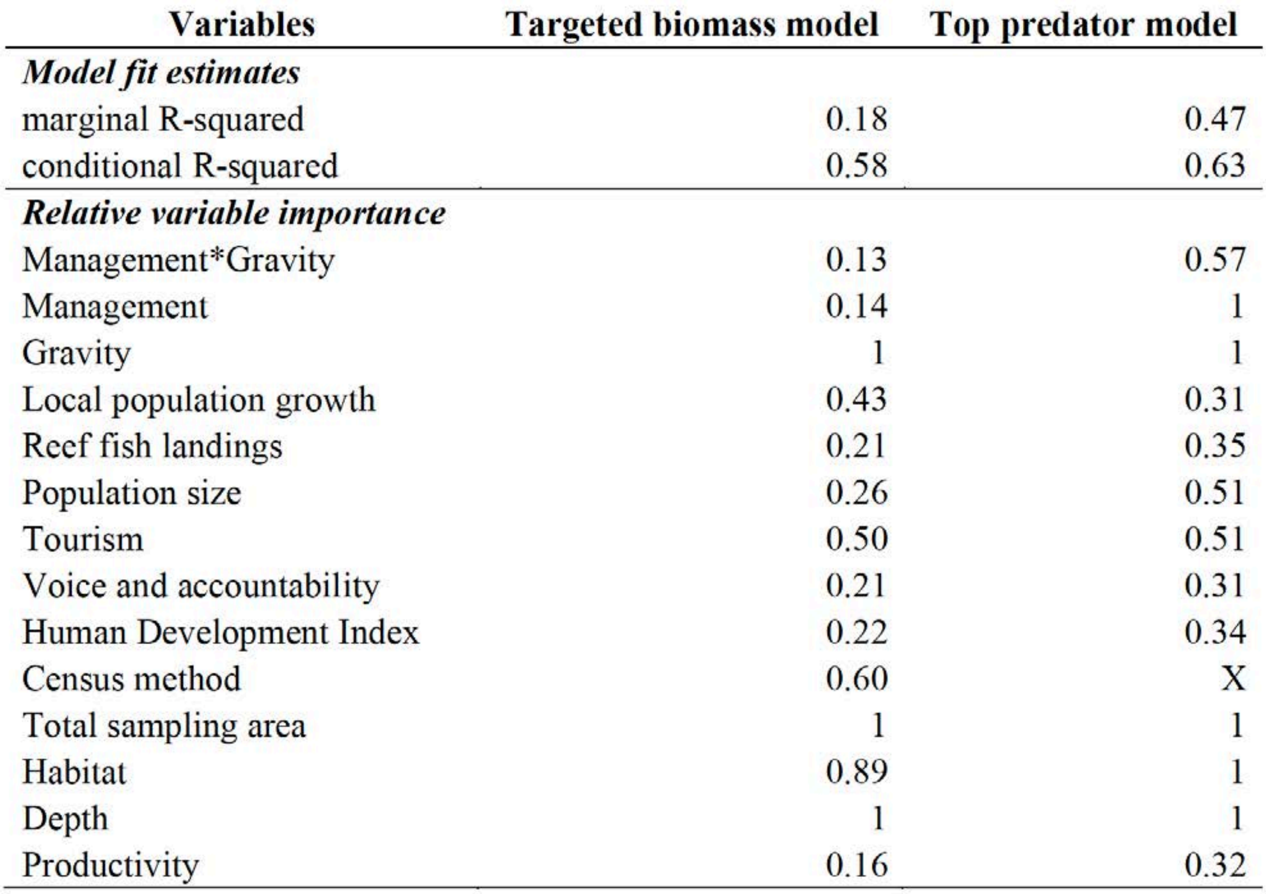
Table IV | Description of households surveyed in Northwest Madagascar. Proportion of households surveyed and total estimated number of households in each community are provided.

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

Table V | 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 VI | 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

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^{TM} 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 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*.

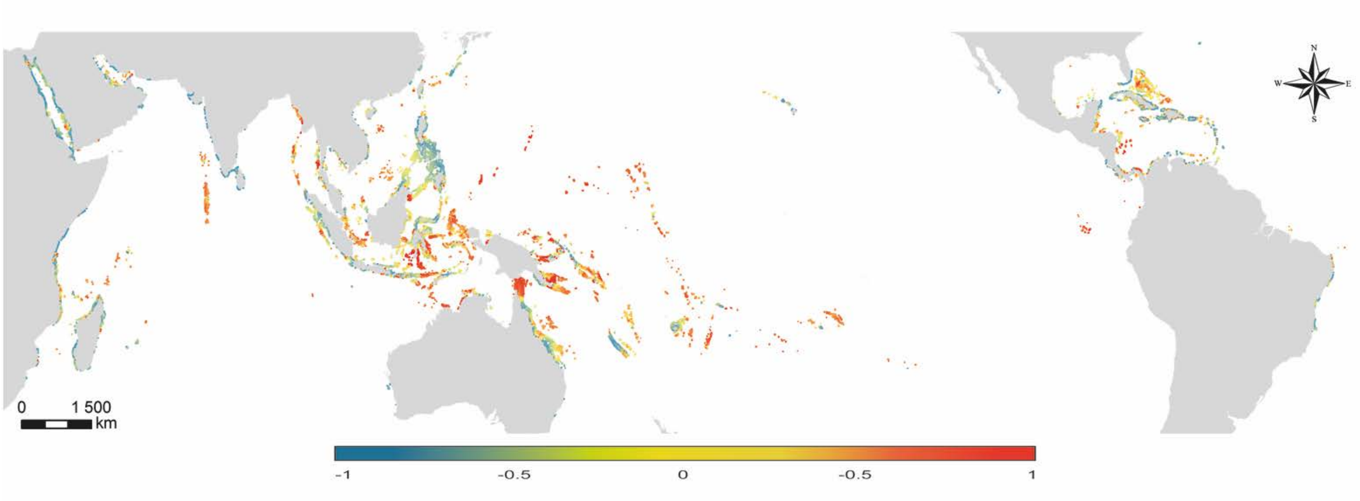
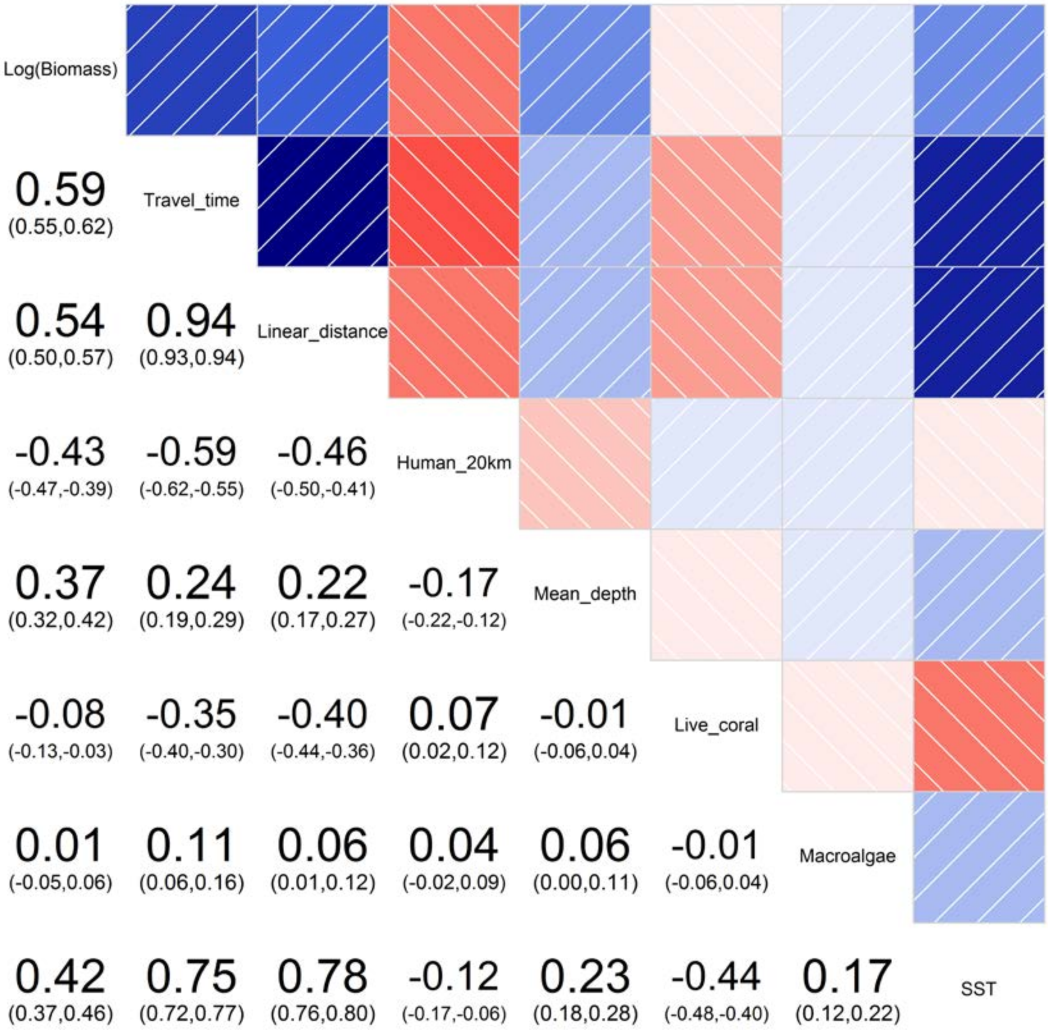


Figure III | Pairwise Pearson correlations between variables used to predict reef fish biomass in New Caledonia. Pearson coefficient of correlations and confidence intervals between all pairs of variables (total reef fish biomass, human, habitat and environmental variables) are presented into the lower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



Log(Biomass)							
0.59 (0.55,0.62)	Travel_time						
0.54 (0.50,0.57)	0.94 (0.93,0.94)	Linear_distance					
-0.43 (-0.47,-0.39)	-0.59 (-0.62,-0.55)	-0.46 (-0.50,-0.41)	Human_20km				
0.37 (0.32,0.42)	0.24 (0.19,0.29)	0.22 (0.17,0.27)	-0.17 (-0.22,-0.12)	Mean_depth			
-0.08 (-0.13,-0.03)	-0.35 (-0.40,-0.30)	-0.40 (-0.44,-0.36)	0.07 (0.02,0.12)	-0.01 (-0.06,0.04)	Live_coral		
0.01 (-0.05,0.06)	0.11 (0.06,0.16)	0.06 (0.01,0.12)	0.04 (-0.02,0.09)	0.06 (0.00,0.11)	-0.01 (-0.06,0.04)	Macroalgae	
0.42 (0.37,0.46)	0.75 (0.72,0.77)	0.78 (0.76,0.80)	-0.12 (-0.17,-0.06)	0.23 (0.18,0.28)	-0.44 (-0.48,-0.40)	0.17 (0.12,0.22)	SST

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 | Contributions and scores (cos2) of each variable integrated in the PCA linking market access and social characteristics of local communities. Five social indicators were considered: the proportion of households who ranked fishing as primary activity (Fishing), the proportion of households who ranked farming as primary activity (Farming), the livelihoods diversity: the mean number of livelihood activities that households are involved in (Nb. Livelihoods), the mean number of community groups people are involved in (Social connection), the proportion of households consuming fish at least once a day (Fish consumption) and were related to market access (Travel time from market). The supplementary variable (Management) was also represented. All variables were properly represented (cos2 > 0.4) by the two first components (PC1 & PC2) except the proportion of households who ranked fishing as primary activity (Fishing).

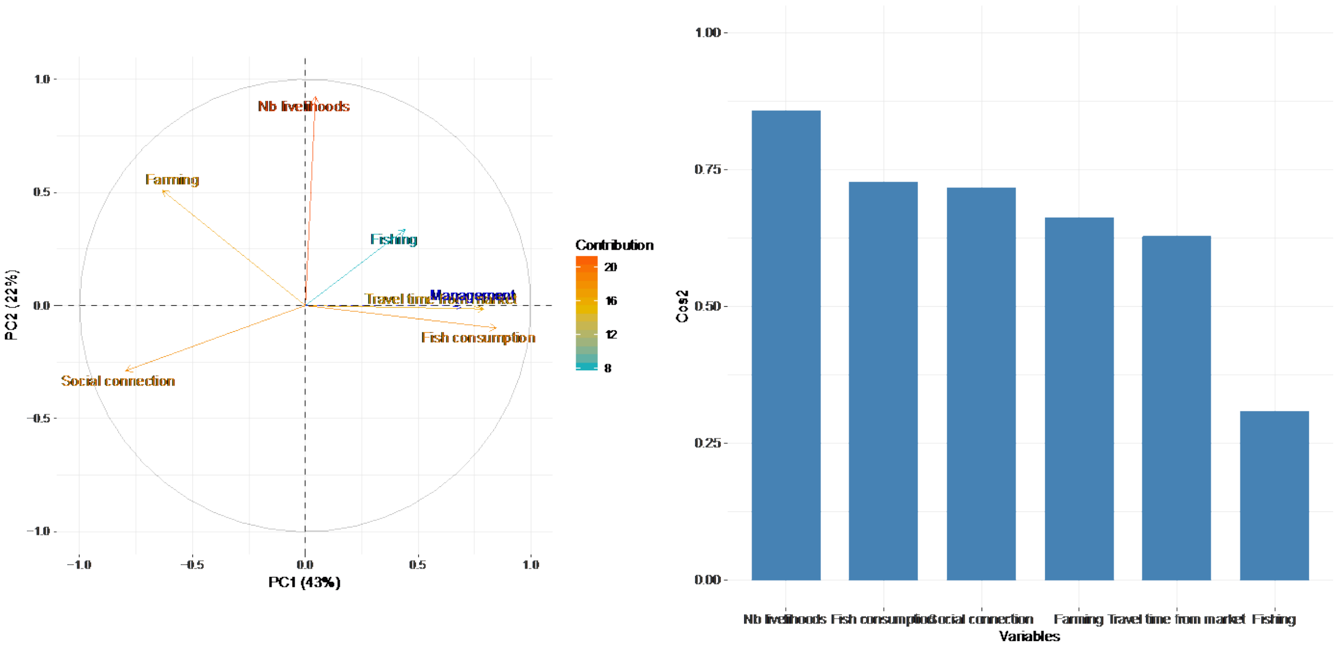


Figure VII | Contributions and scores of each variable integrated in the PCA linking market access and fishing households. Only households engaged in fishing activities were considered and for each community were assessed: the proportion of fishing households who used as main gear nets (Net) or selective gears (Select. gear) respectively and the proportion of fish catches sold (Prop. fish sold) that were related to market access (Travel time from market). As market accessibility and management actions had confounding effects in the study area (marine reserves are disproportionally located far from markets), one supplementary variable (Management) was included to take into account this effect. The supplementary variable (Management) was also represented. All variables were properly represented (cos2 > 0.4) by the two first components (PC1 & PC2).

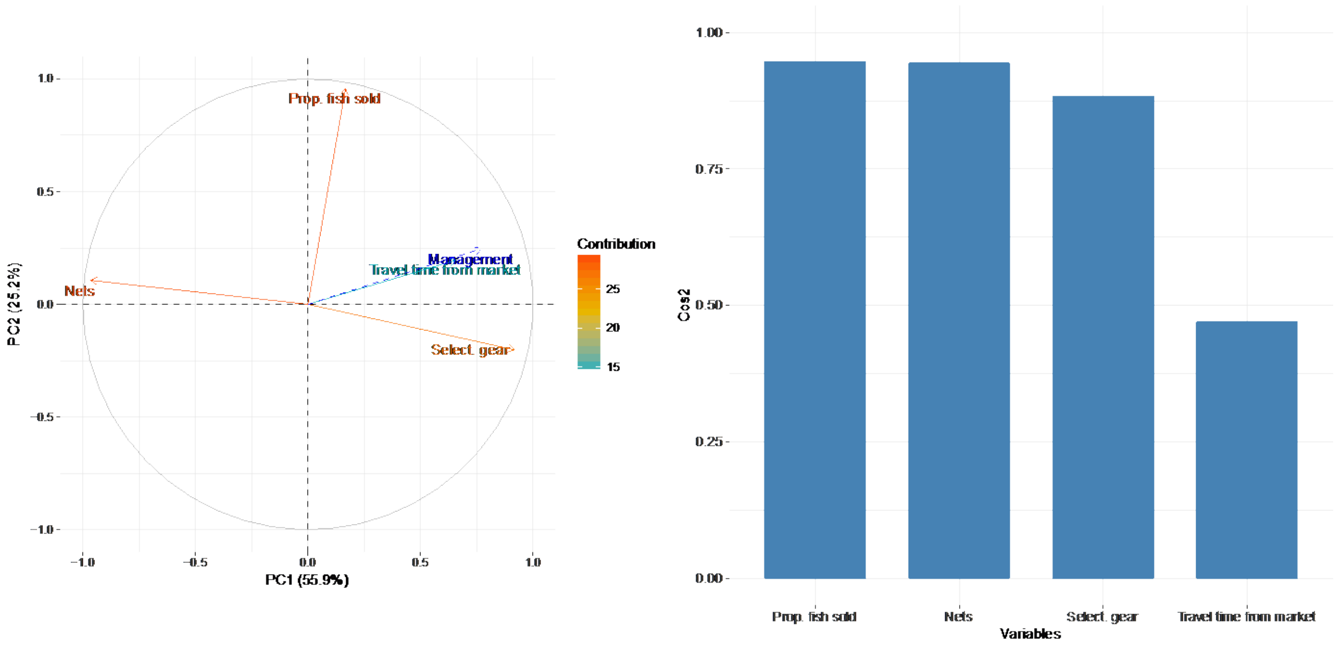


Figure VIII | Standardized effect size of social drivers and environmental covariates, including 95% uncertainty intervals (thin lines), and 50% (thick lines) for (A) the full biomass model (including top predators); (B) targeted fish biomass model (excluding top predators); (C) the top predators presence/absence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

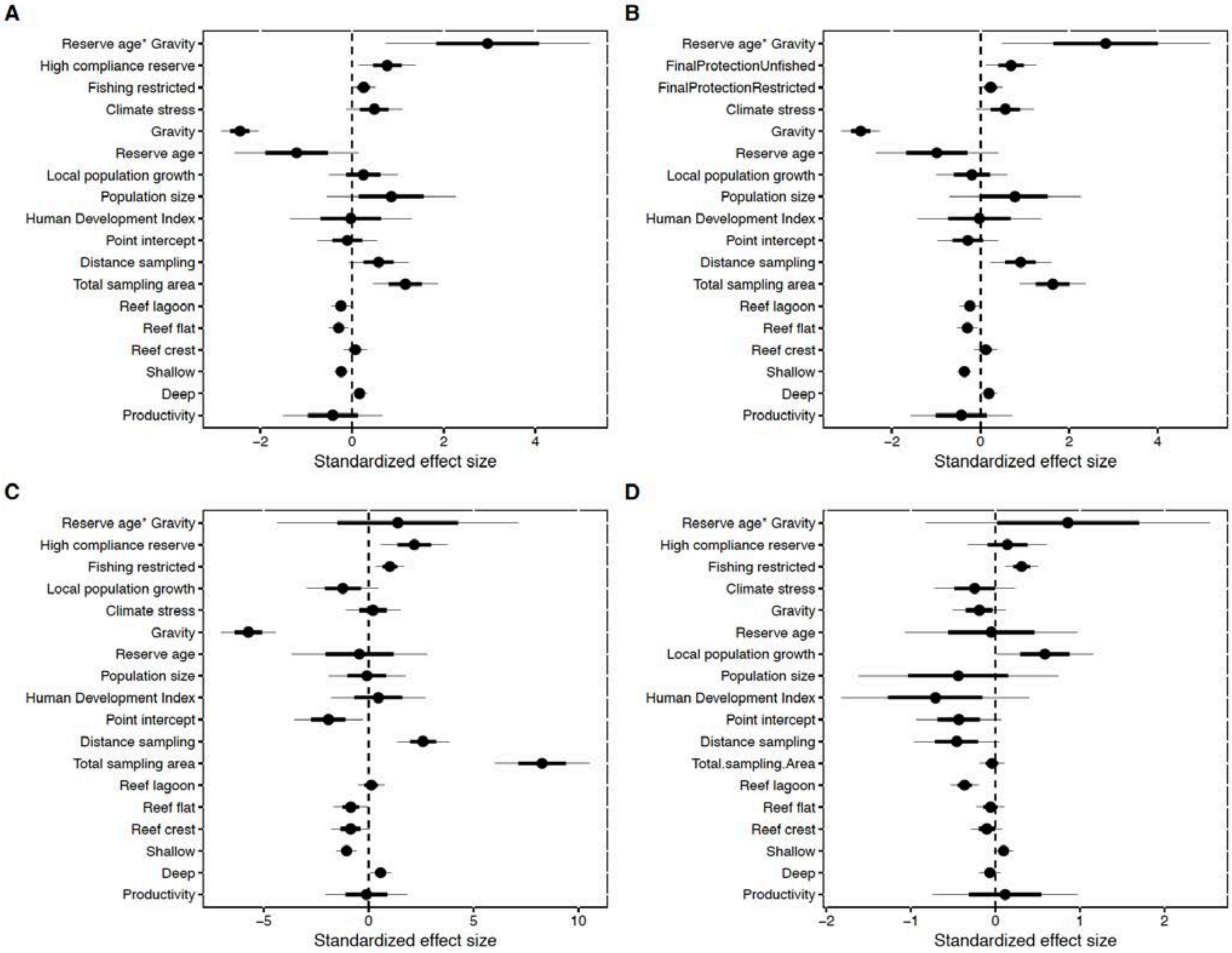


Figure IX | Model-predicted relationships for targeted-only fish biomass excluding top predators. Blue = marine reserves, red=openly fished, green= restricted fishing. Shaded areas represent 95% confidence intervals.

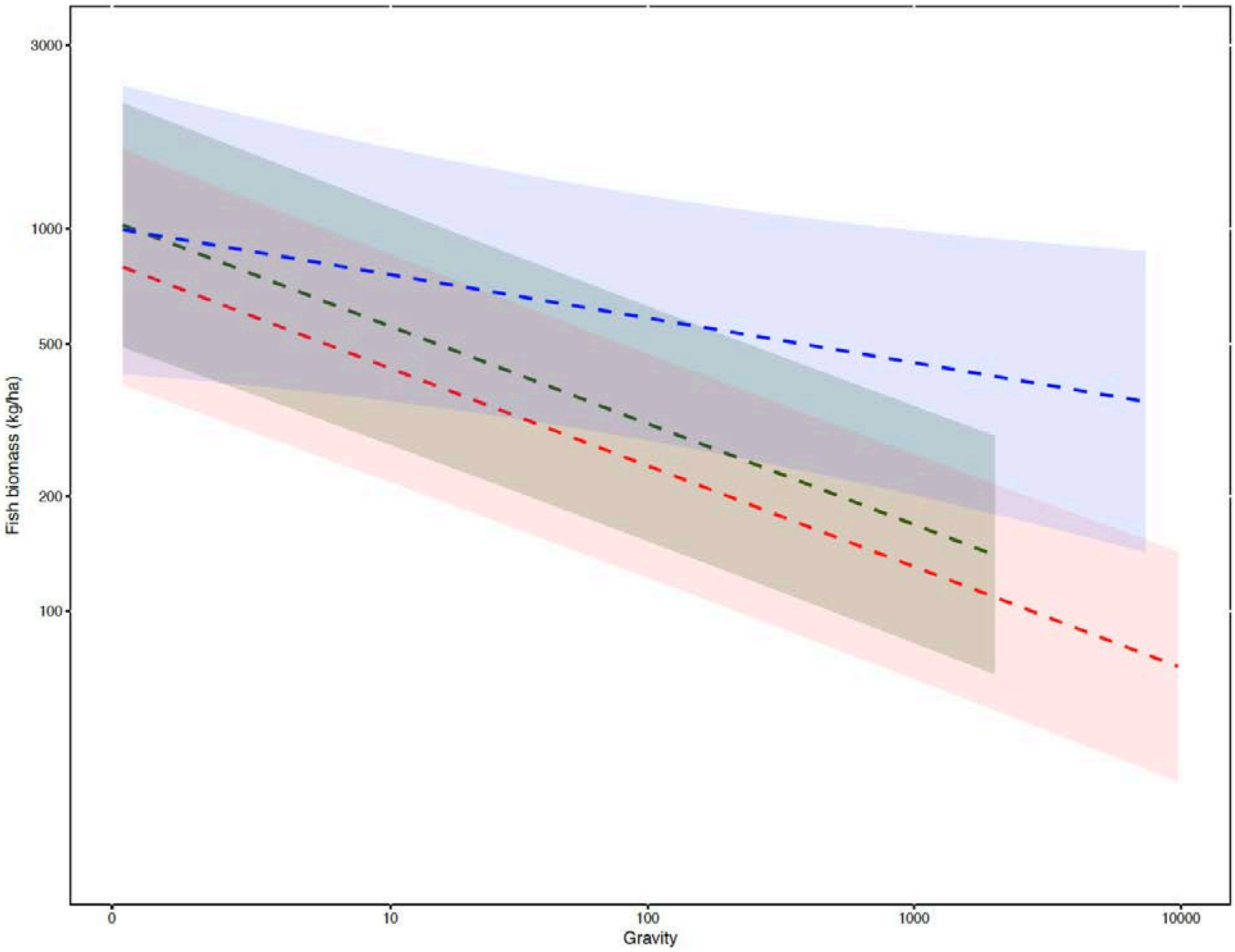
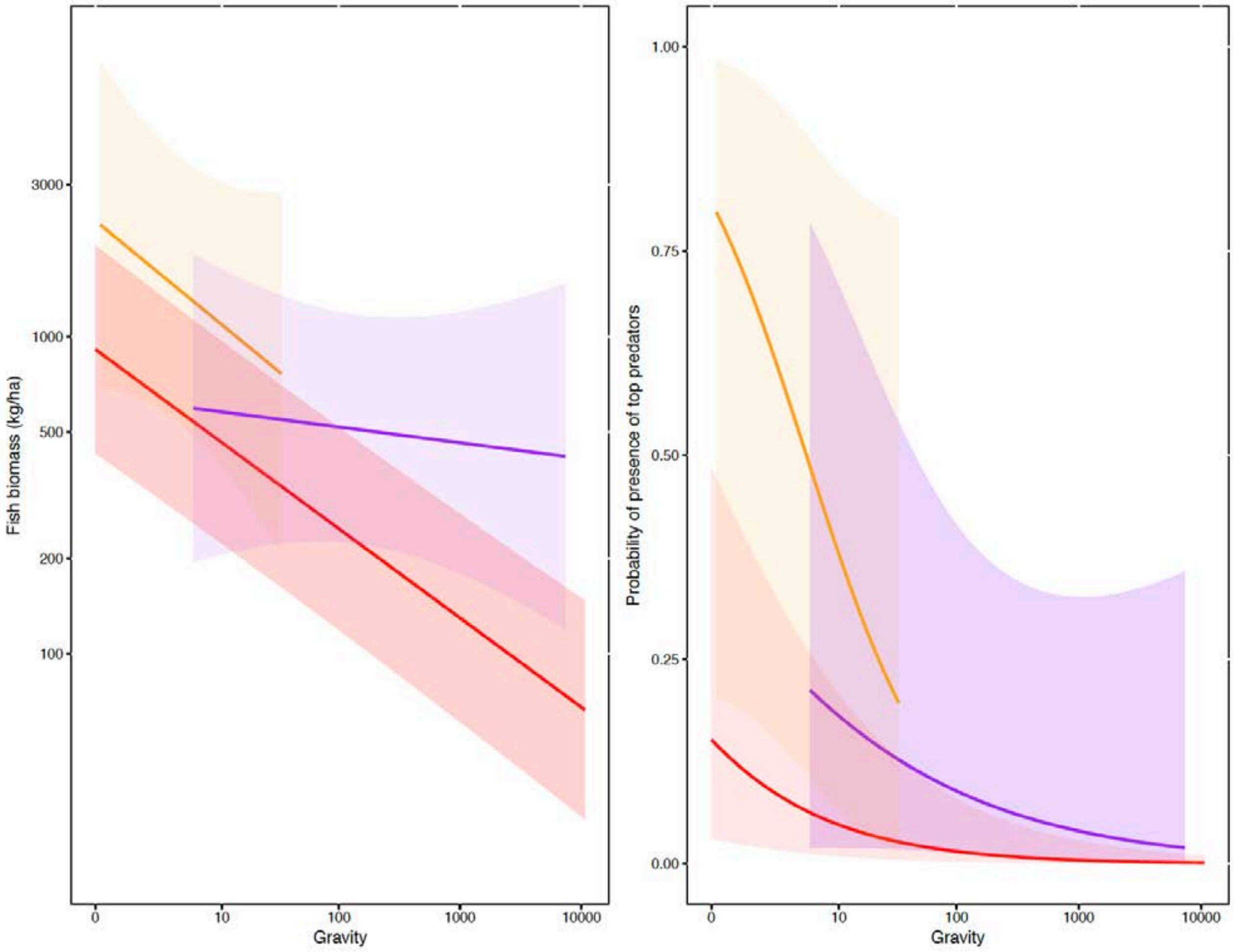


Figure X | Model-predicted trends in fish biomass (left) and probability in encountering top predators (right) with reserves broken into small (<28km^2, purple) and large (orange). Shaded areas represent 95% confidence intervals.



8.3. Supplementary procedure and material for Chapter 5

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 99th and 95th 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.

Figures and Tables

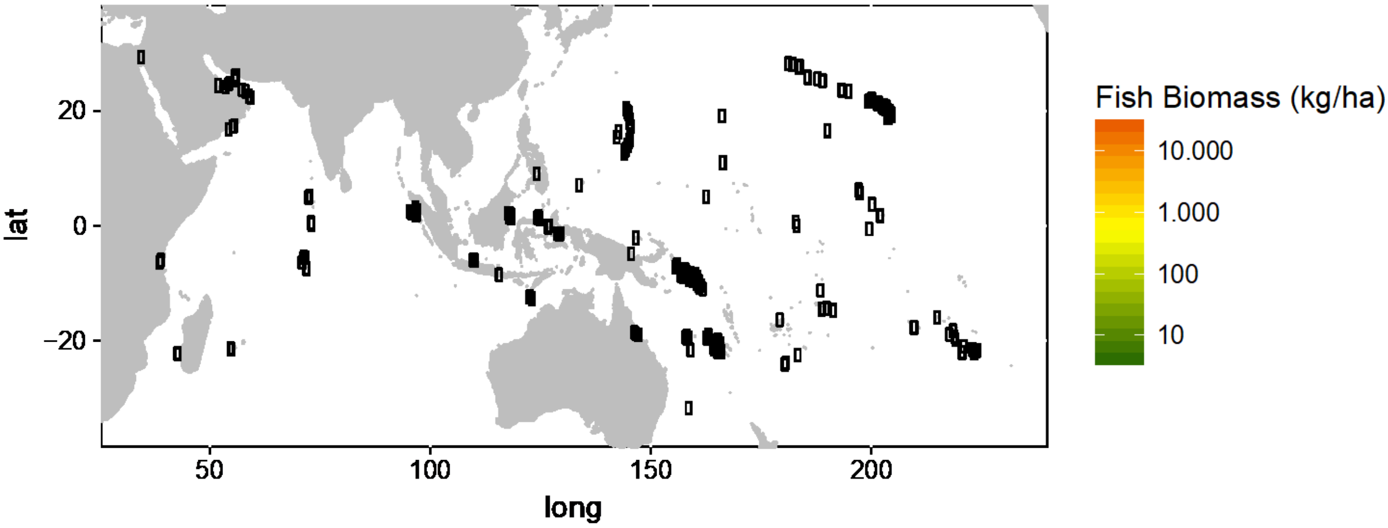


Figure S1 | Map of the reef fish biomass observed in 1,824 reefs located in the Indo-Pacific.

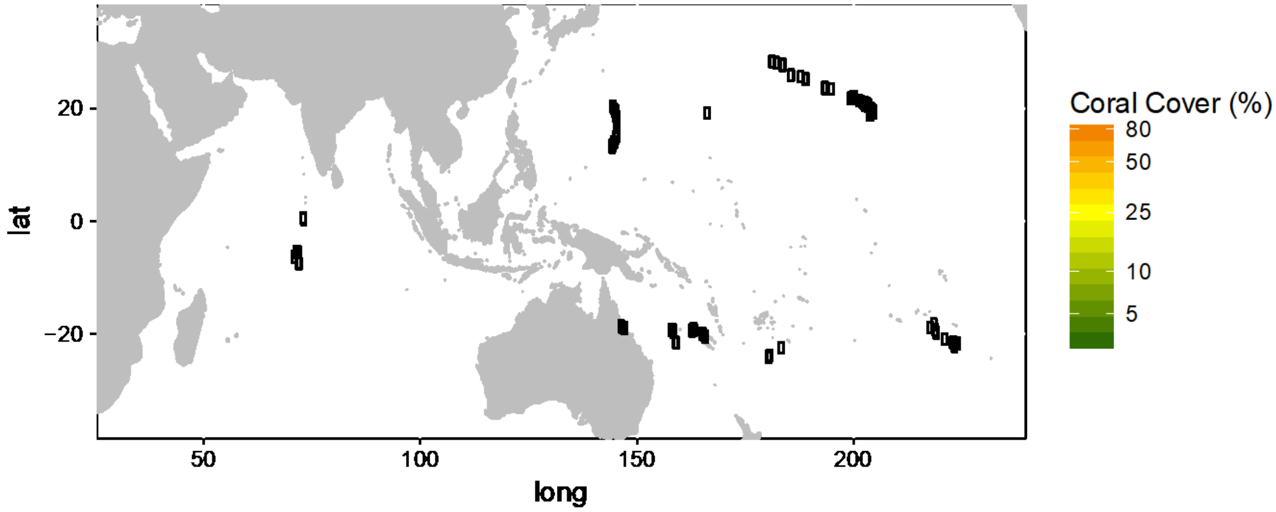


Figure S2 | Map of the live coral cover observed in 741 reefs located in the Indo-Pacific. Information on coral cover was not available for all sites at which reef fish biomass was surveyed.

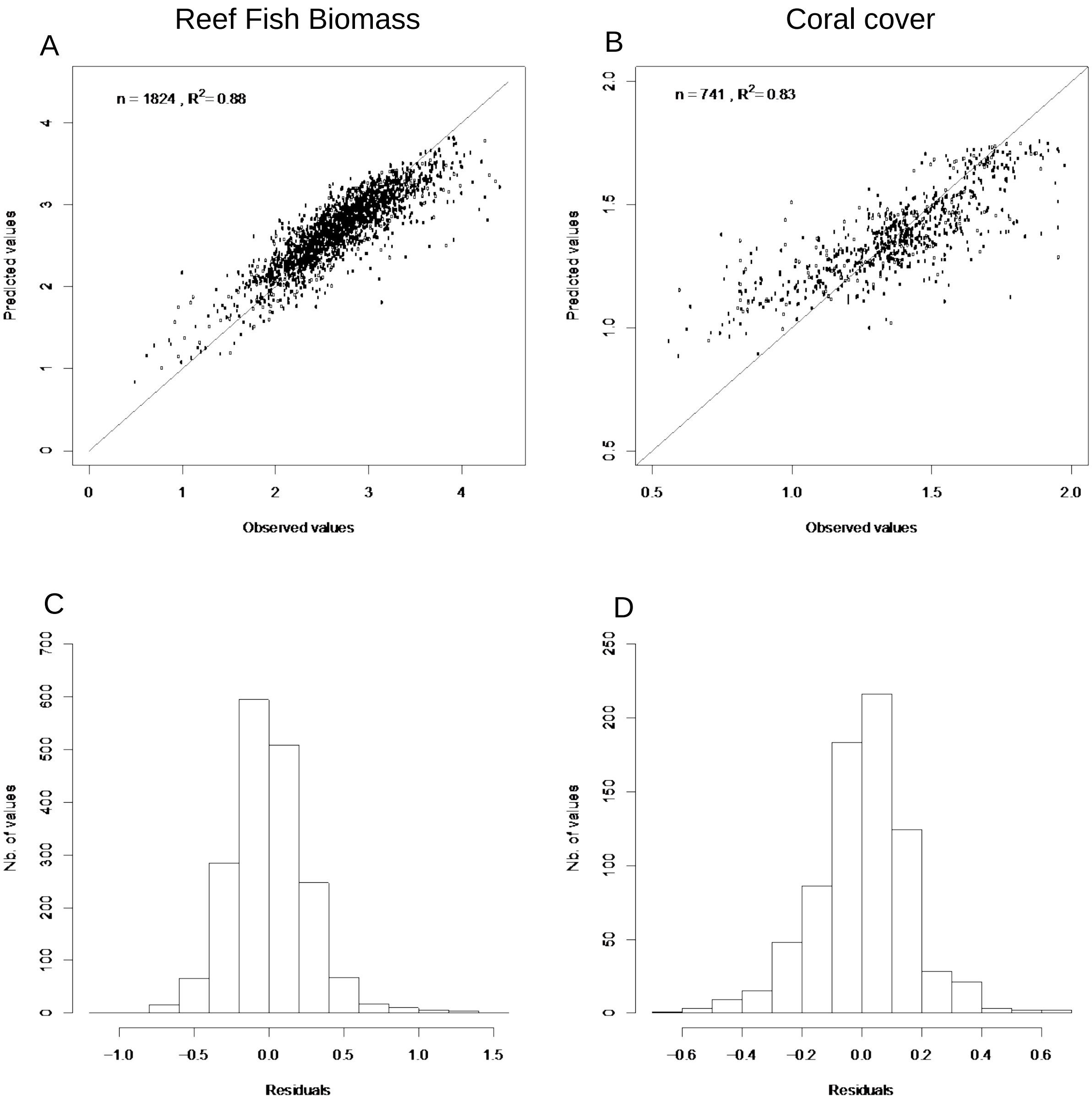


Figure S3 | Accuracy and residuals of the two initial models (fish biomass and coral cover). The accuracy of each model is assessed using the Pearson correlation between predicted and observed values which came to 88% for biomass (A) and 83% for coral cover (B). We checked that residuals of the initial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

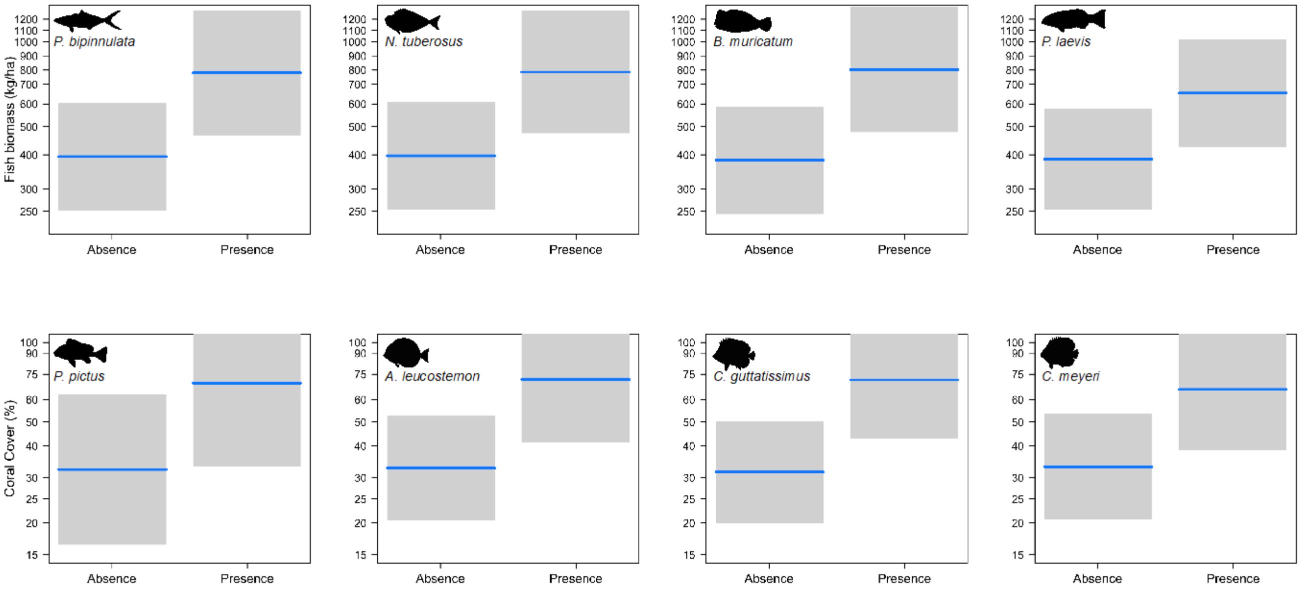
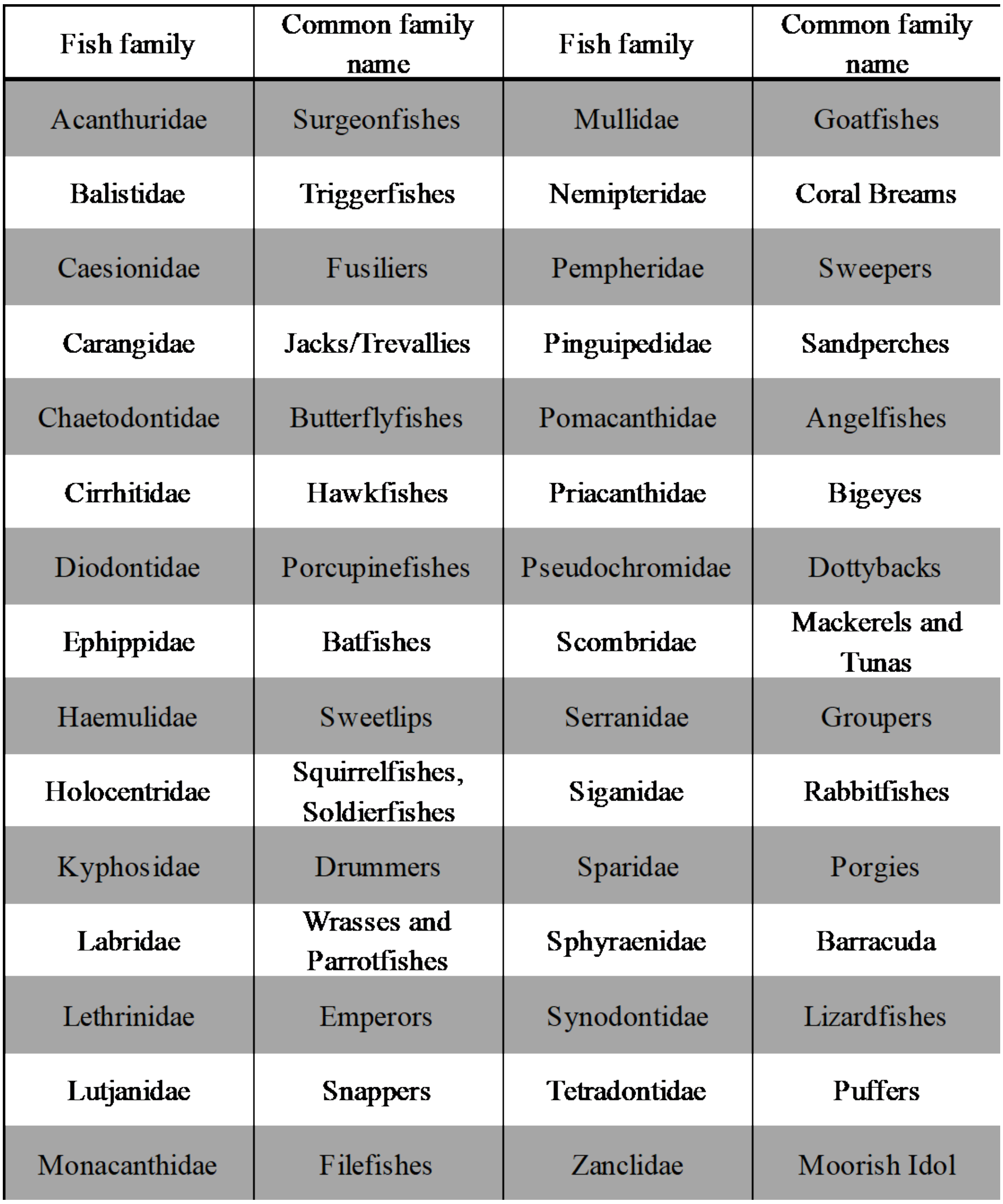


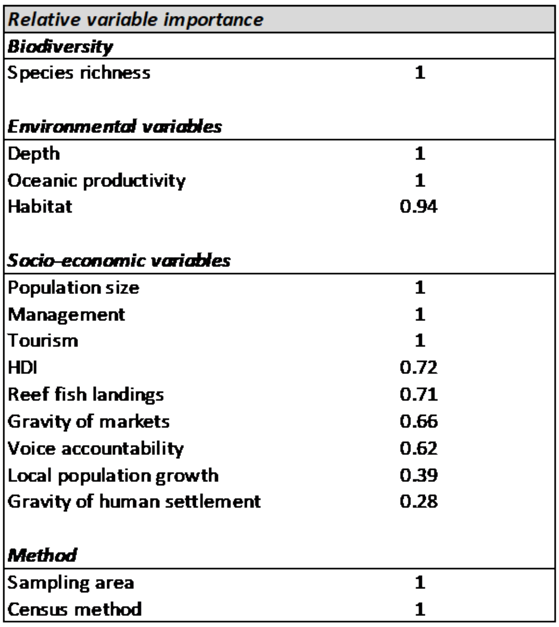
Figure S4 | Net effect of the 4 key fish species linked to the highest levels of fish biomass (top) and live coral cover (bottom). We extracted the pure effects of all the key species and determined which were related to the highest levels of biomass and coral cover respectively, using a partial plot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



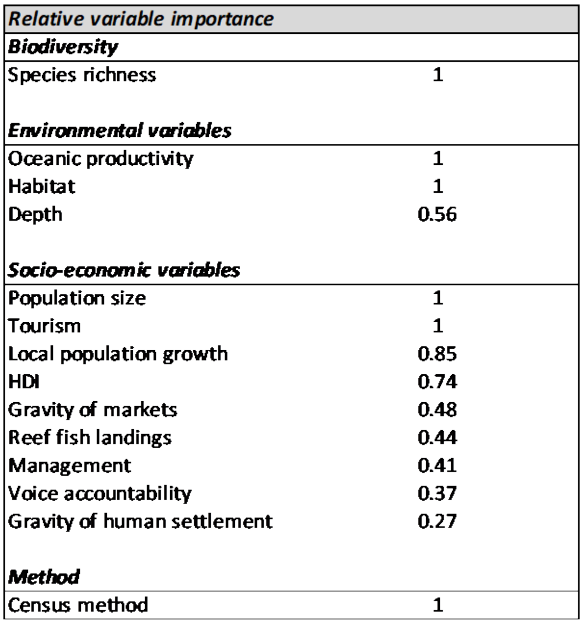
Fish family	Common family name	Fish family	Common family name
Acanthuridae	Surgeonfishes	Mullidae	Goatfishes
Balistidae	Triggerfishes	Nemipteridae	Coral Breams
Caesionidae	Fusiliers	Pempheridae	Sweepers
Carangidae	Jacks/Trevallies	Pinguipedidae	Sandperches
Chaetodontidae	Butterflyfishes	Pomacanthidae	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

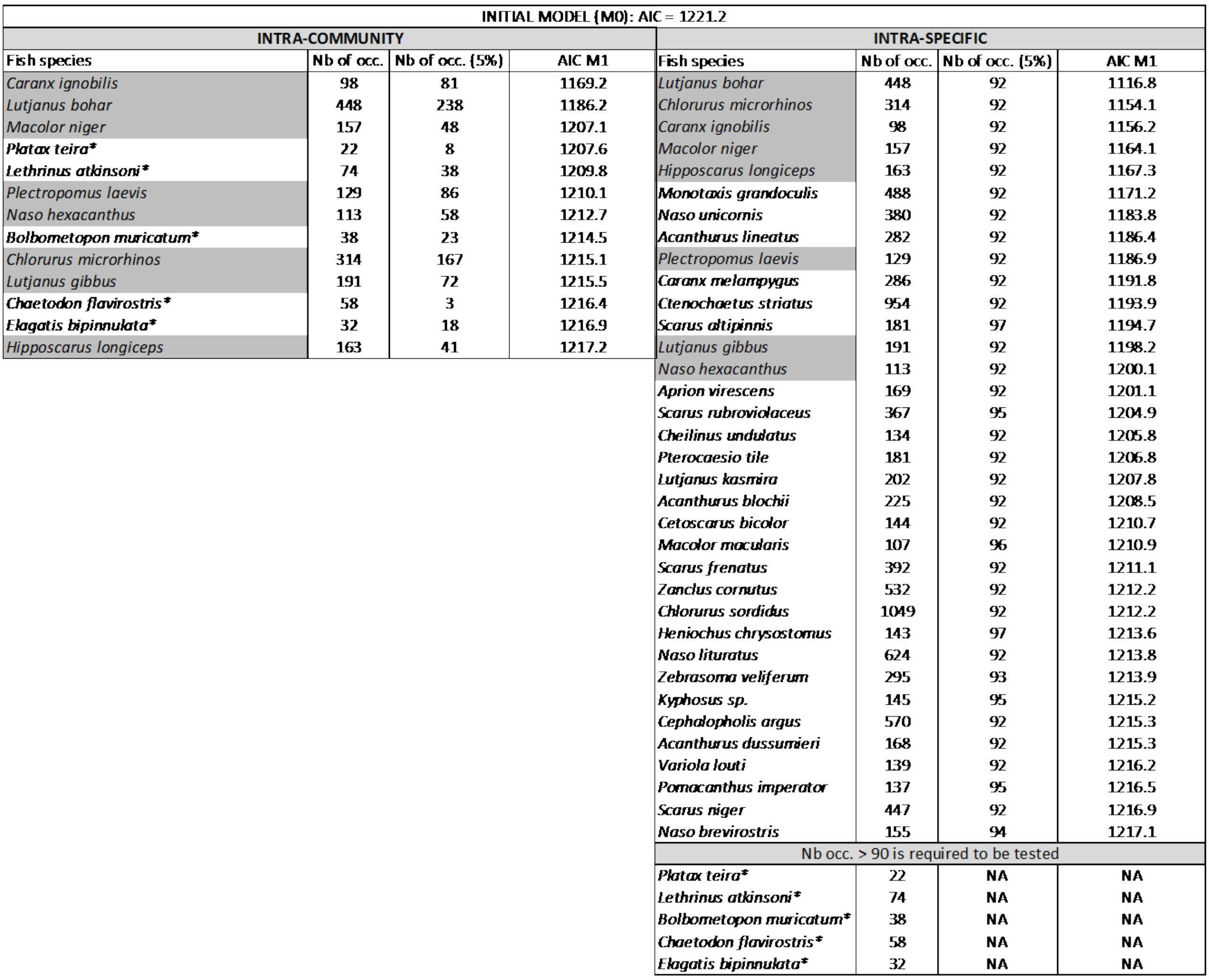
Table S6 | Functional traits of key fish species for reef fish biomass and live coral cover. 23, 25 and 3 fish species are significantly related to biomass (BM), live coral cover (CC) or both (BOTH) of those proxies of coral reef services respectively. Each species is described using six traits: *(1)* 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				**INTRA-SPECIFIC**			
Fish species	Nb of occ.	Nb of occ. (1%)	AIC M1	Fish species	Nb of occ.	Nb of occ. (1%)	AIC M1
Caranx ignobilis	98	96	1166.6	*Caranx ignobilis*	98	19	1157.1
Lutjanus bohar	448	332	1185.0	***Lutjanus gibbus***	191	19	1177.5
Plectropomus laevis	129	116	1199.3	*Macolor niger*	157	19	1177.8
Chlorurus microrhinos	314	285	1202.3	*Naso hexacanthus*	113	19	1183.8
Bolbometopon muricatum	38	35	1206.1	*Lethrinus atkinsoni*	74	19	1188.2
Naso tuberosus	51	46	1206.6	*Bolbometopon muricatum*	38	20	1188.4
Macolor niger	157	100	1209.8	*Hipposcarus longiceps*	163	19	1191.6
Aprion virescens	169	151	1210.9	***Scarus altipinnis***	181	19	1192.8
Hipposcarus longiceps	163	107	1211.5	*Chlorurus microrhinos*	314	20	1194
Naso hexacanthus	113	86	1212.6	***Lutjanus kasmira***	202	19	1196
Lethrinus atkinsoni	74	58	1213.3	*Lutjanus bohar*	448	19	1197.3
Elagatis bipinnulata	32	28	1214.6	*Plectropomus laevis*	129	19	1202.2
Naso caesius	31	22	1216.7	*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).

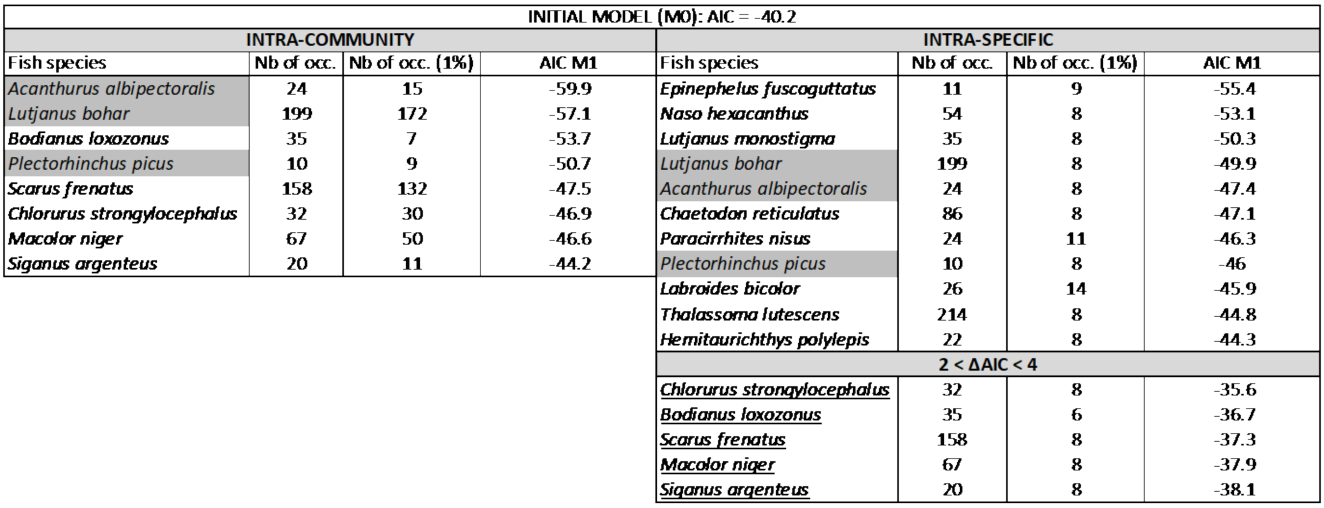


INITIAL MODEL (M0): AIC = 1221.2

INTRA-COMMUNITY			
Fish species	Nb of occ.	Nb of occ. (5%)	AIC M1
Caranx ignobilis	98	81	1169.2
Lutjanus bohar	448	238	1186.2
Macolor niger	157	48	1207.1
Platax teira*	22	8	1207.6
Lethrinus atkinsoni*	74	38	1209.8
Plectropomus laevis	129	86	1210.1
Naso hexacanthus	113	58	1212.7
Bolbometopon muricatum*	38	23	1214.5
Chlorurus microrhinos	314	167	1215.1
Lutjanus gibbus	191	72	1215.5
Chaetodon flavirostris*	58	3	1216.4
Elagatis bipinnulata*	32	18	1216.9
Hipposcarus longiceps	163	41	1217.2

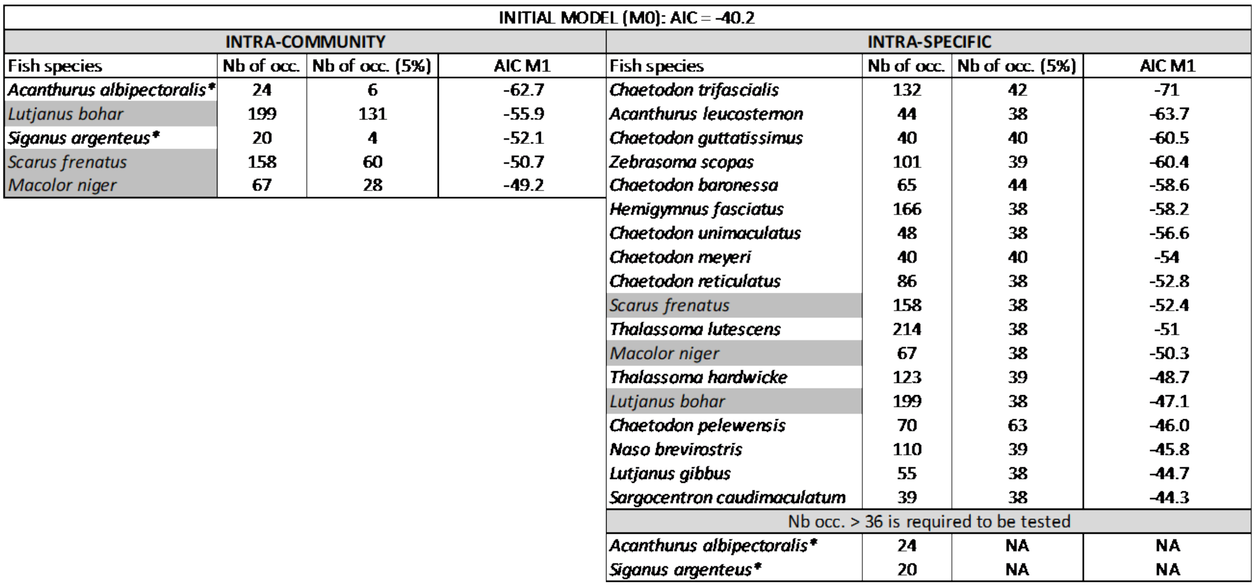
INTRA-SPECIFIC			
Fish species	Nb of occ.	Nb of occ. (5%)	AIC M1
Lutjanus bohar	448	92	1116.8
Chlorurus microrhinos	314	92	1154.1
Caranx ignobilis	98	92	1156.2
Macolor niger	157	92	1164.1
Hipposcarus longiceps	163	92	1167.3
Monotaxis grandoculis	488	92	1171.2
Naso unicornis	380	92	1183.8
Acanthurus lineatus	282	92	1186.4
Plectropomus laevis	129	92	1186.9
Caranx melampygus	286	92	1191.8
Ctenochaetus striatus	954	92	1193.9
Scarus altipinnis	181	97	1194.7
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 leucostemon	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

9. 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

Barneche, D.R., Rezende, E.L., Parravicini, V., **Maire, E.**, Edgar, G., Stuart-Smith, R.D., Arias-Gonzalez, J.E., Ferreira, C.E.L., Friedlander, A.M., Green, A.L., Luiz, O.J., Rodríguez-Zaragoza, F.A., Vigliola, L., Kulbicki, M., Floeter, S.R. Body size drives global gradients in reef-fish species richness across space? *Global Ecology and Biogeography*, doi: DOI: 10.1111/geb.12851.

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