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Abstract

Coral reefs are sanctuaries for a large portion of our planet's biodiversity, but their rapid decline begs critical questions about what exactly is being lost, what driving forces determine decline or resilience, and what implications for life on Earth. To help address these questions, this chapter synthesizes the state of knowledge on the diversity of coral reef life forms at different scales of biological and ecological organization, encompassing variability in

genes, biomolecules, cells, organs, organisms, populations, communities, ecosystems, socio-ecosystems, and biogeoclimatic systems, with a particular focus on French tropical overseas. We discuss research pathways to address knowledge gaps in various scientific disciplines, covering genetics (genomics, transcriptomics, proteomics, metabolomics), morphology, ethology, bioacoustics, demography, functional ecology, macro-ecology, landscape ecology, human and social sciences, bioclimatology, and their cross-disciplinary interactions. Based on contributions from coral reef experts working in different coral reef regions around the world, our synthesis supports a better understanding of the various dimensions of coral reef biodiversity and proposes future research orientations for improving knowledge and conservation. Given the rapid disappearance of coral reefs and how much is still unknown, this chapter underscores

Synopsis

This chapter provides a holistic vision of coral reef biodiversity across vast scales of biological and ecological organization, from genes and molecules to ecosystems and their geoclimatic and social environments. We compare biodiversity metrics among key ecological communities and regions as we synthesize the current state of knowledge on coral reef biodiversity, pinpoint important knowledge gaps, and identify prospective research.

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the urgency of cross-scale biodiversity assessments for a systemic understanding of the distribution and dynamics of biodiversity.

Keywords

Systems science · Biodiversity distribution · Collaborative cross-system research · Coral reef management · Sustainability

10.1 Introduction

10.1.1 Coral Reefs in the Twenty-First Century

Coral reefs are arguably the most biodiverse and productive ecosystems on Earth (Fig. 10.1). They host an estimated 38% of all marine species (Fisher et al. 2015) and contribute fundamental benefits to humanity and the natural world (Moberg and Folke 1999; Speers et al. 2016; Woodhead et al. 2019; Carlot et al. 2023) despite making up a mere 0.08% of the ocean floor (Smith 1978), or 0.17% including associated lagoonal habitats (Spalding et al. 2001), and lying in tropical waters that are poor in nutrients (de Goeij et al. 2013). However, coral reefs are declining due to the high vulnerability of several of their ecologically key functional groups to human-driven and climatic stressors (Brandl et al. 2019a; IPBES 2019; Calvin et al. 2023). In particular, unsustainable rapid growth in coastal development, pollution, fishing, and climate change are increasingly reducing the regeneration of reef habitats by their slow-growing foundational species, the calcifying corals, and altering the capacity of the food webs to preserve their functional equilibrium (Fig. 10.2; Vajed Samiei et al. 2015; Hoegh-Guldberg et al. 2017; Hughes

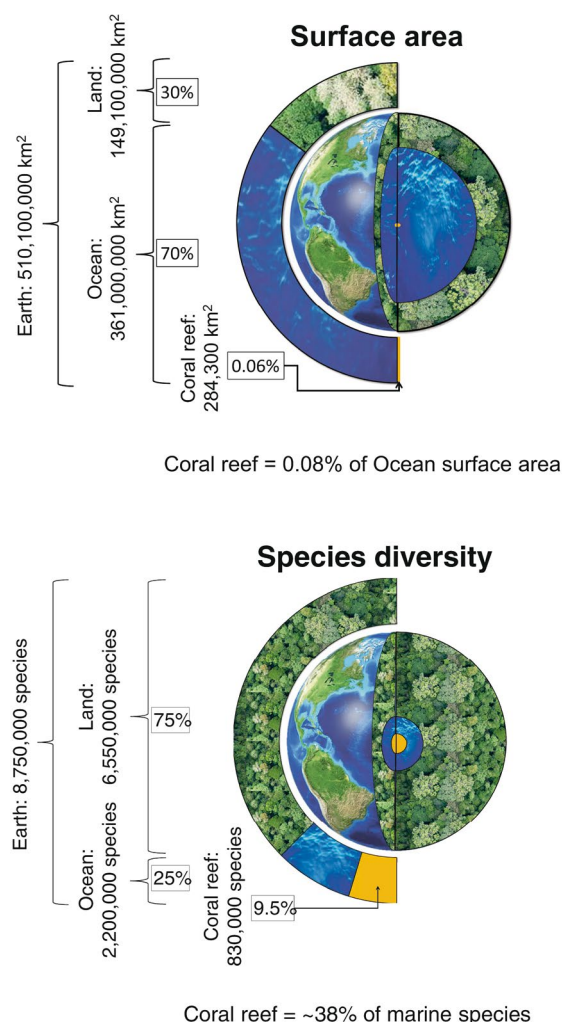


Fig. 10.1 Coral reef contributions in terms of surface area and species diversity, based on total species number estimates according to Mora et al. (2011) and Fisher et al. (2015)

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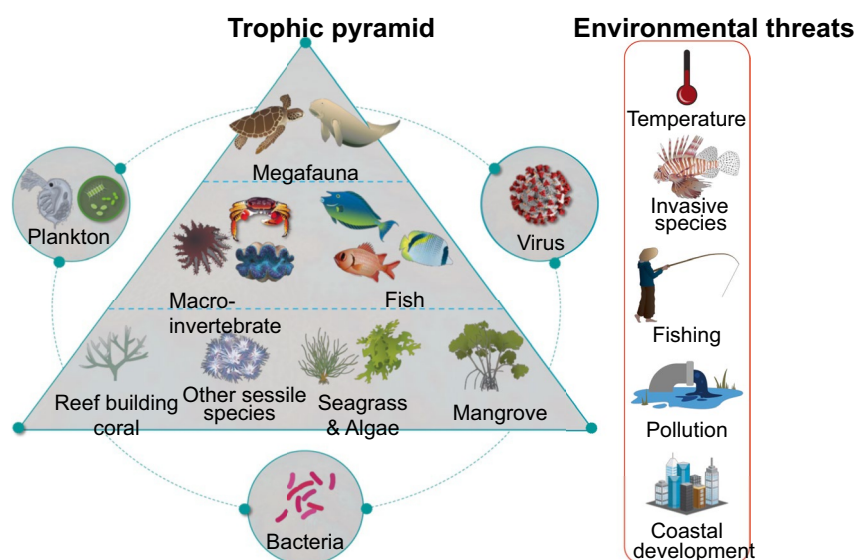
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Fig. 10.2 Key ecological communities of coral reef ecosystems and associated seagrass and algae beds, mangrove forests, and sandy lagoonal plains. The communities are organized in a trophic pyramid, with species occupying distinct ecological niches and contributing a set of ecological functions that enable ecosystem functionality in a state of relative stability. Environmental stressors alter species abundances, threatening the equilibrium and functionality of the system



et al. 2018; Quattrini et al. 2020; Ouédraogo et al. 2021, 2023; Andreello et al. 2022). In many places, eutrophication and overfishing have reduced the capacity of herbivores to control algae communities, leading to major ecosystem shifts (Hughes et al. 2017; Schmitt et al. 2019). The widespread decline of coral reefs and consequently of the benefits they provide to society has made coral reef conservation a societal priority in many regions and a major target for humanity globally (IPBES 2019; Maxwell et al. 2020; Eddy et al. 2021). Within these efforts and in the larger scope of knowledge and conservation of the Earth's biodiversity, it is fundamental to comprehend the extent to which coral reefs contribute to biodiversity, biodiversity distribution in relation to coral reef conditions and human influences, and the consequences of coral reef decline for marine life and humanity. To begin, what exactly is coral reef biodiversity?

10.1.2 What Is Biodiversity?

Biodiversity is defined as the variability of life forms. Despite the simplicity of the concept, biodiversity remains a major scientific mystery, as variability of life is found at a multitude of biological and ecological scales, from the very small to the very large (Fig. 10.3). In longer terms, as defined by Article 2 of the Convention on Biological Diversity (www.cbd.int): “biological diversity means the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems.” In fact, variability of life is characterized in as many dimensions as there are metrics to assess, resulting in a plethora of biodiversity measurements and

disciplinary sub-definitions. While this fractal nature of biodiversity measurements has complexified interdisciplinary interactions, biodiversity assessments remain largely incomplete, as most existing metrics have not yet reached a final estimate and biodiversity metrics continue to increase with the development of new scientific tools and disciplines (Caley et al. 2014; Guerra et al. 2020; Galand et al. 2023). Overall, a global evaluation of Earth's biodiversity is necessary for a better understanding of the organization of life on our planet and the consequences of the biological losses it suffers (Costello et al. 2013; IPBES 2019; Bradshaw et al. 2021). As sanctuaries for a large portion of marine biodiversity, coral reefs are a good place to begin this endeavor.

10.1.3 Objectives of the Chapter

Using contributions from a team of coral reef experts working in different coral reef ecoregions around the world, we compile information from various scientific disciplines of biology and environmental sciences to synthesize knowledge on major metrics of coral reef biodiversity at different scales of biological (i.e., relating to organisms) and ecological organization (i.e., relating to interactions among organisms and with their environments), from genes to ecosystems and their natural and human-associated environments (Fig. 10.3). We evaluate differences among key coral reef biological communities and geographical regions, identify major knowledge gaps, and discuss prospective research. Our synthesis provides an understanding of the various dimensions in which coral reef biodiversity takes form and highlights future research for improving our knowledge of nature and its preservation.

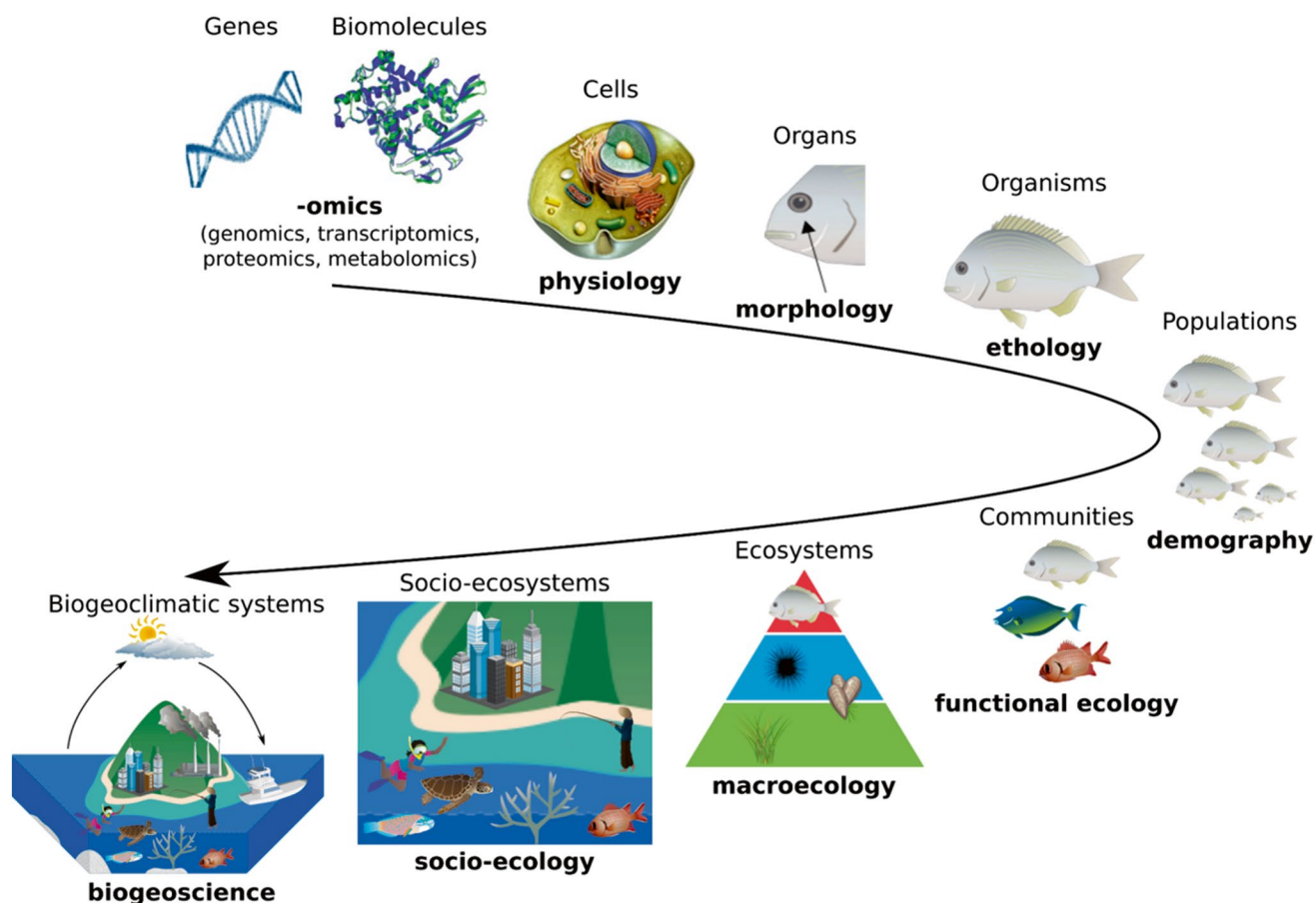


Fig. 10.3 Hierarchical organization of the living, from genes to biogeoclimatic systems, from which biodiversity is the result of variabilities at the different scales. Text indicates the different scales of

biological and ecological organization (top) and the corresponding scientific disciplines (bottom)

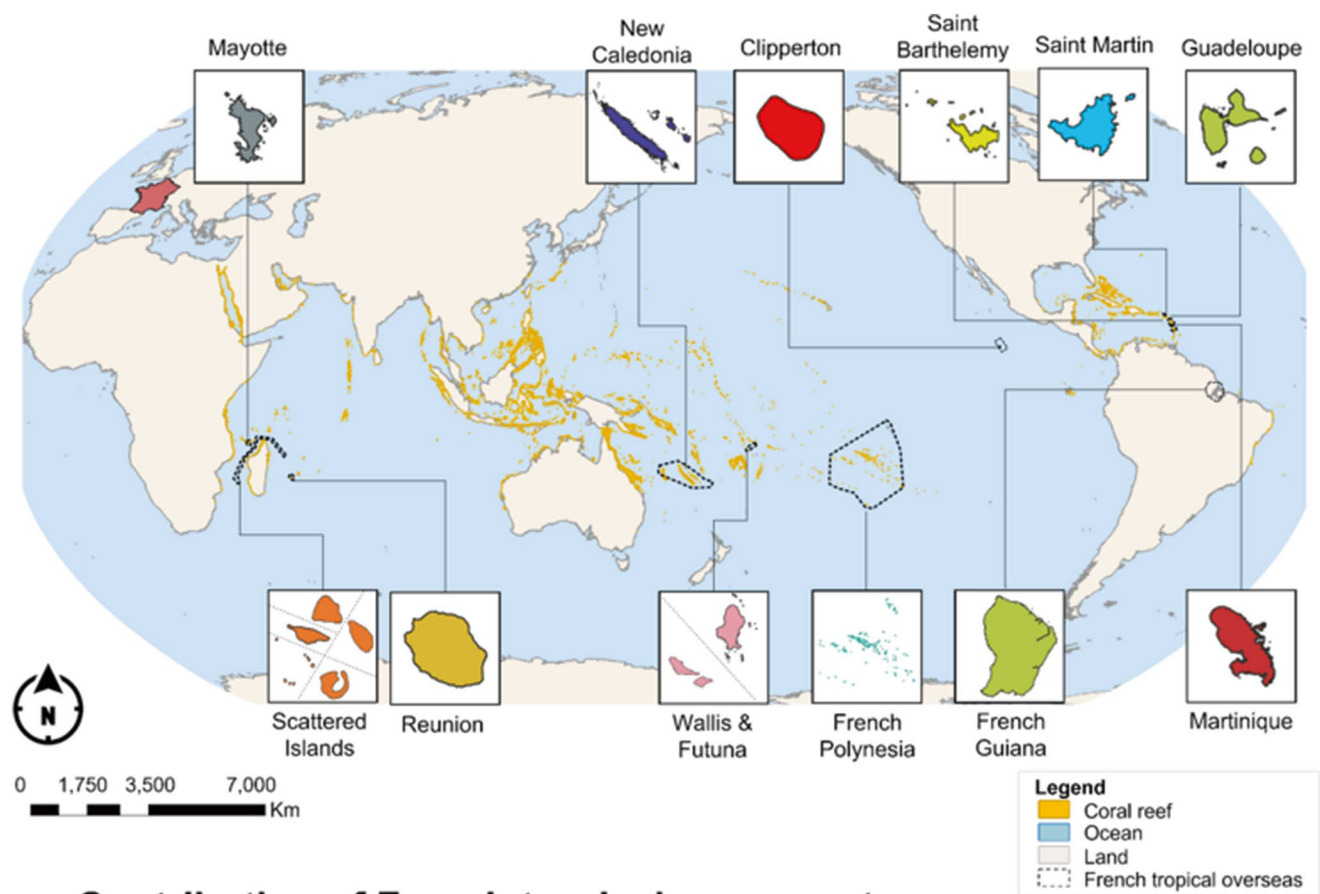
10.2 Methods

We have leveraged the coral reef expertise of the French Laboratory of Excellence LabEx CORAIL network across 12 French tropical overseas localities situated in the Caribbean, Indian, and Pacific regions (Fig. 10.4). This represents ~5% of the world's constructed hard-substrate reefs, ~9% of all coral reef surface area when including associated sandy lagoonal habitats, and encompasses 46° of latitude (18°N–28°S) and all major coral reef basins (Smith 1978; Spalding et al. 2001; Andréfouët et al. 2008).

We characterize coral reef biodiversity at the different scales of biological and ecological organization, from genes to biogeoclimatic systems, by compiling quantitative metrics from the various scientific disciplines (Fig. 10.3) for different coral reef biological communities and regions (Fig. 10.4). Our focus is on major biological groups considered as key ecological compartments of coral reef ecosystems, including reef-building corals and other sessile animals (soft-corals, sponges, ascidians, bryozoans), micro- and macroalgae, vag-

ile invertebrates (crustaceans, mollusks, echinoderms, annelids, platyhelminthes, sipunculid worms, hemichordates), fish (actinopterygians, elasmobranchii), megafauna (sea turtles, dugongs, dolphins, whales, sharks and rays, sea snakes), bacteria, and viruses (Fig. 10.2). Data on seagrasses, mangroves, and sandy lagoonal plains are also integrated as adjacent ecosystems with species distributions that often overlap with coral reef habitats (Moberg and Folke 1999; Andréfouët et al. 2008; Guannel et al. 2016). Environmental data consists of metrics characterizing the geologic, climatic, and societal aspects of the coral reef systems.

Biodiversity data is gathered thanks to the contribution of experts from various disciplines and regions, complemented with data obtained from literature and global databases. Particular attention has been given to the most documented and commonly used biodiversity metrics, and those viewed as essential biodiversity variables (<https://geobon.org/ebvs/>; Pereira et al. 2013). Experts have also been asked to identify major knowledge gaps and prospective research to address them.



Contribution of French tropical overseas to coral reef surface area

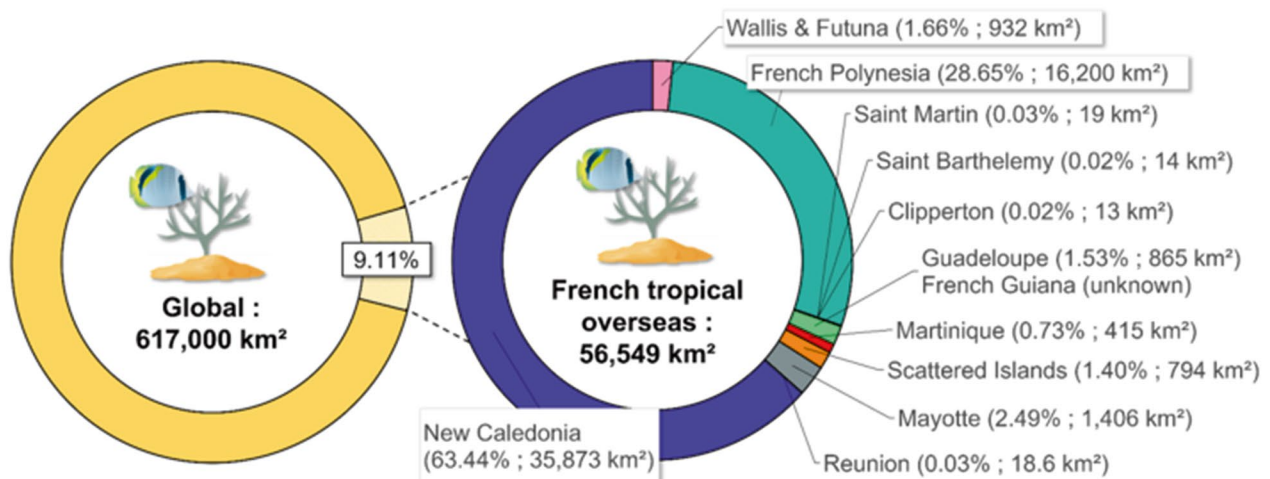


Fig. 10.4 Map of the world's coral reefs and contributions of French tropical overseas. Coral reef surface areas account for constructed hard reef and sandy lagoonal plain habitats (cf. Spalding et al. 2001)

All maps and graphics have been produced using the R software environment (R v4.2.3, R Core Team 2023) complemented with the “ade4,” “stringr,” “ggplot2,” “png,” “RcolorBrewer,” and “Cowplot” packages. Graphics are complemented with iconography from <https://ian.umces.edu> and <https://biorender.com>.

10.3 Results and Discussion

10.3.1 On the Challenge of Assessing Coral Reef Biodiversity

Quantifying biodiversity is a daunting exercise given the colossal task of considering the various scales of biological and ecological organization through the lenses of different scientific tools and disciplines (Fig. 10.3), particularly as most are in their infancy and none have achieved a finite estimate of biodiversity (Costello et al. 2013; Caley et al. 2014; Guerra et al. 2020; Galand et al. 2023). Nevertheless, estimating biodiversity is a necessity for humanity when rapid biodiversity loss is a global reality with irrevocable consequences for life on Earth (Kayal et al. 2019; IPBES 2019; Calvin et al. 2023). Due to their central role in hosting a large portion of the world’s biodiversity and their vulnerability to collapse, coral reefs are certainly a good focus point for this endeavor. The following sections synthesize coral reef biodiversity based on a multitude of metrics that characterize variability of coral reef systems at various biological and ecological scales, providing a snapshot of the work in progress.

10.3.2 Genes

Unknown until recent times, the birth of molecular biology in the 1950s opened paths to a fascinating new vision of how biological features are controlled by inheritable biological units, otherwise known as genes, organized in long sequences of deoxyribonucleic acid, or DNA (Gayon 2016). This revelation confirmed early work by Mendel (1865) on biological inheritance. Since, genetic investigation has been in constant acceleration, with the development of new tools and techniques providing means to deepen our exploration of biological diversity at the level of genomes. Despite significant increases in the number of studies in recent years, the genetic exploration of coral reef ecosystems remains in its infancy. Genomic resources have been developed for some model species within different ecological communities (Fig. 10.5), providing various metrics for measuring genetic diversity within and among taxa, including length, composition, and organization of coding and noncoding sequences (Fig. 10.6) and their degree of similarity between different evolutionary

paths (Fig. 10.7). These metrics can be accessed at the DNA and RNA levels, the latter also providing functional information in the form of gene expression data (transcriptomics). Such studies are particularly relevant to ecological investigations of species responses to environmental changes and other forms of selective pressure (Gingeras 2007; Fuller et al. 2020; Nielsen et al. 2020; Levy et al. 2021).

Increasing availability of genetic data has enabled exploring genetic variation at the population and meta-population levels (e.g., heterozygosity, parentage analysis, introgression, demographic connectivity) and across species distribution ranges (i.e., phylogeography) in key organisms of ecological or scientific importance. This also contributes ecological knowledge regarding population connectivity and regeneration capacity, and species origination and dispersal, therefore supporting biodiversity conservation (Baums 2008; Cowman and Bellwood 2013; Edmunds et al. 2016; Siqueira et al. 2019; Dubé et al. 2020; Swain et al. 2021; Cantalice et al. 2022). Exploring both the spatial and temporal nature of genetic variation is paramount to identifying genetic diversity hotspots and the mechanisms underlying adaptation to changing environments, a field that necessitates further investigation (Fig. 10.5). New approaches combining genetic exploration with descriptors of environmental condition and biodiversity at larger scales of bioecological organization will help in this endeavor (Nielsen et al. 2020; Selmoni et al. 2020; Manel et al. 2020; Bongaerts et al. 2021).

By enabling species identification based on short signature sequences, barcoding data represents the prevalent and accessible form of genetic resource, particularly useful for accessing hidden communities such as bacteria, viruses, symbionts, and cryptic organisms using environmental-DNA (eDNA) approaches (Robbins et al. 2021; Galand et al. 2023). GenBank (www.ncbi.nlm.nih.gov/genbank/) is the main public repository of genetic data in the public sphere (Leray et al. 2019), though project-specific datasets are also available. Recent decreases in the cost of sequencing have led to a sharp increase in shallow genomic surveys. Low-coverage DNA sequencing provides access to complete organellar genomes as these small molecules are often present in several thousands of copies compared to the larger nuclear genomes present as a single copy per cell. Mitochondrial DNA (mtDNA) data is a favorite molecular tool for the study of species diversity in animals (e.g., Shinzato et al. 2021), whereas chloroplast DNA (cpDNA) data is preferably used in plants and algae, mainly owing to differing rates of sequence evolution in these organisms. In addition to sequence data, complete organelle genomes provide morphological characters in the form of genome organization and molecular conformation, providing insights into genetic expression (Fig. 10.7; Kayal et al. 2012a, b, 2015a, b; Lavrov and Pett 2016).

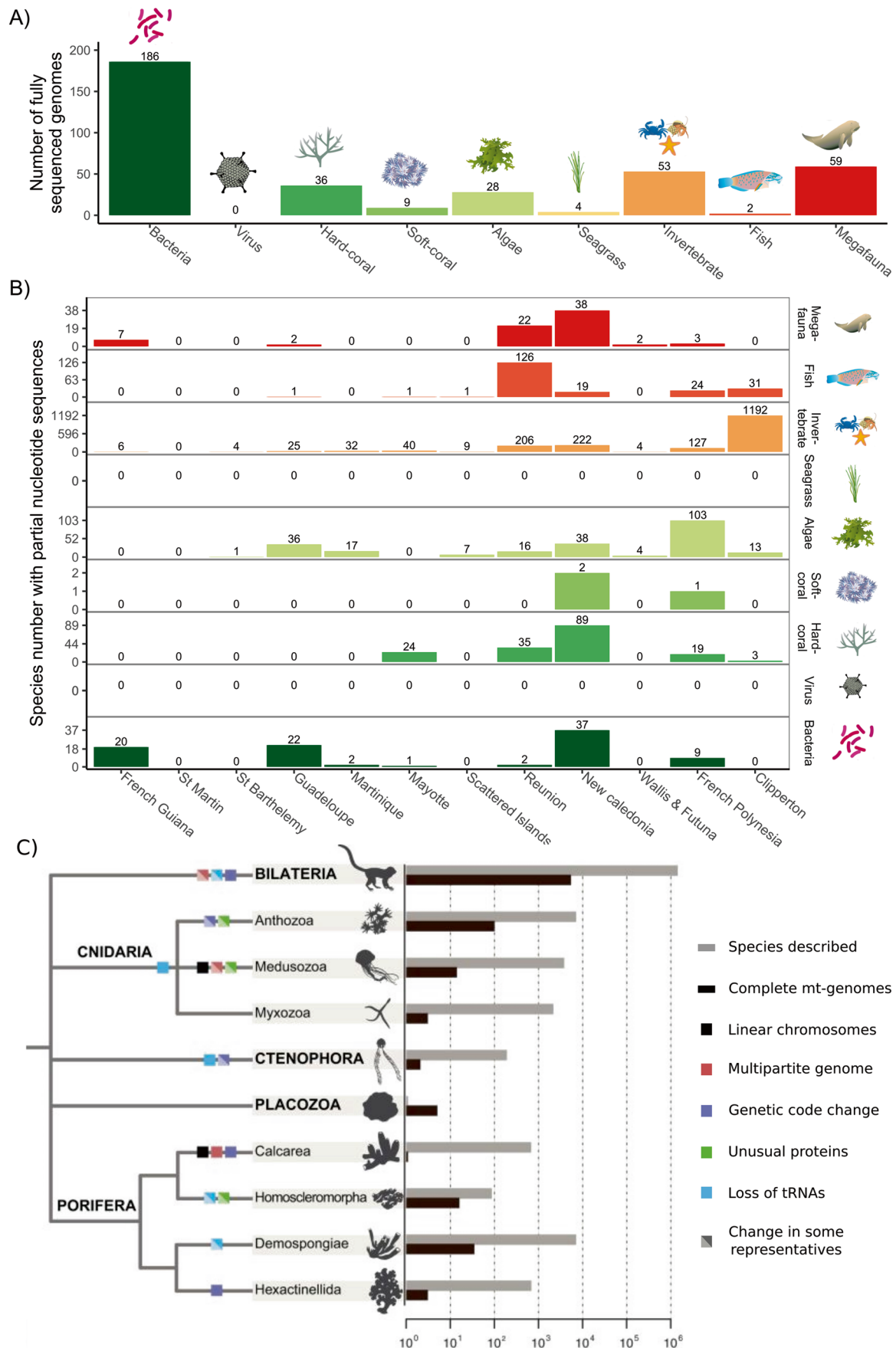


Fig. 10.5 Number of coral reef-associated species with characterized whole-genome sequences (**a**), number of species with available partial DNA sequences across French tropical overseas (**b**), and number of

described species and complete mitochondrial genomes per group (**c**). Data from GenBank (**a**, **b**) and from Lavrov and Pett 2016 (**c**)

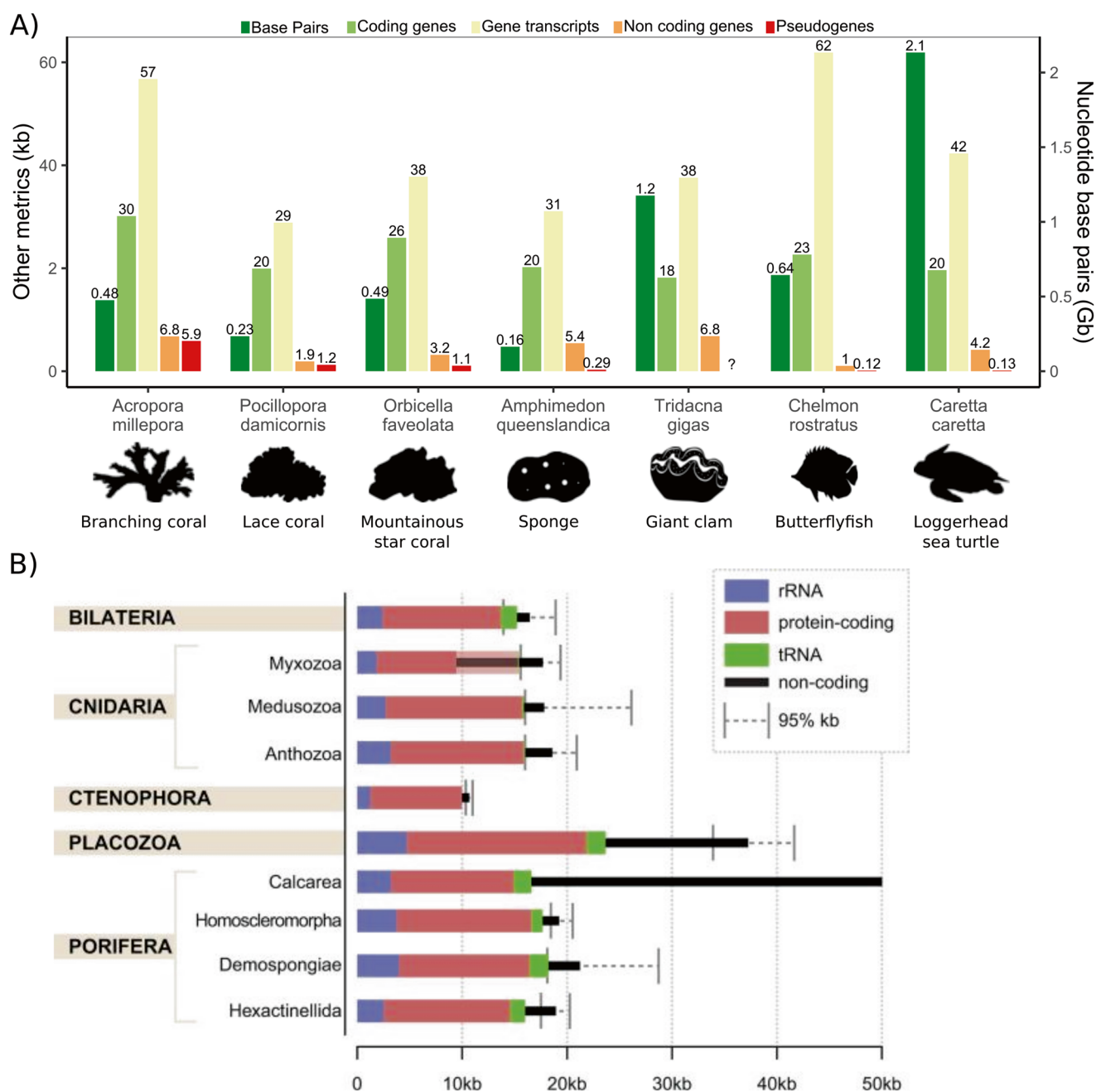
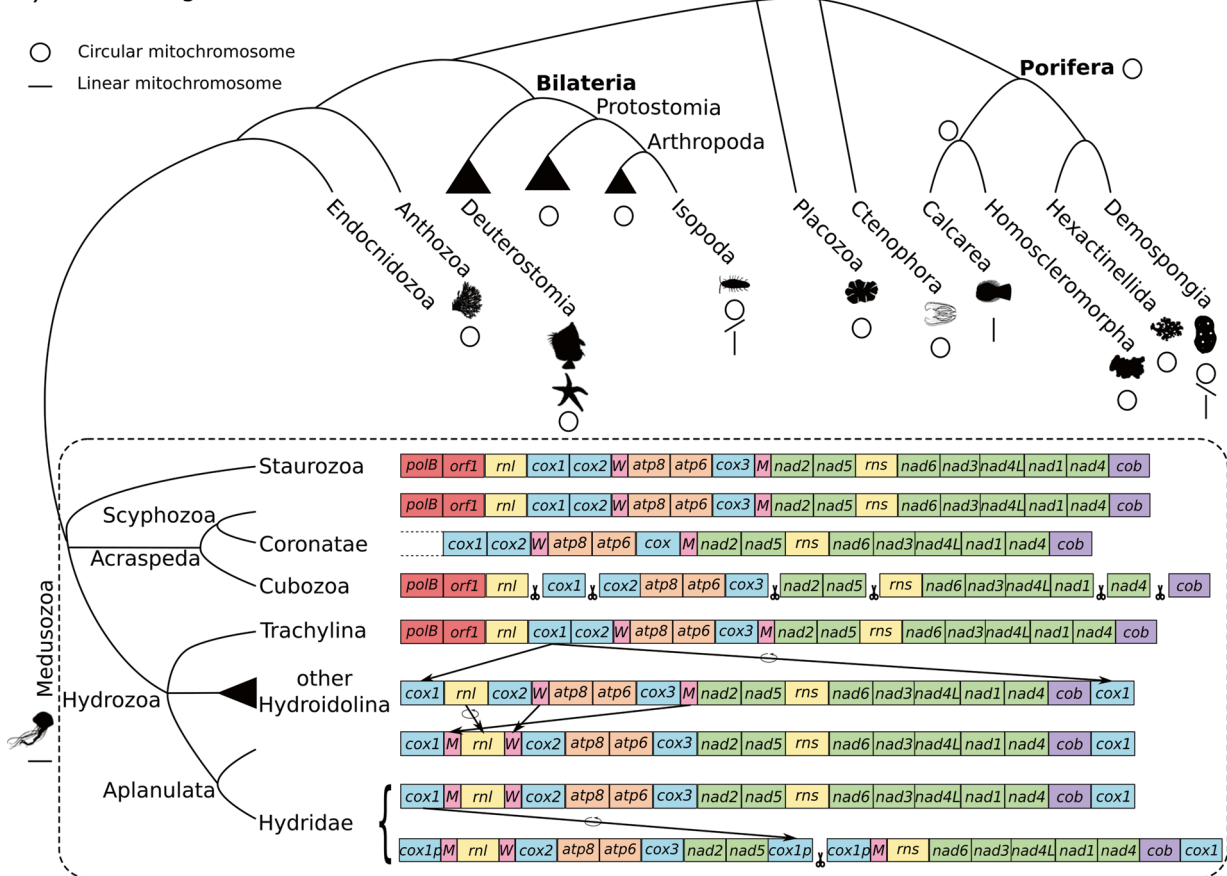


Fig. 10.6 Differences in nuclear (a, data from <https://rapid.ensembl.org>) and mitochondrial (b, from Lavrov and Pett 2016) genome size among key coral reef species groups

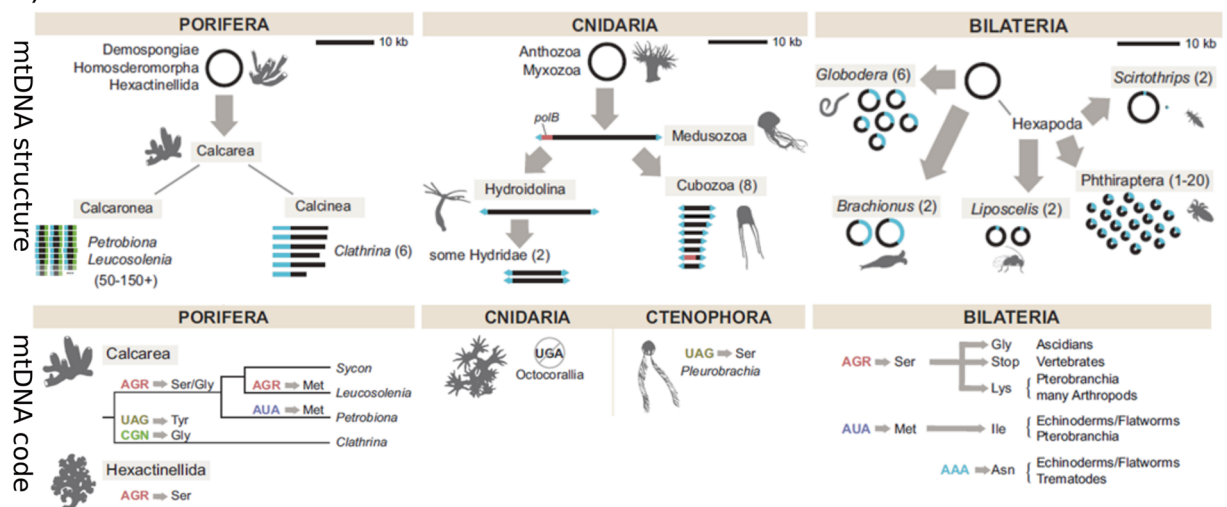
The taxonomic diversity of coral reefs makes them ideal laboratories for exploring evolutionary patterns in living organisms. Taxonomic comparisons indicate a high level of diversity in genome size, composition, and structural organization, with no apparent relationship between genome complexities and species evolutionary positions (Fig. 10.6), although similarity between genetic sequences decreases with increasing evolutionary distance (Ciccarelli et al. 2006). However, genetic characterization of several branches of the

tree of life, including major animal clades such as Porifera, Bryozoa, and Platyhelminthes, remains scarce even in barcode libraries (Mugnai et al. 2021). Such paucity of genetic information is typical of marine, compared to land, ecosystems, impeding large-scale comparisons of genetic and genomic diversity among coral reefs (Fig. 10.5). Cross-regional initiatives such as the recent Tara Pacific campaigns contribute greatly to remedy such shortcomings (Planes and Allemand 2023).

A) mtDNA organization



B) mtDNA code and structure



C) Putative control region and terminal stem-loop found in medusozoan mtDNA

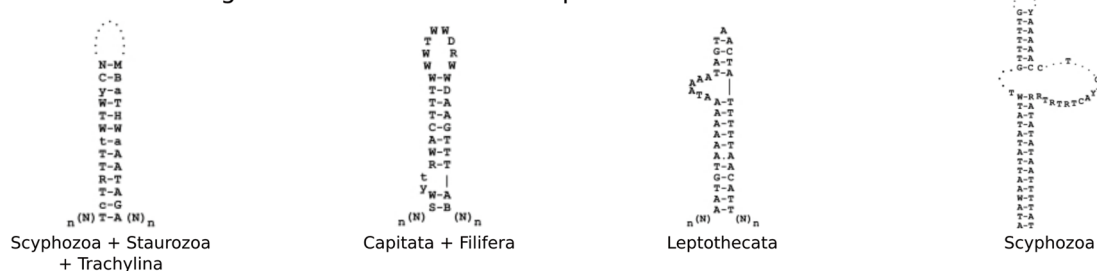


Fig. 10.7 Evolution of mitochondrial DNA (mtDNA) in reef-associated animals with zoom on Medusozoa. Differences in mtDNA result from linearization, fragmentation, gene rearrangement, and

changes in coding sequences, which affect DNA molecular structure and the level of genetic expression. (Adapted from Kayal et al. (2012a, b) and Lavrov and Pett (2016))

10.3.3 Biomolecules

Coral reefs are host to a high diversity of molecular compounds, most of which are still uncharacterized, released by their myriad of local inhabitants. MarinLit (<https://marinlit.rsc.org>) is a major database that documents the diversity of biomolecules of marine origin with medicinal and engineering potentials. Among the ~25,000 marine natural products registered in this database in 2019, a large proportion originates from reef-associated organisms, particularly sponges (33%) and cnidarians (28%) (Fig. 10.8; Carroll et al. 2019). These numbers increase rapidly, with ~1400 new marine biomolecules being described each year, a majority (888 in 2021) originating from tropical regions and sponges and cnidarians (37% in 2021; Carroll et al. 2023). This natural wealth is of particular interest to biopharmaceutical and biotech industries using the bioactive chemicals as cytotoxic, anticancer, pain relief, and antifouling products (Ghareeb et al. 2020; Gomez-Banderas 2022; Wegley Kelly et al. 2022). Research in this field benefits from the attention of active industries and international groups and is likely to uncover many more potential uses as screening of coral reef compounds for natural products continues, notably on less emblematic and cryptic organisms that remain understudied.

By investigating proteins and other small molecules present in organisms and their environments, proteomic and metabolomic approaches provide an additional layer of complexity to molecular biodiversity exploration (Jiang et al. 2021). While regulation of macroalgae is failing on many reefs due to eutrophication and declines in herbivory (Hughes et al. 2017), exploitation of macroalgae can provide a large source for biomaterials and constitute a win-win for humans and ecosystems alike in a time when the sustainable exploitation of ocean resources (i.e., blue economy) is in full expansion (Urban Jr and Ittekkot 2022). Indeed, coral reef macroalgae offer a huge and attractive potential for developing new drugs and biomaterials, an area that is expected to increase with the development of macroalgal farms, especially in French tropical overseas (Stiger-Pouvreau and Zubia 2020).

10.3.4 Cells

Variability in cell organization is a major feature of evolutionary biology, with the acquisition of cellular membranes and organelles being determinant in the development and diversification of life (López-García and Moreira 2023). The large diversity in cell structure and organization found in coral reefs reflects that of taxonomic groups from various portions of the phylogenetic tree, ranging from the most basic virus and simpler prokaryotic cells to the most com-

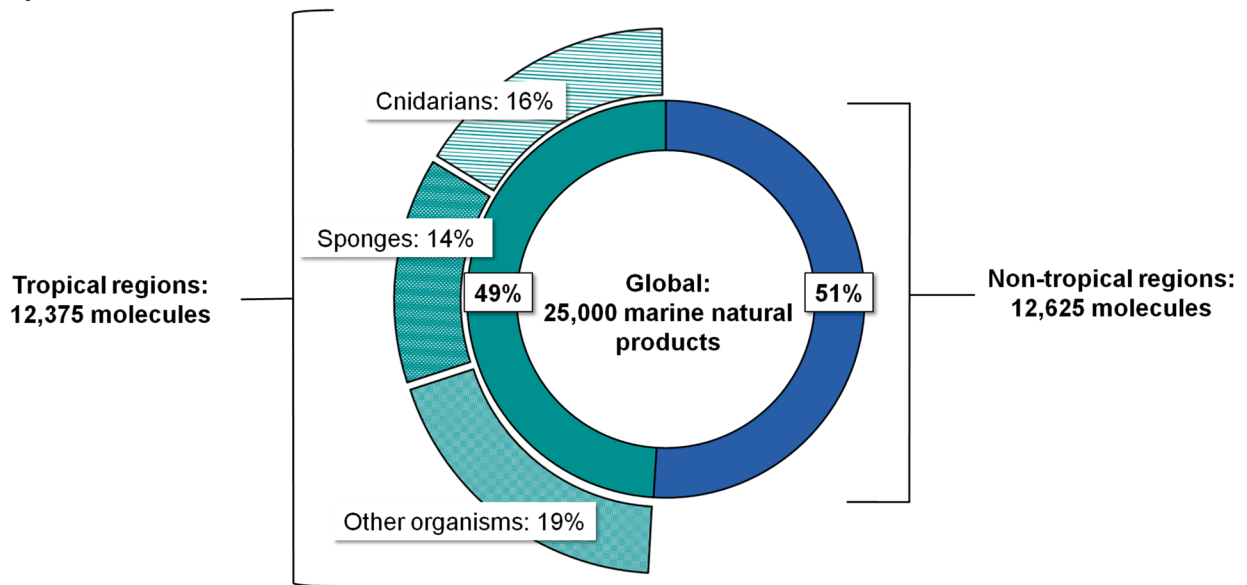
posite cells endowed with complex membranes and organelles acquired through symbiotic associations (Fig. 10.9a). The evolution of multicellularity has enabled cell specialization and the development of organs, leading to a diversification of cell features and functions within organisms (Fig. 10.9b). For instance, one species of reef-building coral harbors 40 different cell types throughout its life cycle (Levy et al. 2021). Such cell diversification confers niche extension and competitive advantage to organisms, influencing biodiversity patterns at higher levels of bioecological organization (population, community).

Cell diversity can reach its paroxysm in symbiotic (paired living beings) and holobiontic (multiple living beings functioning as a unit) organisms, such as reef-building corals finding mutual benefits between heterotrophy in animals and autotrophy in plants to colonize oligotrophic waters (Fig. 10.9b; Jiang et al. 2021). Physiological studies on coral reef species have specifically focused on key metabolic functions, such as respiration, photosynthesis, and calcification, to assess species performances under various environmental conditions, providing insights into their capacity to survive future reef conditions (Vajed Samiei et al. 2015; Hoegh-Guldberg et al. 2017; Andrello et al. 2022). Recent development in genomics, transcriptomics, and proteomics methods enables the exploration of new cell types and functions, providing further insights into the physiological functioning of cells and organisms (Konopka and Wilkins 2012; Levy et al. 2021). New approaches in meta-“omics” (e.g., metagenomics, meta-transcriptomics, meta-proteomics) applied through the lens of the holobiont concept shed light on the hidden functional and cellular diversity of complex marine ecosystems. In fact, marine holobionts are an emerging field of research that shows promising outcomes for our understanding of coral reefs and other ecosystems (Dittami et al. 2021). For instance, monitoring of marine holobionts can provide clues into environmental stressors while providing explanatory mechanisms for adaptation to changing climate (González-Pech et al. 2023). Such knowledge can in turn be used in hierarchical, multi-scale quantitative approaches to bridge the gap to higher bioecological levels such as populations, communities, and ecosystems (Edmunds et al. 2014; Smallegange et al. 2017; Condie et al. 2018; Dubois et al. 2019; Carturan et al. 2020; Morais and Bellwood 2020).

10.3.5 Organs

The diversity of organ shapes and functions was a foundation for Charles Darwin's work on species evolution (Darwin 1859). Work in this realm has paid particular attention to the diversity of key functional organs and transmission of their characters throughout evolutionary pathways, including locomotion, sensory, communication, and reproductive

A)



B)

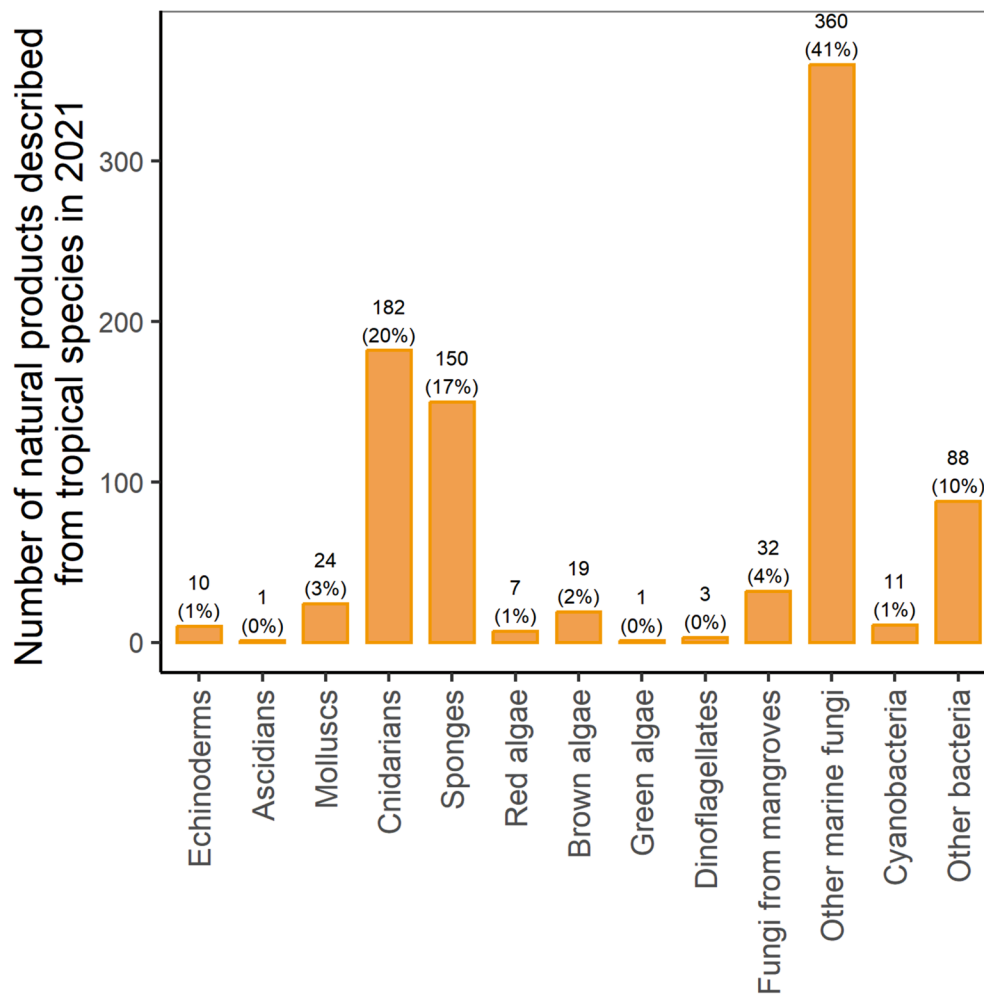


Fig. 10.8 Diversity of biomolecules associated with coral reef species. (a) Proportion of marine natural products associated with tropical reef organisms recorded in the MarinLit database in 2019 and (b) number of

natural marine products described in 2021 extracted from tropical species. (Data from Carroll et al. (2019, 2023))

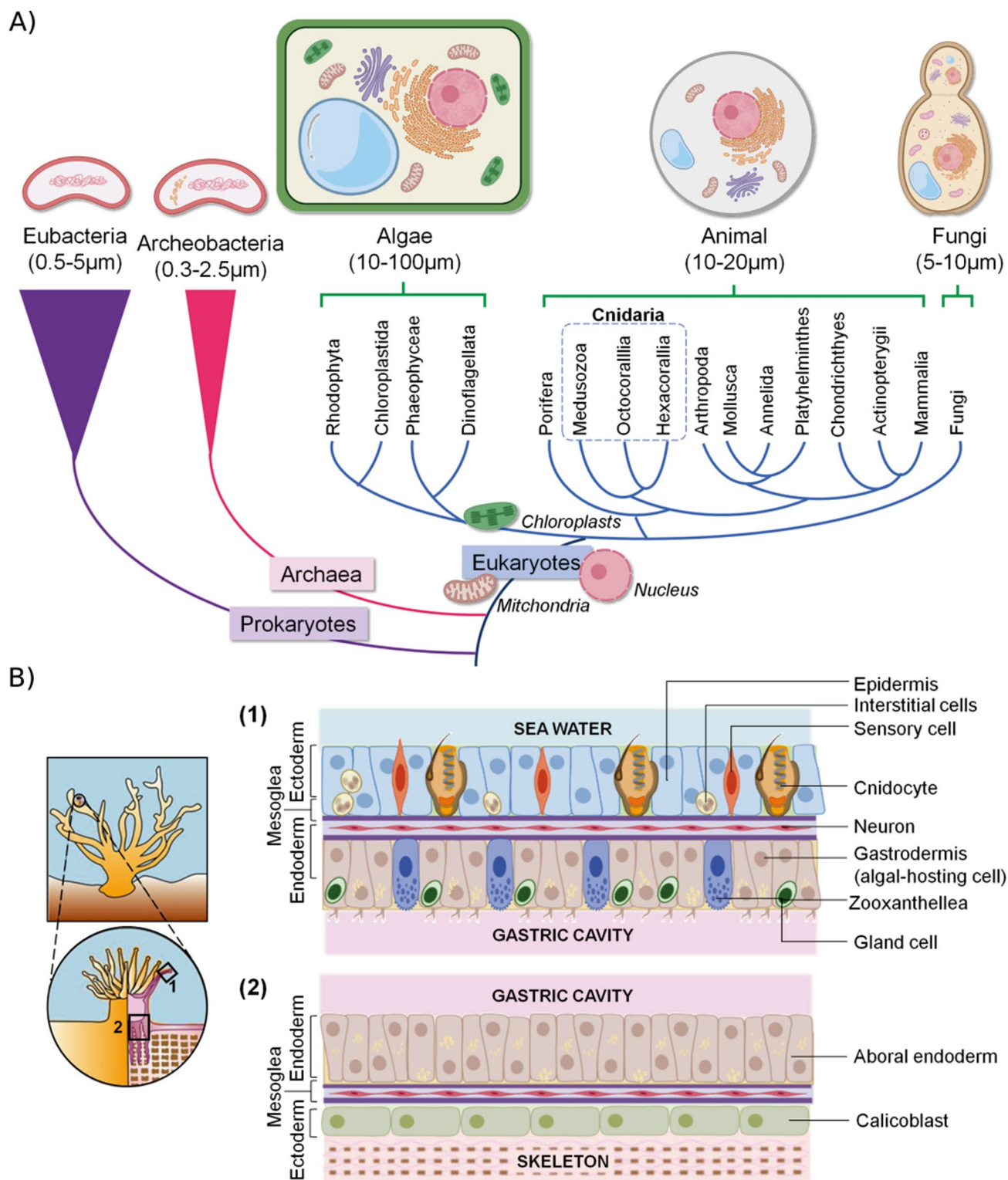


Fig. 10.9 Cell diversity across the tree of life and coral reef organisms. (a) Diversity in cell structures and organelles composition. (b) Cell specialization in reef-building corals. (Adapted from Boilard et al. 2020; Levy et al. 2021)

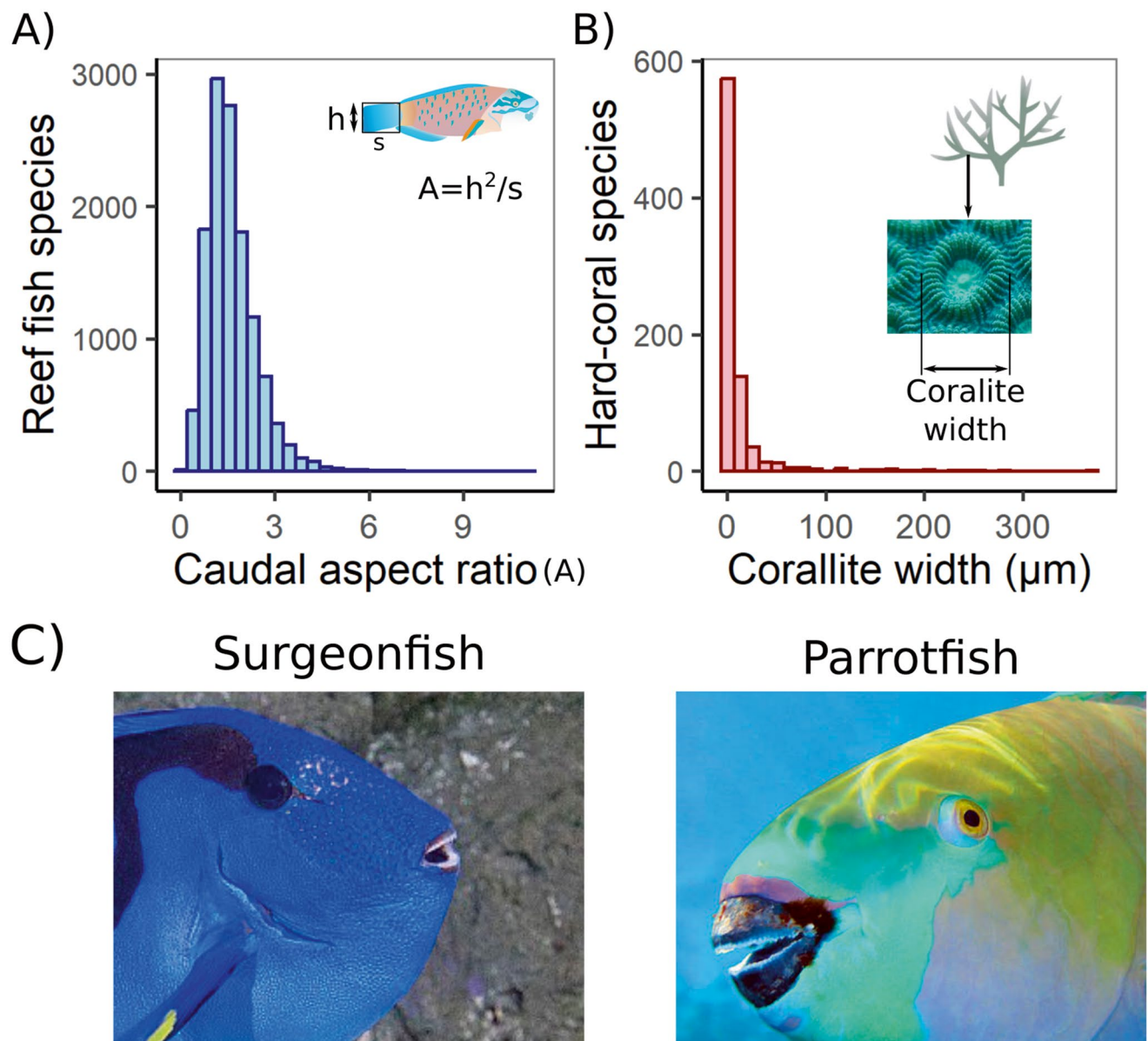


Fig. 10.10 Examples of organ diversity in coral reef species. (a) Variability in the shape of reef fish tails (caudal aspect ratio A) as an indicator of species levels of activity and swimming speeds (Pauly

1989). (b) Variability in the size of reef-building coral corallites. (c) Mouth specialization in herbivorous surgeonfish and microphage parrotfish. (Data from www.fishbase.se and McWilliam et al. (2018))

organs, although often without a specific focus on coral reef species Cernuda-Cernuda and García-Fernández 1996 Maruska 2001 Gregory 2008, Flammang 2014 Fine and Parmentier 2015 Majoris et al. 2021. More focused are studies on species biological traits, which typically rely on organism- and organ-level characteristics for species identification and ecological comparisons (Fig. 10.10). Such information is recorded in reference databases such as <https://coraltraits.org> and www.fishbase.se. While analyses of organ variabilities are scarce, the most common metrics are found for organs used for ecological investigation such as fish otoliths and scales, mineral bodies of the inner ear and surface layer

that are used for sclerochronologic estimations of organism age, and ontologic investigations of diet and life-cycle dynamics (Heather et al. 2018; Morat et al. 2020). Recent advancements in this realm show a similar use of the vertebrate eye lens to explore dietary and spatial variations throughout organisms' lifetime (Quaek-Davies et al. 2018), an area of exploration also investigated in human dental cementum (Bertrand et al. 2022). Similar investigations are performed on marine plants and invertebrates, although using a different set of organs (Duarte et al. 1994; Rypel et al. 2008; Ouréns et al. 2013). In coral reefs, special attention has been given to the diversity of organs associated with

key ecological functions for ecosystem health, such as the role of parrotfishes whose beaks specialize in particular in scraping algae with cyanobacteria, microorganisms, and invertebrate endosymbionts off substrates as compared to the mouths of surgeonfishes more adapted to grazing (Fig. 10.10c; Clements et al. 2017). Physiological and phylogenetic studies investigate the efficiency of such functions and their ecological role in coral reefs, with particular emphasis on the importance of diversity and redundancy of the functions associated with such organs for ecosystem resilience (Guillemot et al. 2011; Siqueira et al. 2019; Pimiento et al. 2020; Robinson et al. 2020).

10.3.6 Organisms

Organisms living in coral reefs vary in many aspects, including in their morphometric sizes and shapes (Fig. 10.11), and biological traits of colors and behaviors, resulting in a level of diversity and curiosity of life-forms that is unique to these ecosystems. Global databases describing these characteristics for reef-building corals and fish include <https://coral-traits.org> and www.fishbase.se.

Variability in the size of organisms relates to differences in species biological traits and also to characteristics intrinsic to individuals (e.g., age) and extrinsic features of their environments (e.g., temperature, food availability). Variability in size is often used as an ecological indicator of species health in given environments, given that body size is easier to measure than age, and is the result of a variety of past demographic processes, such as survival and growth, that are sensitive to environmental conditions, including natural disturbance and human stressors. Body size is also a good descriptor of current species performance capacities in demographic processes that determine the ecological success of populations into the future (Darling et al. 2012; Kayal et al. 2015b; Morais and Bellwood 2020), although other ecological descriptors such as age also play an important role (Rapuano et al. 2023). Typically, the largest individuals are found in the most suitable and less disturbed environments, reflecting species optimal environmental niches and success in ecosystem management (McCook et al. 2010; Cinner et al. 2018; Dietzel et al. 2020).

Body shape is often used for species identification and taxonomic studies on species diversification (Veron 2000; Ramírez-Portilla et al. 2022; Tea et al. 2022), sometimes in relation to species performances in key ecological processes such as fish swimming capacity or wave resistance and light absorption in corals, and the associated energetics (Fig. 10.11a, b; Walker et al. 2013; Madin et al. 2014; Rossi et al. 2018; Cresswell et al. 2020; Kramer et al. 2022; Carlot et al. 2023). A large body of work is particularly dedicated to relating the weight of individual organisms to their body

length for estimations of population biomass, species stock assessments, and ecosystem productivity (Wolfe et al. 2020; Pacey et al. 2023; Tekwa et al. 2023). Using a large sample size of 53,800 specimens from 788 reef species from New Caledonia, Kulbicki et al. (2005) estimated variability in reef fish length-weight relationships to be 9.4% at the species level, 11.4% at the genus level, 13.5% at the family level, and 13.2% within morphological groups (Fig. 10.12b). Based on their analysis of reef fish morphologies, the authors concluded that diversity in fish shapes is constrained by physical limits. There are a dozen major morphological groups in corals and 30 of reef fishes (Fig. 10.11; Veron 2000; Kulbicki et al. 2005). Another major research path focuses on species ecological functions, notably for habitat-forming organisms like corals whose morphologies determine the abundance and diversity of species hosted in their interstices (Darling et al. 2017; Richardson et al. 2017b; Aston et al. 2022).

Diversity in colors is one of the most striking and unique features of (healthy) coral reefs, investigated predominantly in studies on ecosystem health and aesthetics values (Haas et al. 2015; Langlois et al. 2022). Other studies explore the evolutionary and molecular determinants leading to the diversity of colors found on coral reefs, sometimes in relation to jewelry industries, and how some species use colors for communication and camouflage (Marshall 2000; Lemer et al. 2015; Tea et al. 2022). Sometimes, striking colors are indicative of stress, as observed during coral bleaching events (Bollati et al. 2020). However, the mechanisms behind, and consequences of, diversity in colors remain largely to be explored (Hemingson et al. 2019; Hodge et al. 2020).

Relatively little knowledge is available about the behaviors of individual organisms, how they adapt to local environments, and change with human influences. Most studies focus on species of interest for their ecological or societal role. A relatively large portion of studies on marine organism behavior focus on large and charismatic animals which are easier to track and are often a center of touristic attraction and, in particular sharks which can also cause human casualties (Juhel et al. 2019; Taglioni et al. 2019; Lassaue et al. 2020; Maillaud et al. 2022; Riley et al. 2022; Séguigne et al. 2023). The studies also explore habitat use, feeding and mating behaviors, and social interactions of the organisms (Papastamatiou et al. 2006; Mourier et al. 2012; Mourier et al. 2013; Mourier et al. 2016; Guillaume and S  ret 2021; Lassaue et al. 2022; Lassaue et al. 2023), as well as behavioral sensitivity to human stressors (Holles et al. 2013; Gil et al. 2020; Clark et al. 2020; Udyawer et al. 2021). Another center of interest has been the coral predatory seastar, crown-of-thorns starfish (*Acanthaster* spp.), whose population outbreaks are major causes of coral mortality throughout the Indo-Pacific (Pratchett et al. 2014). The studies have particularly focused on movement and feeding behaviors of the sea-

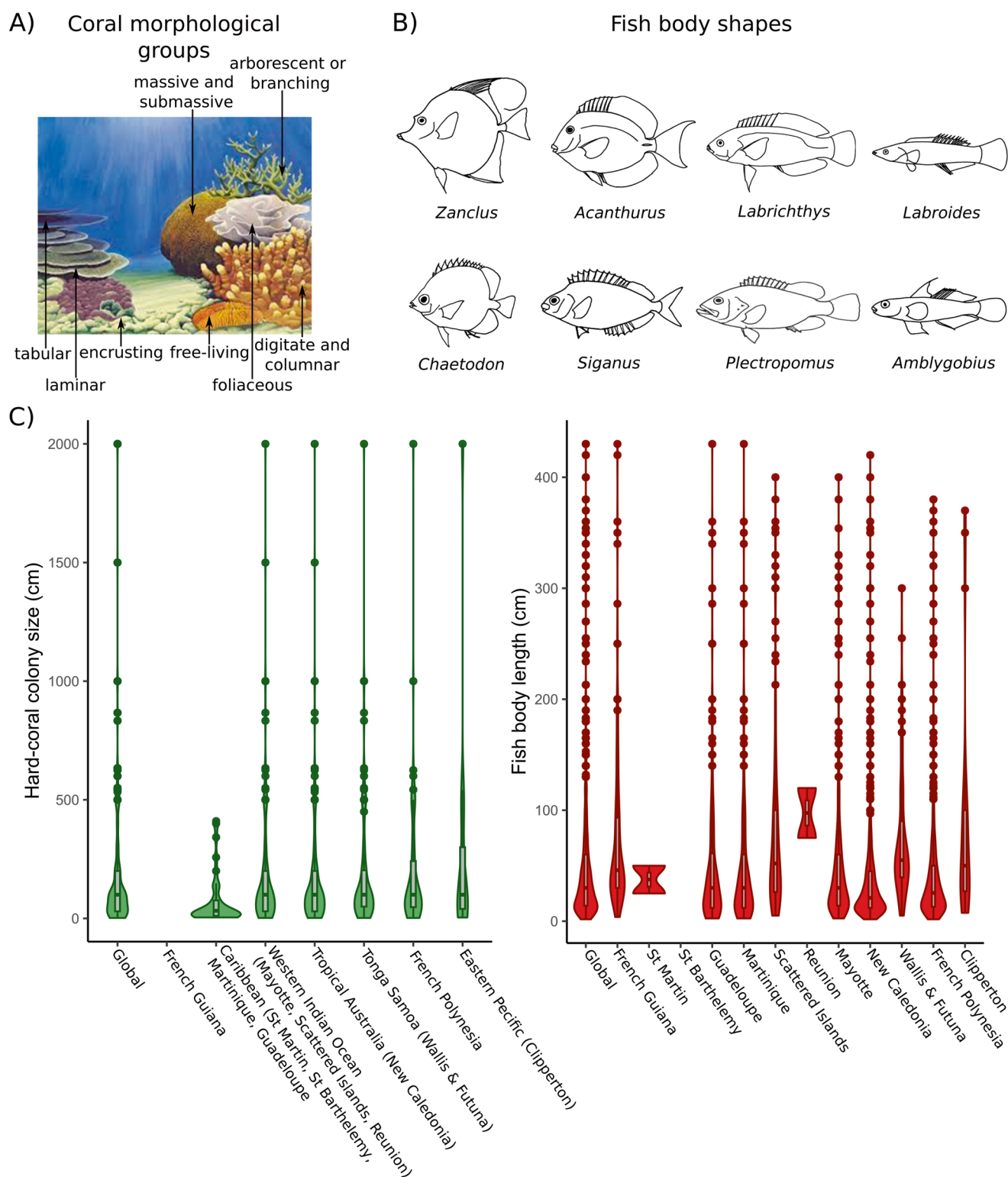


Fig. 10.11 Variability in coral and fish shapes and sizes. Major morphological groups in corals (a, adapted from Veron (2000) and fish (b, adapted from Walker et al. (2013)). Examples of size distribution (whiskers plots presenting median, first and third quartiles, and outliers; vio-

lin plots presenting data densities) in corals and fish among French tropical overseas (c, data extracted from McWilliam et al. (2018) for corals and from www.fishbase.se for fish)

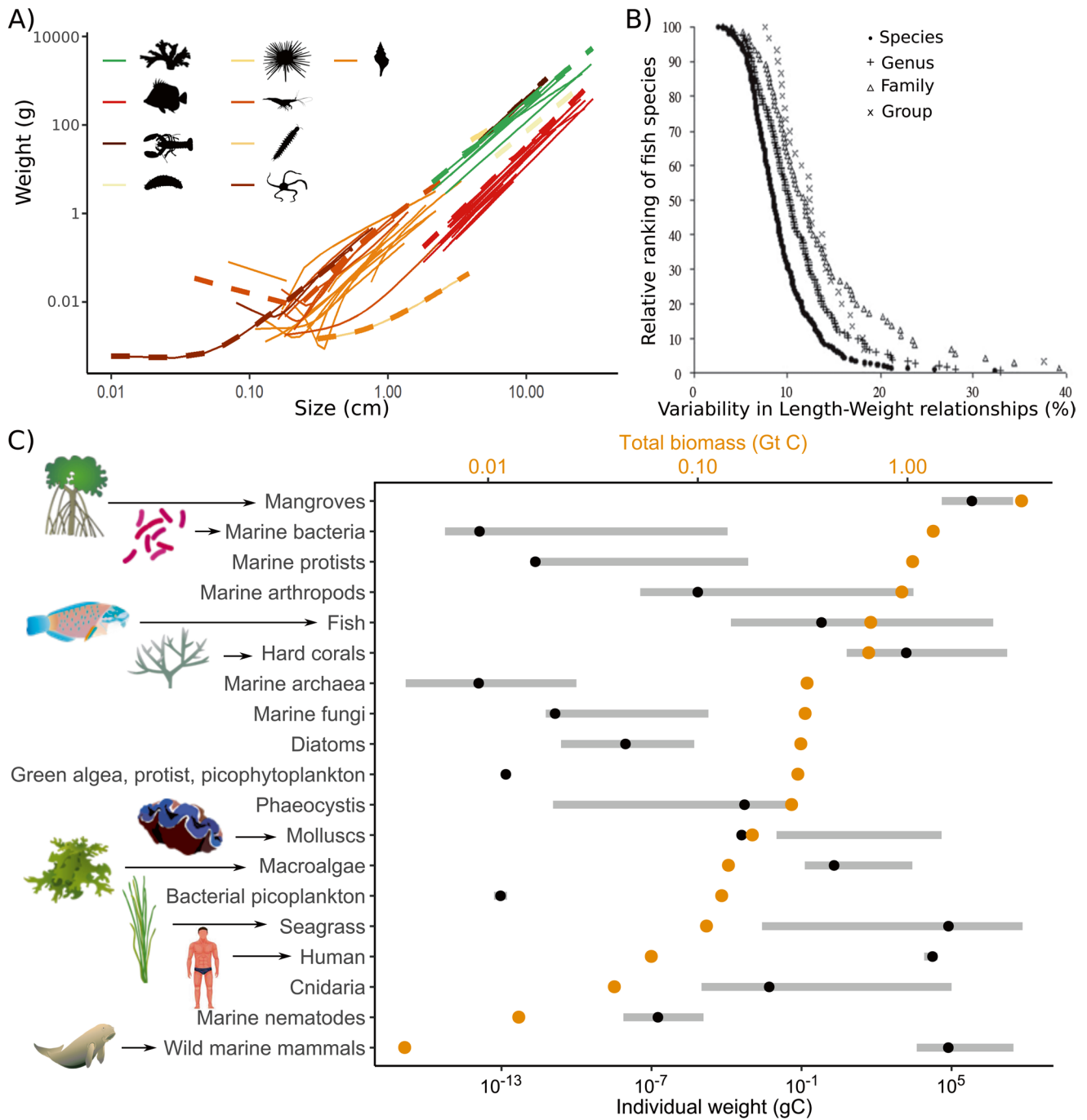


Fig. 10.12 Length-weight relationships (a) of various coral reef organisms by species (solid lines) and species groups (dashed lines), variability in length-weight relationships among species, genera, families, and morphological groups of coral reef fish in New Caledonia (b, adapted from Kulbicki et al. 2005), and individual body weight (range and median) and global biomass of various marine species as compared to humans (c). Length-weight relationship data in (A) from Akiona

et al. (2022) for fish, Pacey et al. (2023) for corals; Wolfe et al. (2020) for Annelida, Mollusca, Arthropoda, and Echinodermata; Lee et al. (2018) for Holothuria; Rahman et al. (2012) for urchins; Aisyah and Triharyuni (2017) for lobsters. Individual body weight and global biomass data in (c) from West et al. (2009), Bar-On et al. (2018), Tekwa et al. (2023)

star as key drivers of coral decline De'ath and Moran 1998; Pratchett 2001; Kayal et al. 2011, 2012b, 2017a, b; Petie et al. 2016; Pratchett et al. 2020) and the identification of its natural predators, which can help mitigate the outbreaks (Bos et al. 2008; Cowan et al. 2017; Kayal and Lenihan 2025), recently with the help of DNA technology (Kroon et al. 2020). Other studies investigated predator-prey, competitive, and mutualistic behavior in different reef organisms (Pratchett 2005; Mills and Côté 2010; Leray et al. 2013; Kayal et al. 2017a; Kayal and Adjeroud 2022). Facing widespread coral reef decline, a large body of work on species behaviors is dedicated to finding solutions for mitigating ecosystem vulnerability to disturbance or boosting recovery through active restoration (Kayal et al. 2011; McKeon and Moore 2014; Kayal and Kayal 2017; Gordon et al. 2019). Sometimes, original studies emerge from unplanned, opportunistic observations of species unusual behaviors, such as bleached corals compensating energy loss by feeding on neighboring macroalgae, and more recently on internal symbiotic microalgae, potentially leading to new investigation channels (Marhaver 2011; Wiedenmann et al. 2023). While the level of plasticity of species behaviors in the face of environmental changes remains largely unquantified, the development and democratization of imagery tools such as underwater cameras and drones have greatly increased research capacity in this realm by enabling increased observations of organisms in their natural environments (Cleguer et al. 2021; Heudier et al. 2023). Further developments in artificial intelligence enable more effective analysis of ecosystem imagery and acoustic recordings for characterizing species attributes and behaviors under various natural and human conditions (González-Rivero et al. 2020; Jamil et al. 2021; Ditria et al. 2022; Ouassine et al. 2024).

10.3.7 Populations

Population abundance estimates are commonly used for stock assessments and evaluations of ecosystem health. Common metrics include population size and distribution range, density, biomass, percent-cover, and size-structure (Fig. 10.13; Adjeroud et al. 2018a, b; Dietzel et al. 2020, 2021; Pacey et al. 2023; Tekwa et al. 2023). In coral reefs as in other ecosystems, many species are often observed at population abundances and size-structures that are near their lower bound (Figs. 10.11c and 10.13), while knowledge on ultimate demographic states achievable by populations and the maximum carrying capacity of ecosystems remains limited (Levin 2000). Nevertheless, comparisons between healthy and altered ecosystem states provide insights on near optimal population abundance, distribution, and size-structure, and the degree of reduction imposed by various stressors (McCook et al. 2010; Cinner et al. 2018; Darling

et al. 2019; Morais et al. 2021). Amidst rapid environmental change, key research questions focus on population resilience and the capacity of species to maintain their abundance through the demographic processes of survival, growth, reproduction, and migration (Darling et al. 2012; Mumby et al. 2014; Kayal et al. 2015b; Morais and Bellwood 2020). Global databases with information on these processes include <https://coraltraits.org> and www.fishbase.se. Demographic investigations use empirical measurements of species performances in these processes (Fig. 10.14) to evaluate the diversity of life-history strategies and identify, through quantitative models, the mechanisms leading to population bottlenecks and species ecological success and coexistence in various environments (Madin et al. 2014; Bozec et al. 2016; Kayal et al. 2018; Riegl et al. 2018; Darling et al. 2019; Carturan et al. 2020). While such investigations depend on fine-scale empirical data on species dynamics, data hitherto limited to few highly studied coral reef sites, current developments in imagery approaches are opening paths to their democratization (González-Rivero et al. 2020; Collin et al. 2021; Jamil et al. 2021; Heudier et al. 2023; Kayal et al. 2023). Increased data availability along with amplified computer power has opened paths to pluridisciplinary quantitative investigations for a better understanding of ecosystem processes across biological, ecological, and biogeoclimatic scales (Jones et al. 2015; Condie et al. 2021; Van Woesik et al. 2022; Carlot et al. 2023; Donovan et al. 2023).

As an alternative to comprehensive approaches designed to integrating a multitude of ecological processes driving species dynamics, other investigation routes focus on single indicator processes serving as ecological metrics of species performance and resiliency such as recruitment rates, competitive wars, or recovery capacities (Done et al. 2010; Penin et al. 2010; Osborne et al. 2017; Vercelloni et al. 2019; Kayal and Adjeroud 2022). In particular, coral recruitment is a commonly used, integrated indicator of coral reef resilience capacity, as reflecting both adult coral abundance and reproductive success, and larval dispersal, settlement, and metamorphosis into reef habitats (Adjéroud et al. 2017). It is monitored in different regions using a standardized method quantifying annual settlement rates of coral larvae on artificial substrates (Mundy 2000). Regional comparisons of coral recruitment rates indicate differences in magnitude, taxonomic composition, and seasonality, with maxima observed at mid-latitudinal range in the southwest Pacific, central Great Barrier Reef and southern New Caledonia, where coral communities are dominated by spawning acroporids, with a shift to brooding pocilloporids and spawning poritids in other places (Fig. 10.14e; Hughes et al. 2002a, b; Adjeroud et al. 2017). Quantitative understanding of the coral recruitment process is still nascent but increasing, thanks to dedicated scientific attention (Hughes et al. 2000; Kayal et al.

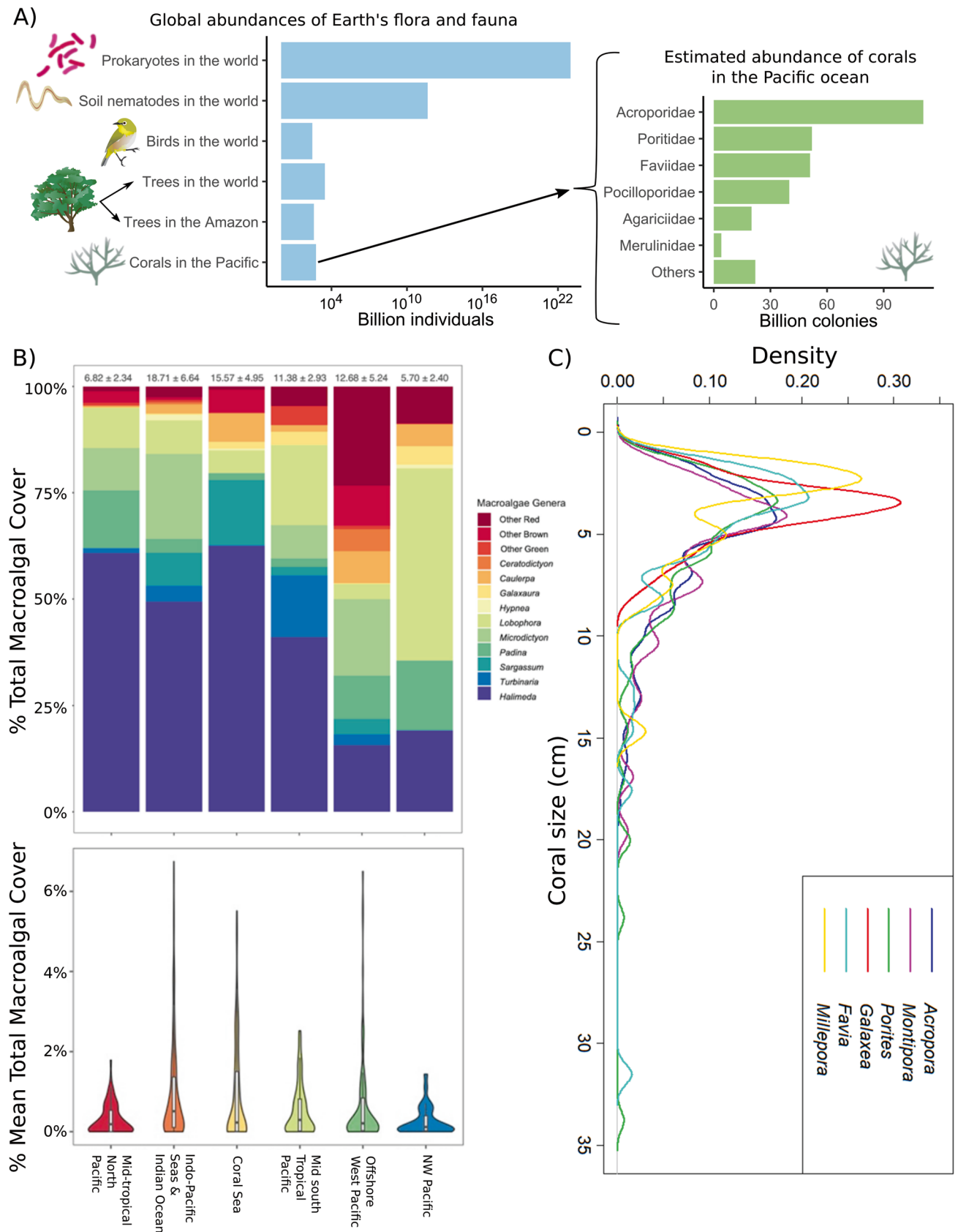


Fig. 10.13 Examples of population state metrics for key coral reef species. Estimated abundance of Pacific reef-building corals as compared to other widespread species (a, data from Dietzel et al. 2021).

Macroalgae cover in the Indo-Pacific (b, adapted from Cannon et al. 2023). Coral size distribution (c, adapted from Kayal et al. 2023)

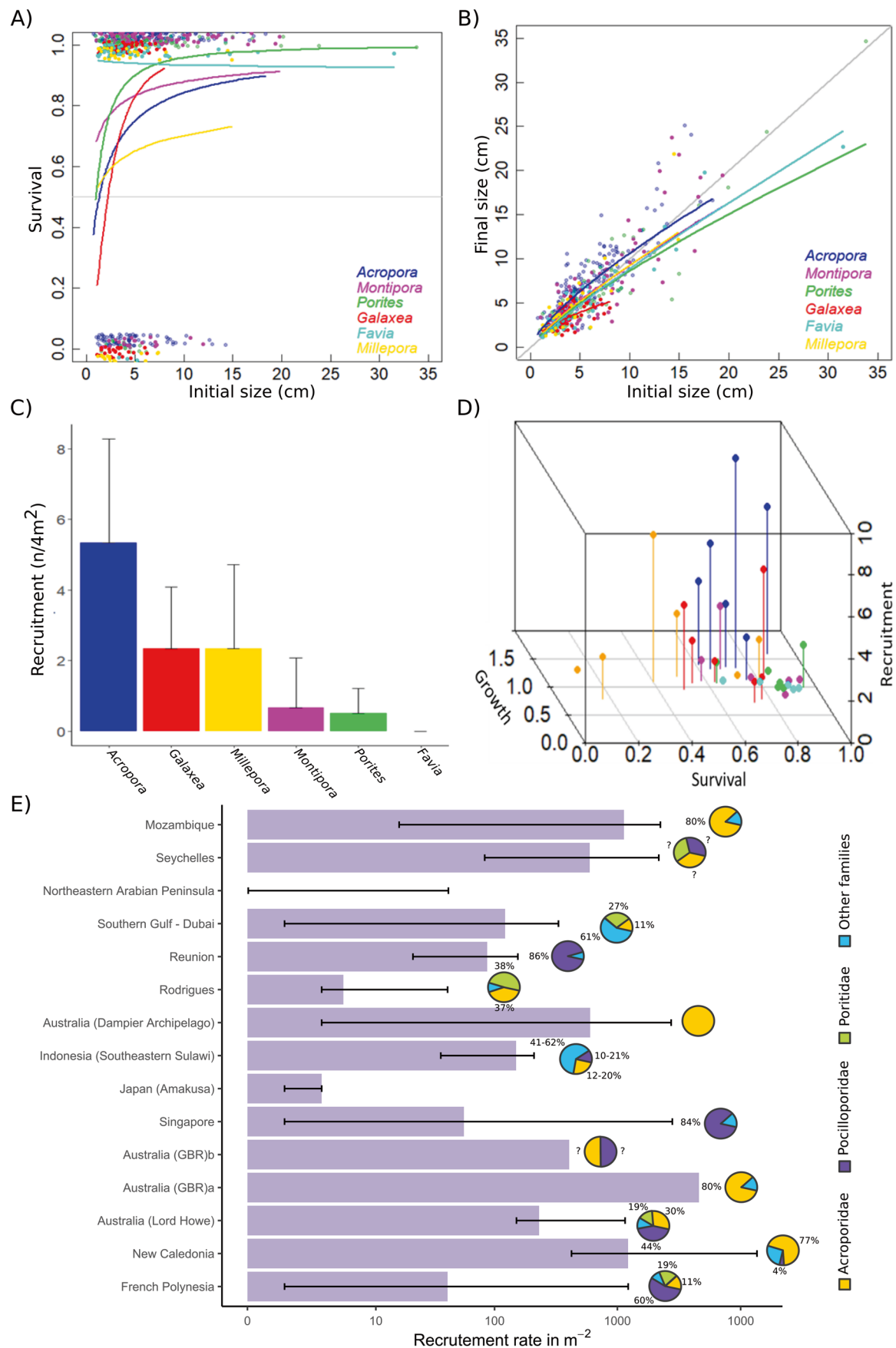


Fig. 10.14 Empirical metrics of coral demographic rates in annual survival (a), growth (b), and recruitment (c), with a visualization of the three processes combined (d, adapted from Kayal et al. 2023), and coral

settlement rates on artificial substrates in different regions (e, data from Adjeroud et al. (2022))

2015b; Bramanti and Edmunds 2016; Doropoulos et al. 2016; Leinbach et al. 2021; Doropoulos et al. 2022). The rise of genetic tools and oceanographic modeling of currents enable estimations of population connectivity in various coral reef species, which exhibit various larval durations and dispersal capabilities (Fig. 10.15; Lester and Ruttenberg 2005; Shanks 2009; Cuif et al. 2014; Cravatte et al. 2015; Edmunds et al. 2016; Hock et al. 2017; Dubé et al. 2020; Lesturgie et al. 2023). Overall, a variety of approaches are deployed to investigate the importance of larval recruitment in the replenishment of coral reef species populations and ecosystem functioning, with direct benefits to biodiversity management and spatial conservation planning (Kayal et al. 2018; Riegl et al. 2018; Brandl et al. 2019b; Manel et al. 2019).

10.3.8 Communities

The number of different species composing a biological community is the most historical and common metric of biodiversity (historically “biological diversity”; Harris 1916). Studies at this scale of observation can be distinguished into two major groups, those focused on taxonomic diversity with the end goal of characterizing community composition and those with an ecological endeavor evaluating changes in community composition and their consequences for ecosystems.

Coral reefs are estimated to host over 2 billion species, including ~830,000 (confidence interval 550,000–1,300,000) multicellular taxa, that is, ~38% of all described marine species (Fig. 10.16; Fisher et al. 2015). Taxonomic work is active in describing new species. Yet large uncertainties surround existing taxonomic delineations in many groups including corals, and species classifications evolve rapidly, particularly through the use of genomics, and many species names are expected to change over time (e.g., Benzoni et al. 2010; Huang et al. 2014a, b; Nakajima et al. 2017; Tea et al. 2022). Up-to-date taxonomic reference databases, such as TAXREF from the Inventaire National du Patrimoine Naturel (INPN, <https://inpn.mnhn.fr>, Gargominy et al. 2022) and the World Register of Marine Species (WoRMS, www.marine-species.org) are essential for ensuring coherence in species designations. Current descriptions distinguish 1681 species of hard corals including 995 associated with coral reefs, 19,772 fish, 55,238 crustaceans, 50,877 mollusks, and 3760 hydrozoans (see Fig. 10.16a, b for all groups). Overall, species descriptions and therefore biodiversity estimates are more complete for large species in shallow habitats such as megafauna which are easier to observe and tend to decrease for smaller and more cryptic habitats and species, including sponges, although genetic meta-barcoding and bioacoustic approaches increasingly enable detection (Elise et al. 2019;

Nichols et al. 2022; Wolfe et al. 2023; Galand et al. 2023). Biogeographic studies on species distributions assess spatial variations in species diversity and the mechanisms behind speciation and extinctions (Cowman and Bellwood 2013; Clements et al. 2017; Tea et al. 2022; Cantalice et al. 2022). Regional comparisons identify a pronounced gradient in species diversity with the spatial extent of coral reef systems (Bellwood et al. 2005) as well as their geographic distance to the center of marine biodiversity situated in Southeast Asia (Hughes et al. 2002a; Dietzel et al. 2021; Lutzenkirchen et al. 2023) and to the equator (Jones et al. 2019), features that are reflected across French overseas (Figs. 10.17, 10.18 and 10.19). These patterns concord with our general understanding that the level of biodiversity of a system is a function of the extent and diversity of ecological niches available, which relates to spatial as well as temporal heterogeneity (e.g., increased seasonality at higher latitudes promoting species coexistence through competitive reversals; Logan 1984; Kayal and Adjeroud 2022), and the variety of organisms able to occupy these niches. Nevertheless, current estimates of species richness should be considered with caution for certain species groups, since estimation methods and sampling efforts may differ among regions and result in potential bias (e.g., differences in coral diversity estimates in Fig. 10.16c). For instance, both molecular and morphological approaches are used to assess species diversity, which often results in contrasting outcomes, and a recent extrapolation-based study accounting for sampling effort suggests that coral diversity may in fact be higher in the western Indian ocean than in the coral triangle (Kusumoto et al. 2020). Overall, how species richness and other biodiversity metrics vary with spatial scales or other units of sampling effort remains poorly understood (Nash et al. 2014; Chase et al. 2018; Donovan et al. 2023).

A large body of work exists on using the dynamics of key communities of ecological or social importance, such as corals and fish, to assess coral reef ecosystem health and associated management strategies (Lamy et al. 2016; Kayal et al. 2018; Adjeroud et al. 2018a; Vercelloni et al. 2019; Carturan et al. 2020; Graham et al. 2020). Some studies investigate more specifically the ecological functions associated with different communities, such as primary production, herbivory, nutrient transport and recycling, and habitat formation or alteration (Brandl et al. 2019a; Pimiento et al. 2020), and the ecological processes through which changes in one community spread to other ecosystem components (Leray et al. 2012; Kayal et al. 2012b; Condie et al. 2018; Dubois et al. 2019). Nevertheless, the complexity of biotic interactions, including predator-prey, competition versus mutualism, symbiosis versus parasitism, and how they are modulated by environmental conditions remains largely unexplored, particularly in biodiverse and ecologically oscillating ecosystems such as coral reefs (Connell 1978; Schmitt et al.

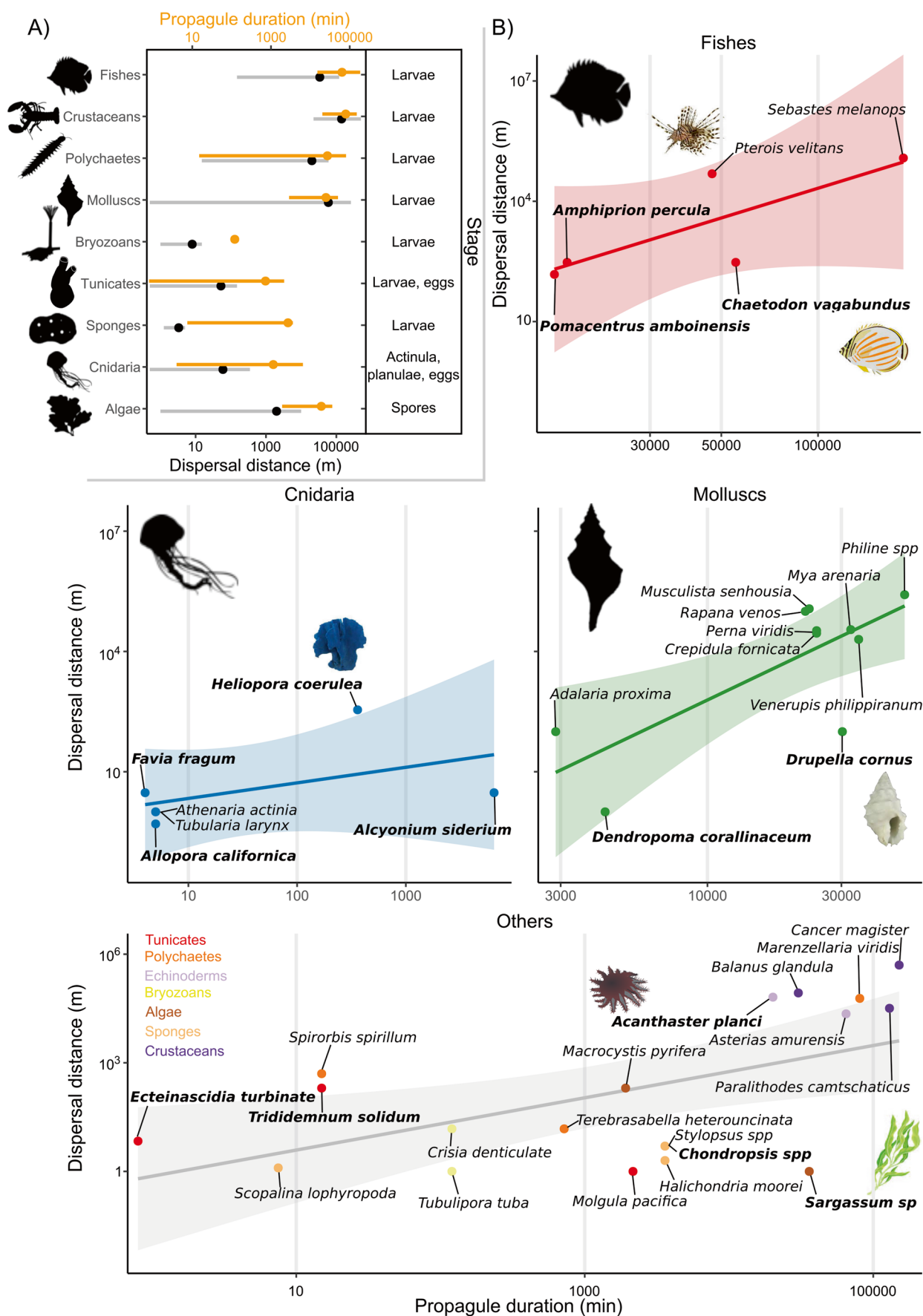
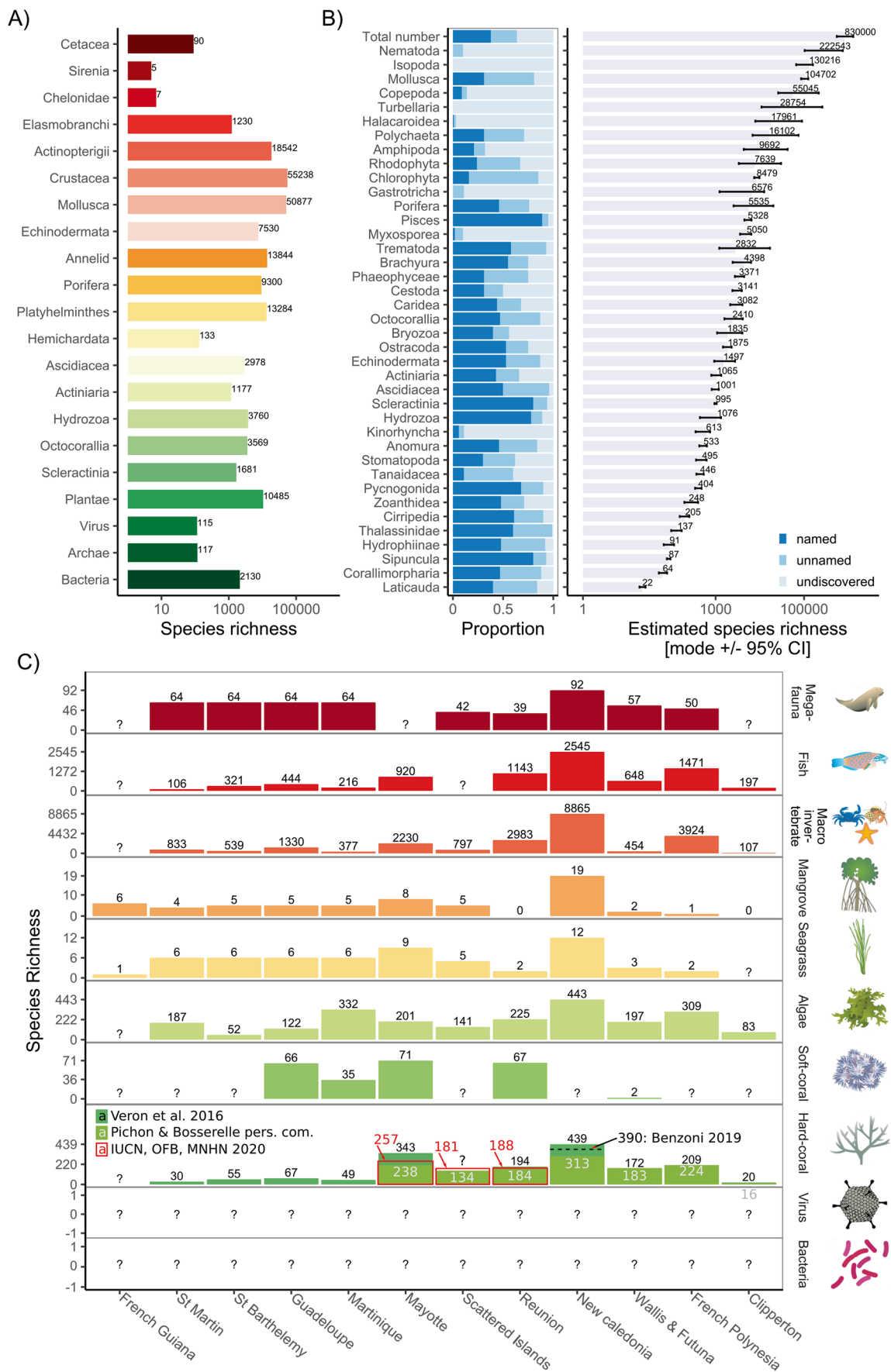


Fig. 10.15 Dispersal capabilities of various marine organisms with characterized propagule duration and dispersal range (not restricted to coral reef species, data from Shanks 2009). (a) Dispersal stage, dis-

tance, and duration (mean $\pm$ range) for different taxonomic groups and (b) relationships between propagule dispersal and duration. Coral reef species are identified in bold



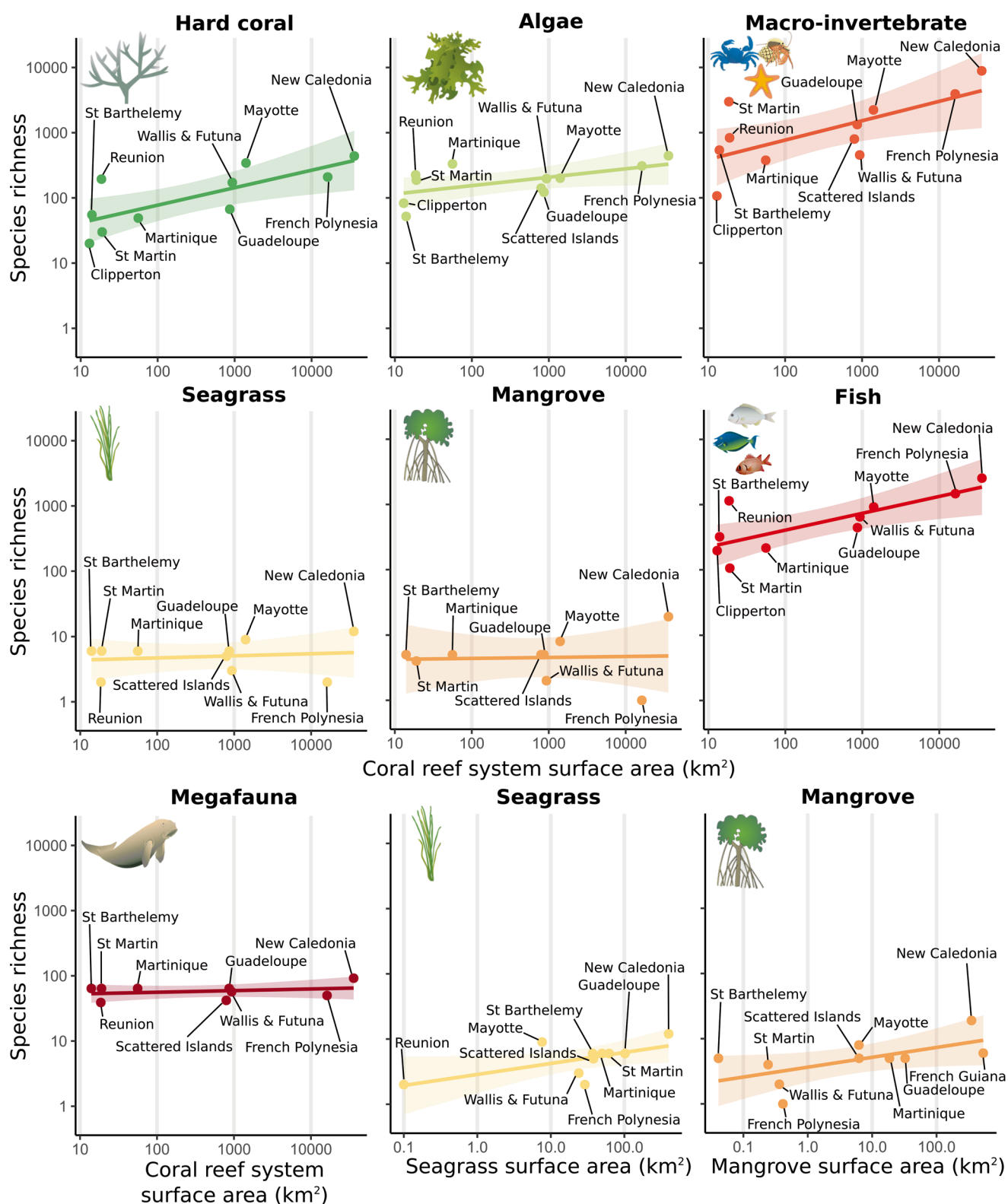


Fig. 10.17 Species diversity of major coral reef ecological communities as a function of ecosystem surface area (coral reef system surface area includes constructed hard-substrate reef and associated lagoonal habitats, c.f. Spalding et al. 2001)

Fig. 10.16 (continued) of coral reef-associated multicellular communities. (Adapted from Fisher et al. 2015). (c) Species richness for key coral reef communities in French overseas. For reef-building corals, estimates from different sources are provided. Data from Pichon and Bosserelle (pers. com.), Benzoni (2019) and IUCN comité français et al. (2020) result from a more in-depth analysis of sample specimens from the area. Megafauna comprises large marine species groups: sea turtles, dugongs, dolphins, whales, sharks and rays, and sea snakes

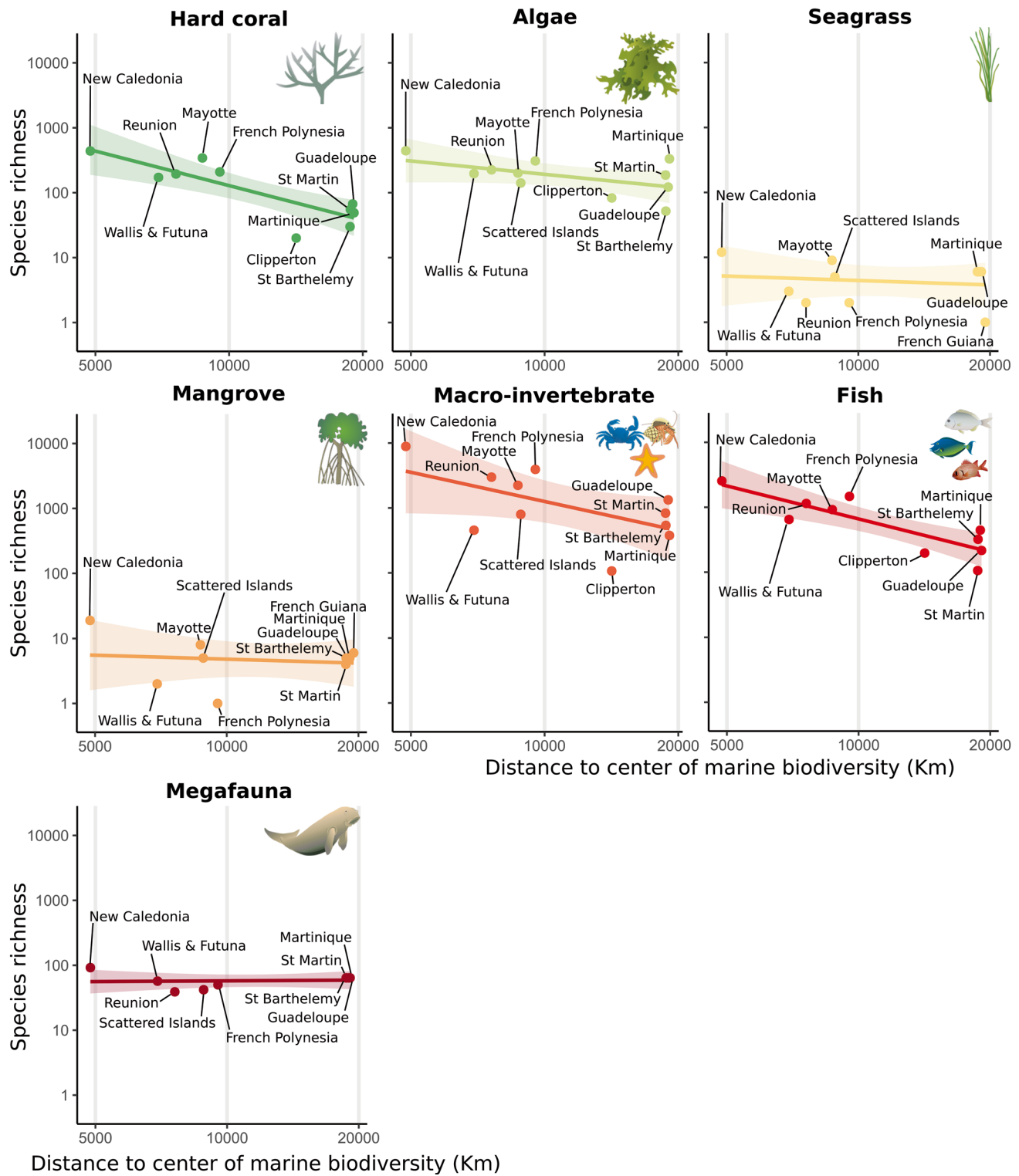


Fig. 10.18 Species richness of major coral reef ecological communities as a function of distance to the center of marine biodiversity (reference point set as western Banda Sea, latitude -5.461885 , longitude 122.936220)

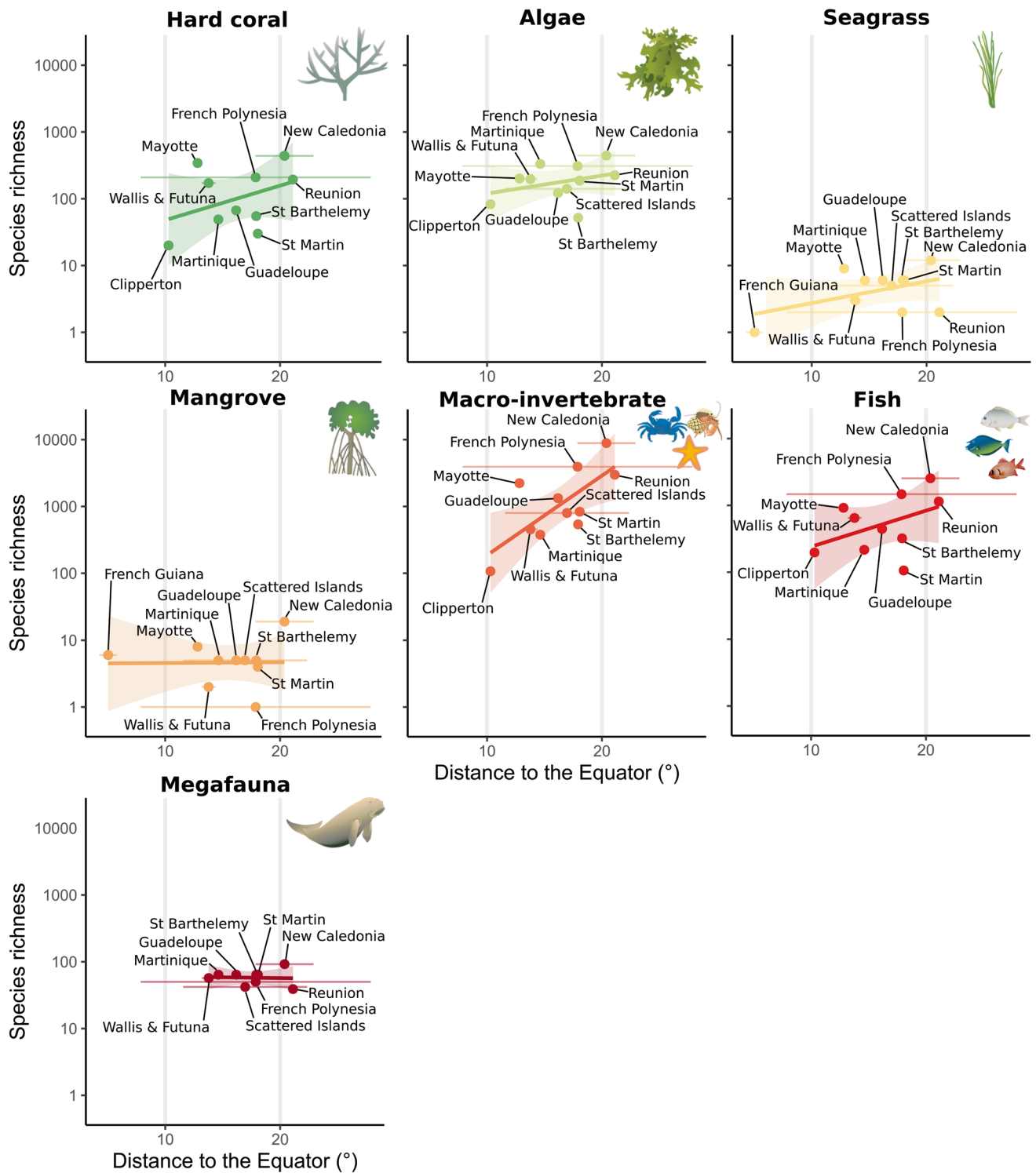


Fig. 10.19 Species richness of major coral reef ecological communities as a function of distance to the Equator (absolute average latitude $\pm$ range, in degree)

2009; Mills and Côté 2010; Kayal et al. 2011; McKeon and Moore 2014; Kayal et al. 2017a; Kayal and Adjerdoud 2022). It is only recently that fine-scale ecosystem time-series data have enabled empirical investigations on major ecological processes driving ecosystem resilience (Mumby et al. 2007; Riegl et al. 2018; Cresswell et al. 2023). To strengthen coral reef conservation actions, more knowledge is needed on the ecological processes driving community dynamics, including on the less emblematic and cryptic communities such as microorganisms, algae, and sponges that are understudied (de Goeij et al. 2013; Brandl et al. 2019b; Cannon et al. 2023; Galand et al. 2023).

10.3.9 Ecosystems

Coral reef ecosystems around the world differ in size, composition, health, and dynamics, resulting in a myriad of ecosystem states with unique ecological features. However, some key ecosystem characteristics enable differentiating coral reef systems into broad functional categories along ecological gradients. At a broad consideration, the size and degree of isolation have strong consequences on the structure and fate of coral reef ecosystems. On one side of the spectrum, large continuous systems in the southwestern Pacific, such as the Australian Great Barrier Reef with 348,700 km² of reef habitats and New Caledonia's reef system with 35,873 km² contrast with small and isolated systems on the other side of the spectrum, such as the atoll of Clipperton with its 13 km² of reefs located approximately 950 km from the closest coral reef system (Romero-Torres et al. 2018; Figs. 10.4 and 10.20). Within this spectrum, many systems of various sizes are found with differing degrees of geographic fragmentation and ecological isolation, sometimes due to the presence of natural barriers to dispersal (Raitos et al. 2017; Hock et al. 2017; Romero-Torres et al. 2018). For example, the 19 km² of coral reefs surrounding the single island of Reunion in the Indian Ocean are situated roughly 200 km from the closest reef system of Mauritius and 700 km from Madagascar, whereas the 16,200 km² of reefs in French Polynesia are scattered among 5 archipelagos, 118 islands, and atolls (1576 land units including islets, Fig. 10.20b) across 2,500,000 km² of ocean in the Central South Pacific. These broad geomorphological characteristics of reef systems are relatively well-known for shallow habitats in clear waters, thanks in big part to satellite imagery, but knowledge decreases rapidly with water depth and turbidity as evidenced by the Great Amazon Reef that was only recently discovered under the Amazonian river plume and extends ~1000 km, including into French Guiana's coastal waters (Moura et al. 2016; Francini-Filho et al. 2018). The size and degree of isolation of the reefs determine the level of chemical and biological connectivity between ecosystems

and therefore the productivity, regeneration capacity, and resilience of the diverse species populations they host (Edmunds et al. 2016; Gounand et al. 2018). In the face of disturbances, small and isolated coral reef systems are therefore generally more vulnerable to full-system collapse and exhibit limited recovery capacities, while for larger interconnected coral reef systems, disturbance impacts are often restricted to small portions, resulting in higher rates of demographic replenishment from adjacent unaffected populations (Wolff et al. 2016; Riegl et al. 2018; Vercelloni et al. 2019; Adjerdoud et al. 2022). Larger reef systems also host higher proportions of biodiversity, thanks to a wider geographical expansion and the amount and diversity of ecological habitats and niches available (Eddy et al. 2021), as illustrated with New Caledonia's large ecosystem surface areas and associated biodiversity metrics (Fig. 10.17). Meta-ecosystem approaches characterizing chemical and demographic flow between ecosystems are still nascent, and their development should deepen our understanding of ecological drivers of ecosystem productivity and resilience (Gounand et al. 2018; Condie et al. 2021).

Ecosystem productivity and trophic organization are other key attributes characterizing different states in coral reef ecosystems. However, comprehensive ecosystem-level evaluations remain scarce, as most ecological investigations are conducted at the population or community scale, seldom integrating the various communities constituting coral reef ecosystems (Fig. 10.2; Rogers et al. 2015; Condie et al. 2018; Dubois et al. 2019). Nevertheless, simplified evaluations based on the representation of a limited number of ecological components or functions capture key species interactions such as habitat provision, predation, and competition, therefore characterizing major ecosystem dynamics (Kayal et al. 2012b; Mourier et al. 2016; Brandl et al. 2019a; Pimiento et al. 2020; Adam et al. 2021; Wolfe et al. 2023). Overall, the studies indicate that the magnitude of ecosystem biomass and its distribution among different ecological compartments vary in space and time as a function of the carrying capacity of the systems, the length and complexity of the food webs, the species richness of the different communities, and their dynamics in relation to the natural and human environments (Trebilco et al. 2013; Jacquet et al. 2020; Nagelkerken et al. 2020; Mehner et al. 2022). As such, healthy coral reef ecosystems situated in protected areas near the center of marine biodiversity tend to be characterized by more developed food webs and higher overall productivity, thanks to a more effective exploitation of ecological niches (McCook et al. 2010; Mellin et al. 2016; Morais et al. 2021; Heudier et al. 2023). In contrast, disturbed, degraded, and less diverse coral reefs tend to show shorter food webs and lower ecosystem productivity due to a limited exploitation of ecological niches, mortality events, and eventually the collapse of most vulnerable species populations (D'agata et al.

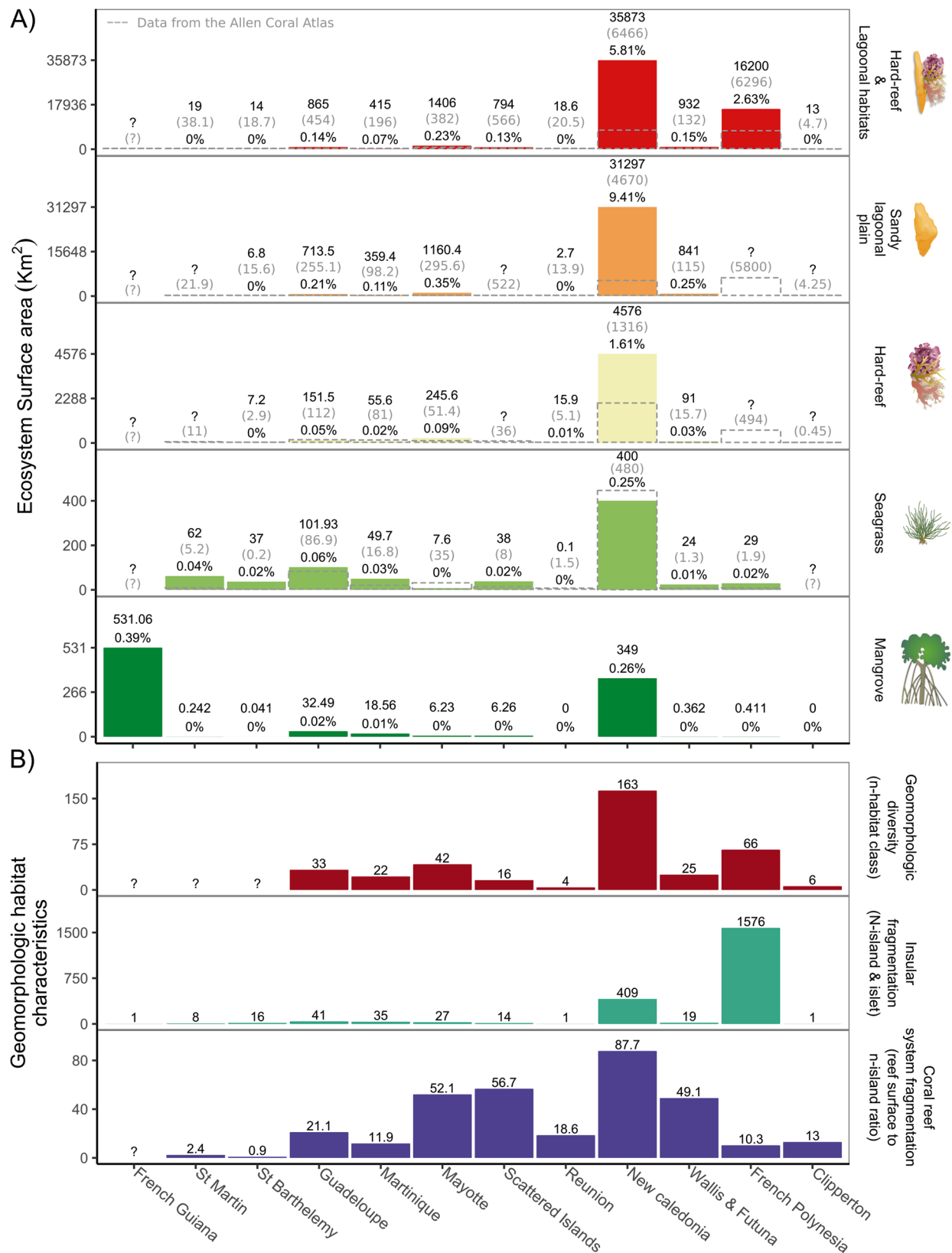


Fig. 10.20 Characteristics of coral reefs and associated ecosystems across French tropical overseas. Ecosystem surface areas and the percentage of the global values they represent are illustrated (data from and Spalding et al. 2001 IFRECOR 2021, as well as <https://allencoralatlas.org> for comparison), along with the diversity in reef geomorphologic habitats (number of level 5 tele-detection classification out of a total of 800 coral reef habitat geomorphologies found on Earth, data from Andréfouët et al. (2008) and system fragmentation indices

for comparison), along with the diversity in reef geomorphologic habitats (number of level 5 tele-detection classification out of a total of 800 coral reef habitat geomorphologies found on Earth, data from Andréfouët et al. (2008) and system fragmentation indices

2016; Cinner et al. 2018; Darling et al. 2019; Duprey et al. 2020; Eddy et al. 2021; Zhang et al. 2023). Coral decline, nutrient discharge, and the collapse of herbivore populations have led to drastic ecosystem upheavals, including shifts in dominance from corals to algae in many places (McManus and Polsenberg 2004; Schmitt et al. 2019; Morais et al. 2020; Adam et al. 2021; Reverter et al. 2022). While the ecological mechanisms controlling ecosystem resistance and resilience to such abrupt transition are generally understood, ecosystem vulnerability to various forms of stressors acting in isolation or in concert remains largely to be quantified. The development of new methods for monitoring coral reef ecosystems such as bioacoustics (Elise et al. 2019; Dimoff et al. 2021), remote-sensing (Hedley et al. 2016), and eDNA (Alexander et al. 2020; West et al. 2020), boosted by machine learning algorithms (Burns et al. 2022; Ditría et al. 2022), can help accelerate data acquisitions and processing, including in cryptic and mesophotic coral reef habitats for which relatively little is known (Brandl et al. 2019b; Pérez-Rosales et al. 2022; Wolfe et al. 2023).

Among the major ecological compartments of coral reef ecosystems, species diversity generally culminates in invertebrates, followed by fishes, corals, and algae, although the relative contributions of the different communities to species diversity vary among regions (Figs. 10.16 and 10.21a). While differences in data availability among regions blurs to some degree the level of certainty on these patterns, furthering these trans-community evaluations will bring heightened understanding of the magnitude and organization of ecosystem biodiversity among regions and taxonomic groups. Inter-regional comparisons indicate a marked contrast in coral reef ecological states between oceanic basins, with corals prevailing as primary constituents of reef habitats in the Pacific Ocean and macroalgae dominating the substrate on Caribbean reefs, with an intermediate state observed in the Indian Ocean (Fig. 10.21b; Reverter et al. 2022). These regional differences in dominance between corals and macroalgae concord with global gradients in coral species diversity and robustness of herbivory, which culminate in the Pacific Ocean and are weakest in the Caribbean (Hughes et al. 2002b; Bellwood et al. 2005; Siqueira et al. 2019; Cramer et al. 2021). Similarly, the abundance of various species groups changes with the latitudinal gradient, including sponges which are more prevalent near the equator and soft-corals at higher latitudes (Reverter et al. 2022). A positive relationship is observed between community diversity and biomass across regions for corals and fish, but not for algae in which the species diversity to biomass relationship is negative (Fig. 10.22). These patterns concord with our general understanding that species diversity supports higher ecological productivity, particularly at higher trophic levels, in structurally complex ecosystems dominated by corals, and declines when reefs are dominated by algae (Mumby and

Steneck 2008; Graham and Nash 2013; Nash et al. 2014; Rogers et al. 2015; Clements et al. 2017). They indicate biomass maxima in coral and fish communities are achieved by species additions and therefore a diversified occupation of ecological niches, whereas high algal productivity tends to be driven by few proliferating species. These community-level differences have cascading effects that spread to other ecosystem compartments through species ecological functions and trophic and other forms of biotic interactions. Diversified coral communities contribute structural habitats for a myriad of organisms, including for species necessitating relatively large and long-lasting structures, therefore amplifying biodiversity and trophic food chains beyond the capacity of algal structures (Richardson et al. 2017a; Urbina-Barreto et al. 2021). This topic necessitates deeper investigation to comprehend the links between biodiversity, ecological productivity, habitat, and spatial scale, and the consequences of the ongoing changes of coral reef ecosystems.

A synthesis of the major environmental disturbances impacting coral reefs across French tropical overseas over the last decades indicates coral reef systems differ in their exposure and vulnerability to different types of disturbance (Fig. 10.23). While some disturbances, such as cyclones and increasingly coral bleaching events, occur globally in the tropics (Hughes et al. 2018; Puotinen et al. 2020), others are restricted to specific regions. This is the case with major diseases causing coral and sea-urchin *Diadema antillarum* die-offs, outbreaks of the holopelagic macroalgae *Sargassum fluitans* and *S. natans*, and rapid population expansions of invasive seagrass *Halophila stipulacea* and lionfish *Pterois* spp. in the Caribbean Sea (Côté and Smith 2018; Winters et al. 2020; Marsh et al. 2021; Hewson et al. 2023). Similarly, outbreaks of the coral predator crown-of-thorns starfish *Acanthaster* spp. are restricted to the Indo-Pacific, whereas tsunami impacts to coral reefs are mostly reported in the southwest Pacific (Løvholm et al. 2012; Pratchett et al. 2014). These large-scale spatial patterns emerging from inter-regional comparisons are also modulated by smaller, intra-system differences, particularly in broad and fragmented coral reef systems such as French Polynesia, New Caledonia, Scattered Islands, and Great Barrier Reef where disturbance impacts are spatially contained (Kayal et al. 2012b; Wolff et al. 2016; Adjeroud et al. 2018a; Mellin et al. 2019; Vercelloni et al. 2019; Pérez-Rosales et al. 2021a).

Despite significant differences in the level of knowledge available on environmental disturbances among regions, it appears that some coral reef systems like the ones in French Polynesia, New Caledonia, and the Caribbean islands are situated in areas prone to high frequency of disturbance, while others in Wallis and Futuna and Scattered Islands (though Tromelin is in a cyclone route) seem to lie in relatively stable environmental sanctuaries that suffer fewer

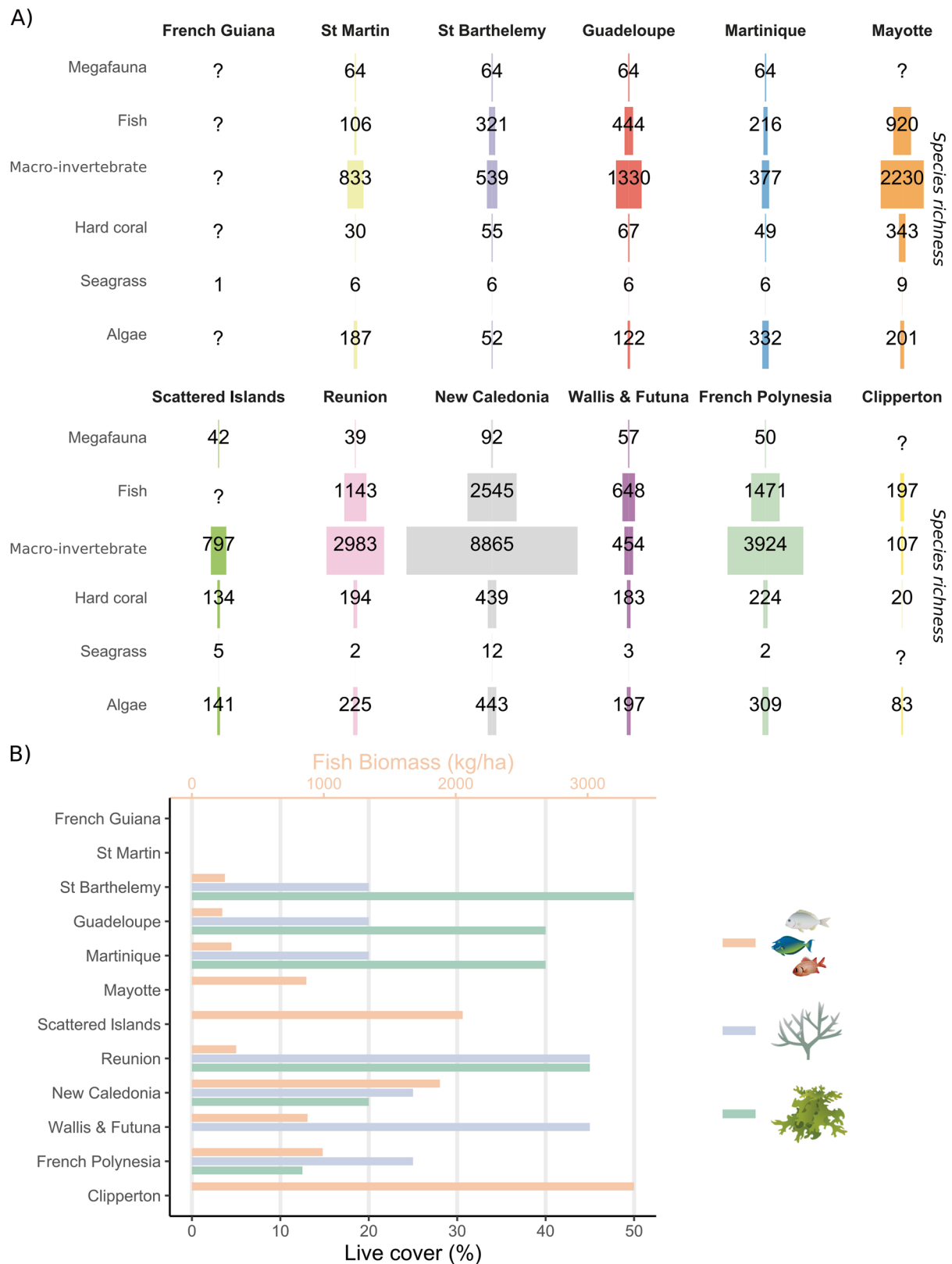


Fig. 10.21 Coral reef ecosystem diversity and productivity across French tropical overseas. Species richness of key ecological communities constituting the coral reef trophic pyramid (**a**, see Fig. 10.16 for

data sources) and percent cover of corals and algae and fish biomass (**b**, data from McClanahan et al. 2019, 2021; Souter et al. 2021)

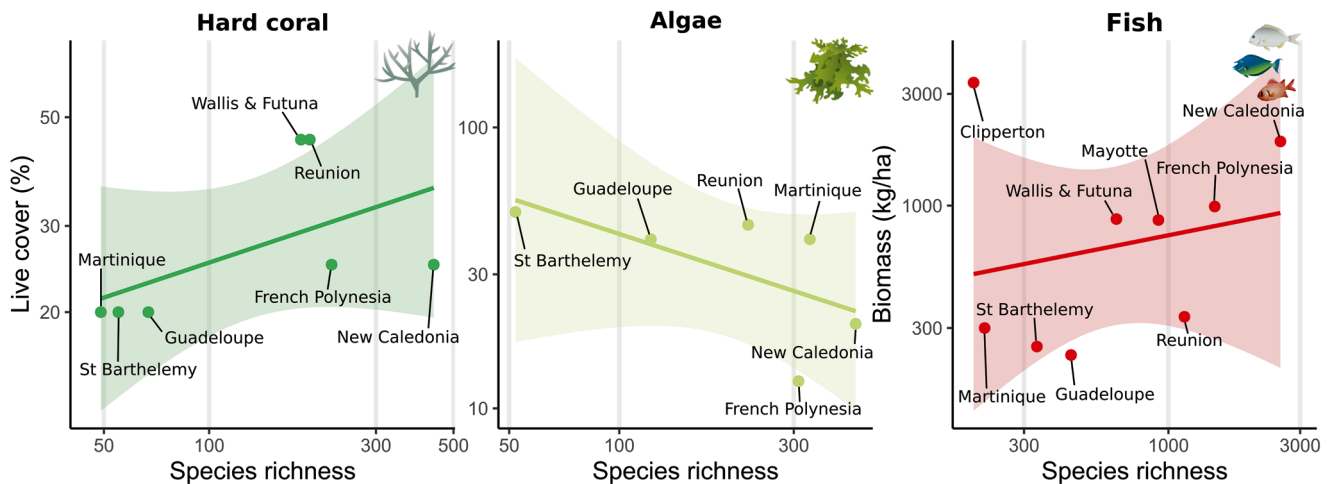


Fig. 10.22 Relationships between species diversity (richness) and biomass (reflected by percent cover in sessile communities) in corals, algae, and fish. Percent cover and biomass data from McClanahan et al.

(2019, 2021) and Souter et al. (2021); see Fig. 10.16 for species richness data sources

disturbance events (Fig. 10.23b; Løvholt et al. 2012; Puotinen et al. 2020; Kuempel et al. 2022). While coral reefs have long evolved with environmental disturbances whose nonequilibrium effects on ecosystems are seen as a major source of their exceptional biodiversity (Connell 1978; Quattrini et al. 2020), the consequences of recent changes in disturbance types and regimes for coral reef resilience and functionality remain insufficiently understood to support adequate management, especially in regions of high exposure and vulnerability Adjeroud et al. 2018a; Vercelloni et al. 2019; Leinbach et al. 2021; Pérez-Rosales et al. 2021a; Carlot et al. 2023; Zhang et al. 2023). Eutrophication and fishing are suspected to generate a higher occurrence and intensity of *Acanthaster* outbreaks and associated mass coral mortality, whereas the frequency and magnitude of temperature anomaly-induced coral bleaching events and cyclonic storms have risen with ongoing climate changes (Sweatman 2008; McCook et al. 2010; Mellin et al. 2016; Vanhatalo et al. 2017; Puotinen et al. 2020; Cresswell et al. 2023). Time-series analyses of coral cover indicate *Acanthaster* outbreaks have resulted in strongest impacts on reefs through mass coral mortality and cascading effects on various reef communities, followed by cyclones and then coral bleaching events, although coral mortality associated with regional and global bleaching is becoming more prominent (Osborne et al. 2011; De'Ath et al. 2012; Kayal et al. 2012b; Adjeroud et al. 2018a; Vercelloni et al. 2019; Pérez-Rosales et al. 2021a; Gilmour et al. 2022). Coral bleaching events have become a common part of coral reef dynamics in most tropical regions, with variable inter-annual occurrences depending on climatic oscillations (El Niño Southern Oscillation, North Atlantic Oscillation) and the ecological state (abundance, composition) of coral communities (Sully et al. 2019).

Higher sea water temperatures have also been related to increases in coral disease (Burke et al. 2023). The National Oceanic and Atmospheric Administration (NOAA)'s (<https://coralreefwatch.noaa.gov>) tool has been a major information source for marine heatwave and coral bleaching alerts and forecasts (and <https://www.nhc.noaa.gov> for tropical cyclones), although its continued availability is uncertain due to current government instability and public service meltdown in the USA.

Over recent decades, much research attention has been dedicated to elucidating the mystery behind *Acanthaster* outbreaks, whose drivers have remained elusive (Pratchett et al. 2014, 2017), although pieces of knowledge add up with new studies performed during each new outbreak cycle. Accumulated evidence points toward the role of nutrient limitations on larval stages (Fabricius et al. 2010; Wooldridge and Brodie 2015), predatory control particularly on juveniles (Sweatman 2008; Cowan et al. 2017; Westcott et al. 2020), and, more recently, the capacity of the juvenile seastars to remain in a latent (ecologically "dormant") herbivorous stage where cryptic populations hidden in dead-coral rubble can build up over years before shifting to corallivory and full-grown mature adults once live coral is abundant (Deaker et al. 2020; Wilmes et al. 2020; Deaker and Byrne 2022). Recurrent observations of outbreak episodes have enabled identification of initiation sites and propagation patterns of outbreaks in several regions, along with a good knowledge of their impacts to coral communities, repeatedly observed patterns that therefore appear predictable (Kayal et al. 2012b; Adjeroud et al. 2018b; Babcock et al. 2020; Wilmes et al. 2020; Condie et al. 2021). Among French tropical overseas, *Acanthaster* outbreaks are recorded in French Polynesia, New Caledonia, and Mayotte with a periodicity of

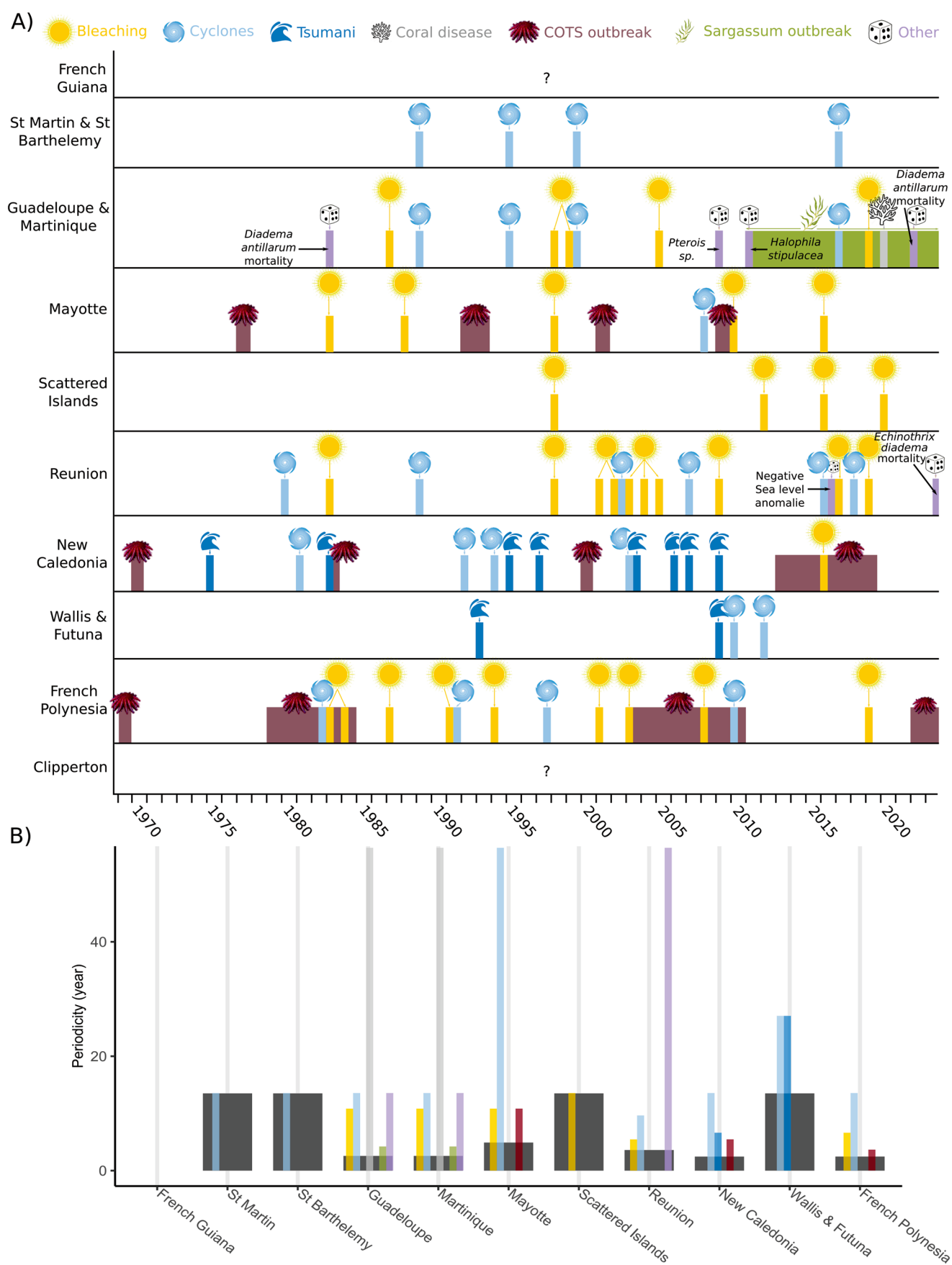


Fig. 10.23 Major environmental disturbances to coral reefs recorded in French tropical overseas over years (a) and mean periodicity of the events (b). In b, occurrence periodicities are shown per disturbance type (color bars) and considering all types of disturbances (black bars)

~15 years (Fig. 10.23), which is consistent with the frequency of outbreaks reported in other regions such as Australia's Great Barrier Reef (Kayal et al. 2012b; Pratchett et al. 2017; Adjeroud et al. 2018a; Babcock et al. 2020; Richards et al. 2021). Occurrences of the outbreaks seem correlated with ocean productivity in relation to regional weather oscillations influencing patterns of temperature, rainfall, and wind (Fabricius et al. 2010; Houk and Raubani 2010; Wooldridge and Brodie 2015; Matthews et al. 2020), with hitherto no direct evidence of recent increases in frequencies or intensities of the outbreaks. Yet, comparative coral reef health assessments highlight the importance of preserving ecosystem integrity for higher chances of resilience in the face of *Acanthaster* outbreaks (Sweatman 2008; McCook et al. 2010; Mellin et al. 2016; Westcott et al. 2020; Kroon et al. 2021). Recently, much effort has been dedicated to identifying reef predators able to keep *Acanthaster* populations in check as a natural solution to outbreaks (Cowan et al. 2017; Desbiens et al. 2023; Kayal and Lenihan 2025). Within-system studies indicate the seastar outbreaks are restricted to reefs subject to coastal influence and propagate from distinct initiation sites that are exposed to high nutrient discharge, including mid-shelf reefs near the towns of Cairns in Australia's Great Barrier Reef and Noumea in New Caledonia and the north shore of the island of Moorea in French Polynesia (Fabricius et al. 2010; Kayal et al. 2012b; Wooldridge and Brodie 2015; Adjeroud et al. 2018b; Adam et al. 2021). As a new cycle of *Acanthaster* outbreaks spreads in the Pacific, inter-regional connectivity between *Acanthaster* populations among adjacent systems and the degree of synchronicity of outbreaks in response to regional weather patterns remain to be explored. Among major environmental disturbances impacting coral reefs, *Acanthaster* outbreaks are the easiest to try to mitigate, and control programs are performed in various regions (Condie et al. 2021; Castro-Sanguino et al. 2023). Yet, culling of the seastar populations is costly, has shown relatively limited efficiency over large spatial scales, and addresses a symptom rather than the root causes of the outbreaks. Nevertheless, despite its notorious reputation as a harmful species, a pest (Pratchett et al. 2014; Kayal et al. 2017b), *Acanthaster* is also recognized for its role as a keystone predator benefiting biodiversity by feeding preferentially upon competitive acroporids (particularly genera *Acropora* and *Montipora*) that otherwise have the capacity to outcompete other corals (Kayal et al. 2011; Darling et al. 2012; Pratchett et al. 2017; Kayal and Adjeroud 2022). The degree to which *Acanthaster* outbreaks are triggered by large abundance of their preferred prey species remains to be investigated, though long-term observations in Moorea, French Polynesia, indicate swarms of seastars emerge

when competition for space among corals is particularly prevalent (Fig. 10.24).

10.3.10 Socio-ecosystems

Coral reef socio-ecosystems around the world come in a variety of forms, combining differing levels of natural ecosystem and human society features (Figs. 10.20, 10.21, 10.22, 10.23 and 10.25). The prevalence and impacts of human populations, as well as their ties to ecosystems for coastal protection, food, and economic resources, are key to ecosystem health and the resulting level of sustainability and benefits to nature and society (McCook et al. 2010; Cinner et al. 2018; Comte and Pendleton 2018; Williams et al. 2019; Darling et al. 2019; Castro-Cadenas et al. 2022). Small natural systems supporting large human populations tend to suffer from stronger impacts from coastal development, overexploitation, and pollution, resulting in reduced ecosystem health, management deficiencies, and limited socio-ecosystem resilience (Duprey et al. 2020; Boyce et al. 2020; Ouédraogo et al. 2021; Andrello et al. 2022; Ouédraogo et al. 2023). This begs the long-standing question of the carrying capacity of natural systems, not only in terms of the size of the human population they can support but most importantly the overall level of stress they can sustain without declining. Other socio-ecosystem aspects, including the ecological and geomorphological contexts as well as the economic and cultural ties to the reef, further contribute to the vulnerabilities of the systems (Mumby et al. 2007; Anthony et al. 2015; Siqueira et al. 2019; Cramer et al. 2021). When management strategies fail to preserve coral reef ecosystem health, declines in biodiversity, biological productivity, and ecological functionality reduce the level of ecosystem services provided to society, often with a rise of negative interactions and ecosystem disservices (Speers et al. 2016; Woodhead et al. 2019; Carlot et al. 2023). Harmful algal blooms such as outbreaks of benthic ciguatera-producing dinoflagellates occur more frequently in degraded environments where dead coral skeletons and macroalgae surfaces provide substrate for the microorganism, with strong societal consequences for human health and economy (Fig. 10.26; Alves de Souza et al. 2022). Described for centuries in French tropical overseas, ciguatera poisonings are on the rise under the possible influence of global changes (marine heat waves, ocean acidification, etc.), and the distribution range of ciguatera-producing species and their accumulation in trophic food webs is expanding to subtropical/temperate regions, though the statistics of human poisonings remains highly underestimated as most cases go undocumented (Fig. 10.27; Rongo et al. 2009; Chinain et al. 2021). The CiguaWatch Initiative, led by French Polynesia,

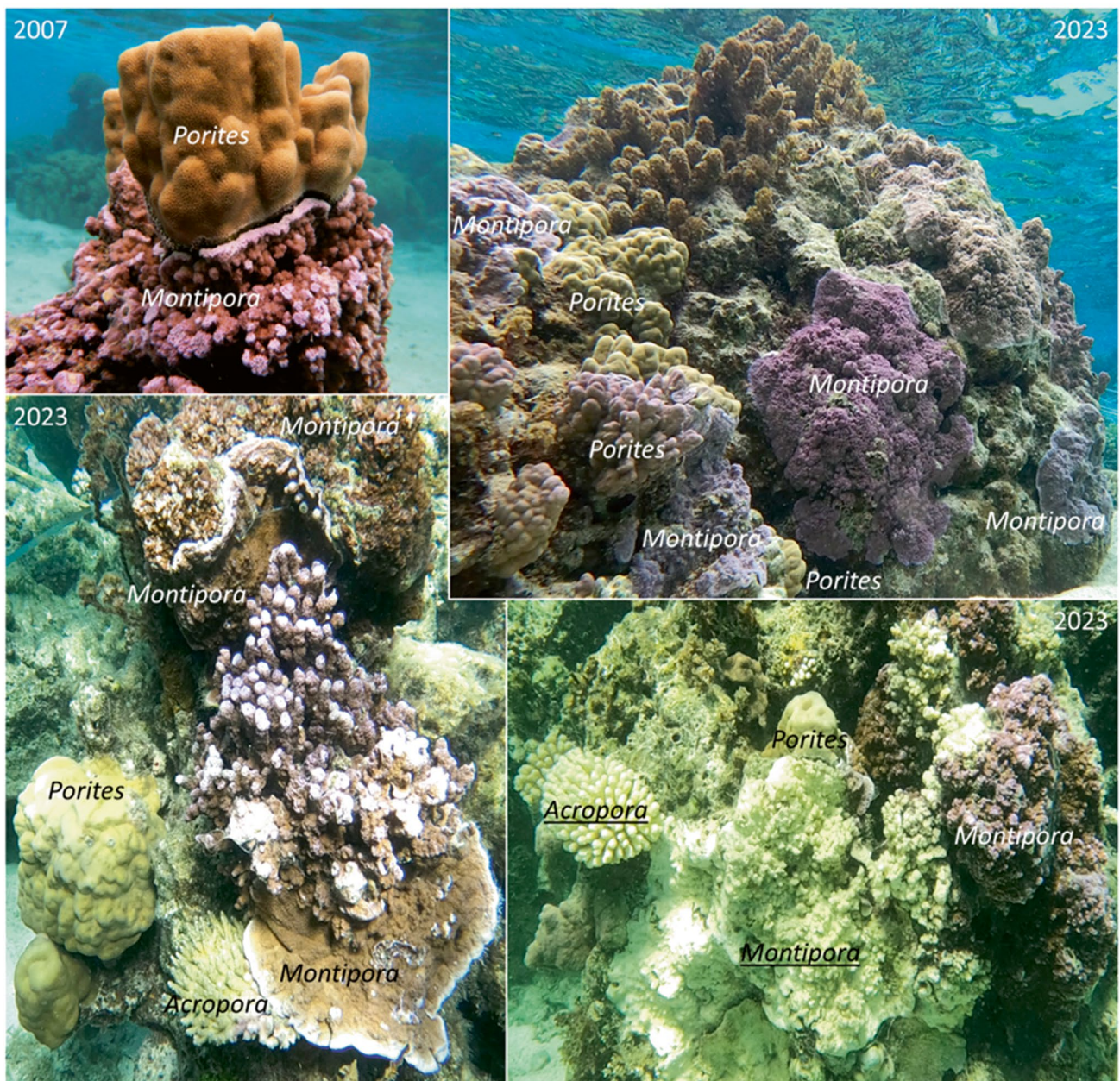


Fig. 10.24 Photographs illustrating the co-occurrence of outbreaks of the coral predatory seastar crown-of-thorns starfish (*Acanthaster*) with periods of high abundance of their favorite prey, the acroporid corals (particularly genera *Acropora* and *Montipora*). Photographs were taken in the lagoon of Moorea, French Polynesia, at the onsets of two distinct episodes of *Acanthaster* outbreaks occurring ~15 years apart and causing widespread coral mortality (Fig. 10.23). The pictures show the capacity of encrusting *Montipora* to overgrow other corals, particularly

massive *Porites* which is foundational to forming large habitat structures in the lagoon. Because *Acanthaster* preferentially preys upon acroporids, their episodic outbreaks prevent *Montipora* to fully out-compete *Porites*, promoting species coexistence. Bottom-right picture shows *Acropora* and *Montipora* colonies (underscored names) bearing white feeding scars characteristic of recent predation by the seastar. See text for references on the topic

provides a regional platform for training and data sharing on Ciguatera poisoning surveillance in the South Pacific (<https://ciguawatch.ilm.pf>). Ongoing research particularly seeks a better understanding of ciguatera-related algal bloom ecology for anticipating and monitoring outbreaks, evaluating their consequences on societies, and improving

ciguatoxin detection tests, patient diagnostic tools, and medical care (Rongo et al. 2009; Chinain et al. 2020; Chinain et al. 2021). Other examples of negative feedback from system alterations include recent concerns about increasing outbreaks of the coral predatory seastar *Acanthaster* throughout the Indo-Pacific and *Sargassum*

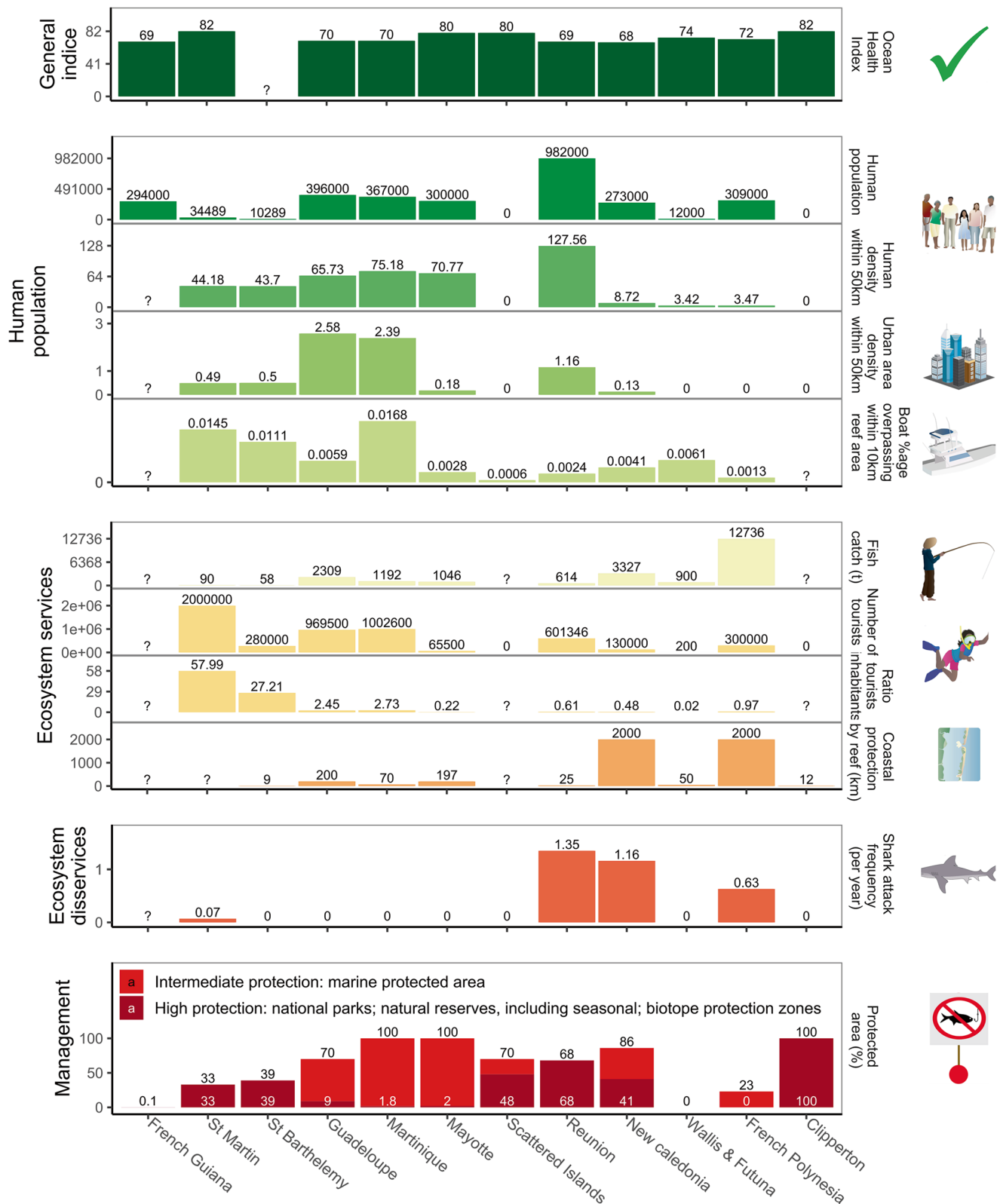


Fig. 10.25 Differences in coral reef socio-ecosystems among French tropical overseas. The Ocean health index summarizes ecosystem state and resilience on a scale of 0–100 (Halpern et al. 2012). Shark attack

frequency was calculated over the 1980–2023 period. (Data from <https://oceanhealthindex.org>, <https://recifs.epfl.ch>, <https://www.iedom.fr>, <https://public.opendatasoft.com> and IFRECOR (2021))

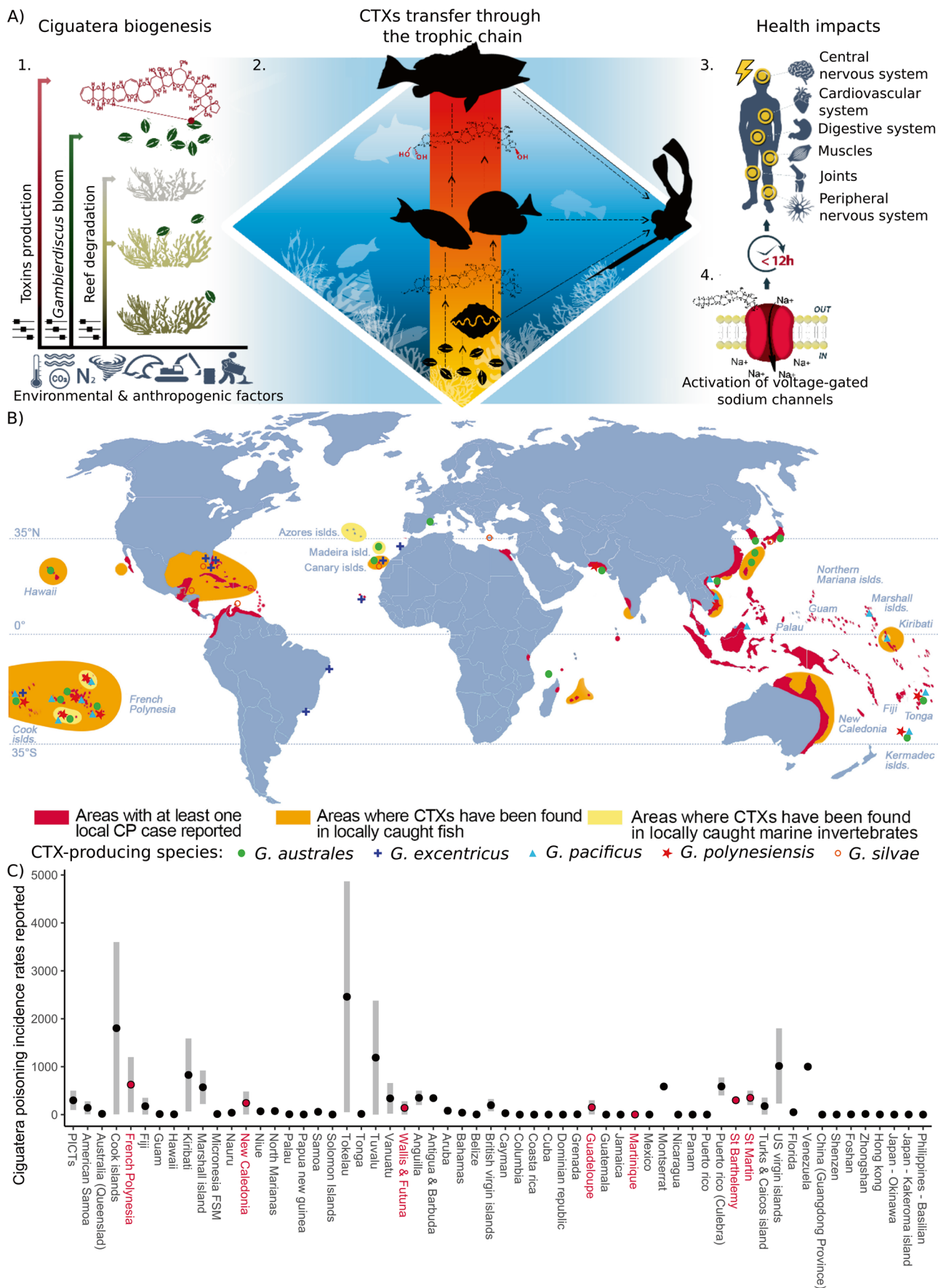


Fig. 10.26 Ciguatera poisoning biogenesis and transmission (a, adapted from Chinain et al. 2023), distribution of ciguatera (CTX) producing species (*Gambierdiscus* spp.) Ciguatera poisoning prevalence areas (b, adapted from Chinain et al. 2021), and Ciguatera poisoning (CP) incidence rates among regions (c, data adapted from Chinain et al. 2021 and references therein). PICTs for Pacific Island Countries and Territories

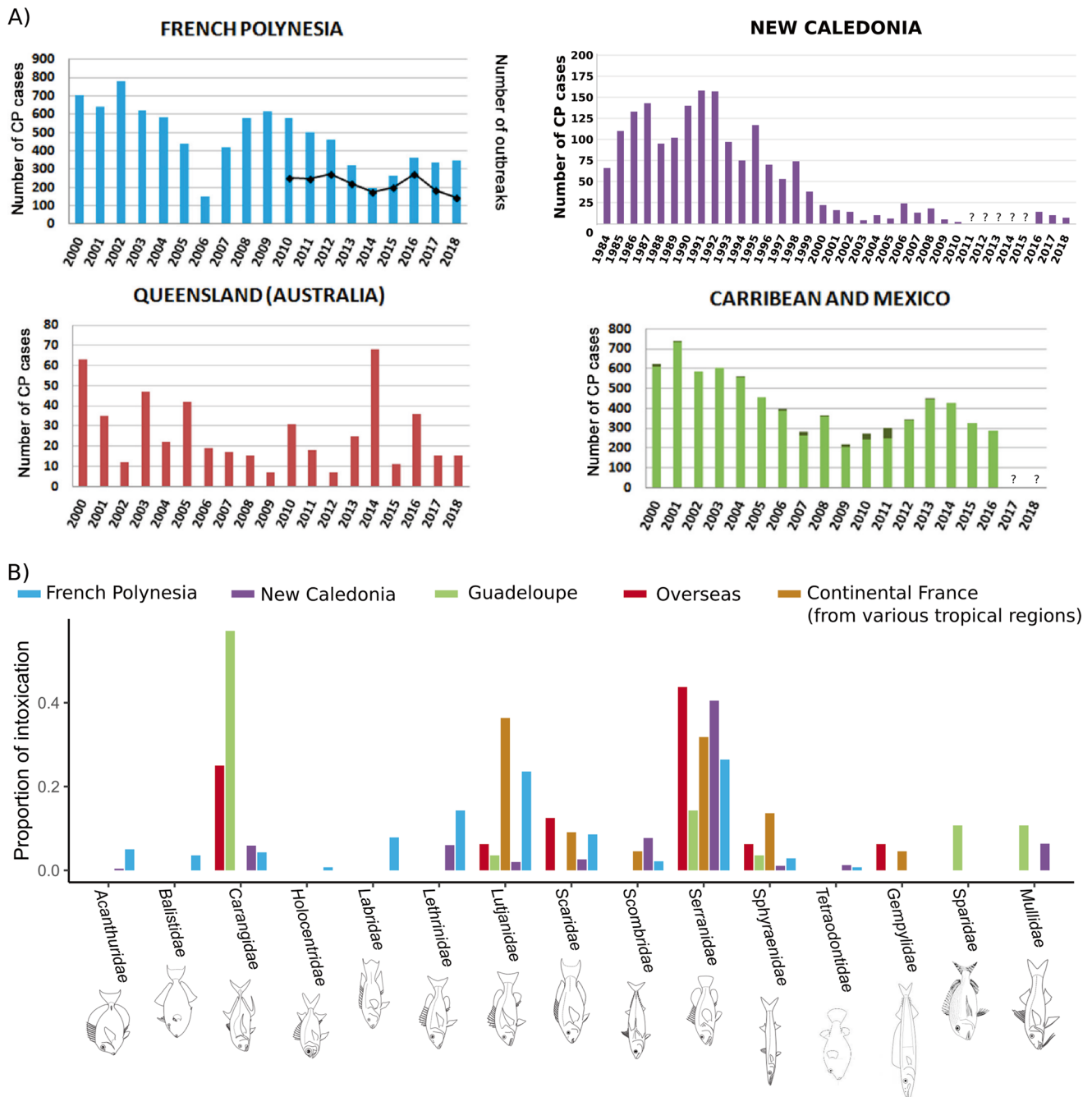


Fig. 10.27 Documented number of human ciguatera poisoning (CP) cases through time per region (**a**, adapted from DASS 2018; Chinain et al. 2021) and vectors implicated in both autochthonous and imported

poisonings (**b**, data from Boucaud-Maitre et al. 2017; DASS 2018; Gatti and Chinain 2023)

strandings in the Caribbean (Fig. 10.23; Pratchett et al. 2014; Matthews et al. 2020; Marsh et al. 2021) and critical shark attacks on humans in Australia, Reunion, and New Caledonia (Fig. 10.25; Taglioni et al. 2019; Maillaud et al. 2022; Riley et al. 2022), although there is still limited understanding of underlying drivers. In the face of uncertainties and lack of incentives to address root causes, *Sargassum* removals and culling of *Acanthaster* and shark

populations are common practice in different coral reef socio-ecosystems, practices that are often hotly debated (Papastamatiou et al. 2006; Vanhatalo et al. 2017; Pratchett and Cumming 2019; Babcock et al. 2020; Condie et al. 2021; Gray et al. 2021; Maillaud et al. 2022; Borsa et al. 2023). Fortunately, positive examples of human-wildlife interactions with potentially deadly animals also exist, although the mechanisms determining sustainability and

their thresholds remain in big part to be understood (Udyawer et al. 2021).

Coral reef biodiversity and associated ecosystem productivity and services have long supported the development of human societies in the tropics. Yet in various places, rapid and ecologically unsustainable growth has caused coastal alterations that are beyond the tolerance capacity of ecosystems, threatening the sustainability of the coral reef socio-ecosystems (Woodhead et al. 2019; IPBES 2019; Duprey et al. 2020). Achieving sustainable coral reef socio-ecosystem development is however not easy, as local human activities often impact marine ecosystems over large spatial scales and are increasingly combined with global environmental changes (Donovan et al. 2023), as many human concentrations have already caused significant and long-lasting damage to their surrounding ecosystems and as many societies still prioritize unsustainable development paths (Brodie and Waterhouse 2012; Cinner et al. 2018; Daskin and Pringle 2018; Kayal et al. 2019; Darling et al. 2019; OECD 2020; Cramer et al. 2021; Ouédraogo et al. 2021; Ouédraogo et al. 2023; Calvin et al. 2023). The most extreme disturbances in French tropical overseas took form as nuclear testing in 1966–1996 on the islands of Mururoa and Fangataufa in French Polynesia, of which 41 were conducted above ground and 140 in volcanic rock under the coral reef (Philippe et al. 2022), and broad use of the highly toxic and long-lasting organochlorine pesticide chlordane in Guadeloupe and Martinique in 1973–1993 (Multigner et al. 2016), with, apart from cancers in local human populations, largely unknown consequences on the coral reef socio-ecosystems and life more broadly.

Among the >500 million people living in tropical coastal areas protected from erosion and storm waves by coral reefs, ~100 million live below 10 m elevation within 10 km of a coral reef (Ferrario et al. 2014; Beck et al. 2018; Carlot et al. 2023). Among these, ~three million people live in French tropical overseas, mostly in Reunion, Martinique, and Guadeloupe where coastal urbanization and human density are the highest, followed by French Polynesia, Mayotte, New Caledonia, and French Guiana, although the latest is largely dominated by mangroves (Figs. 10.20 and 10.25). Coastal protection by coral reefs is particularly prominent in New Caledonia due to the high exposure to tsunamis, particularly on the eastern coasts, as well as in French Polynesia where relatively young barrier reefs protect the small Central Pacific island community from storm waves (Sahal et al. 2011; Løvholt et al. 2012; Burke and Spalding 2022). Fishing rates are the highest in French Polynesia where seafood constitutes a highest portion of the diet and fish exportation a significant part of the economy (Morin et al. 2016; FAO 2022), whereas tourism is particularly developed in the Caribbean, followed by Reunion and French Polynesia. The degree of reliance of tropical coastal societies on coral reefs

varies from one system to another, though decline in coral reef health has strong consequences for exposure to flooding, food security, and economic opportunities (Pendleton 2010; Comte and Pendleton 2018; Alves de Souza et al. 2022; Carlot et al. 2023).

Coral reef socio-ecosystem vulnerability depends in big part on the ability of societies to durably manage ecosystems by preventing degradation and overexploitation through implementation of effective environmental regulations, exploitation quotas, and protected areas (McCook et al. 2010; Anthony et al. 2015; Rogers et al. 2015; D'agata et al. 2016). Overall, there are four major management strategies that target social and ecological vulnerabilities: environmental mitigation, ecosystem protection, restoration, and adaptation, though trade-offs and synergies between the different strategies and prerequisite conditions for success are largely unevaluated (Comte and Pendleton 2018; Thiault et al. 2020a). Comparisons across socio-ecosystems indicate that key characteristics of success include strong regulation enforcement and community engagement in management strategies (Cabral et al. 2018; Thiault et al. 2020a; Thiault et al. 2020b; Maxwell et al. 2020). Coral reef management across French overseas currently includes different levels of regulatory-designated marine protected areas, varying from 0% of ecosystem surface area in Wallis and Futuna to 100% in Clipperton (Fig. 10.25), though this does not account for other forms of locally recognized management. Limitations to design, implement, and enforce sustainable environmental management are often economic in nature, related to the level of inequality, dependency on natural resources and global market, and capacity of protection from local and international poaching (McCook et al. 2010; Cabral et al. 2018; Januchowski-Hartley et al. 2020; Thiault et al. 2020b; Maxwell et al. 2020; FAO 2022). The governance of socio-ecosystems and how different societal actors take part in management decisions are also important factors in socio-ecosystem trajectories (Morrison et al. 2020; Thiault et al. 2020a).

Coral reef socio-ecosystems exhibit a multitude of governance systems, as observed in French tropical overseas characterized by different degrees of decision-making centralization and a hierarchy of bodies performing policy-making, public safety, and territorial planning roles with different jurisdictions (Fig. 10.28). Given increasing environmental changes, and that many coral reefs may already be approaching their maximum tolerance limits, governance systems face the challenge of adapting rapidly while engaging a variety of societal actors at different scales (Donovan et al. 2023). Success in achieving healthy and resilient coral reef systems may depend on the capacity of socio-ecosystems to anticipate and adapt to future challenges (Rogers et al. 2015). Socio-ecosystemic diversity is a key attribute of French tropical overseas that are characterized by

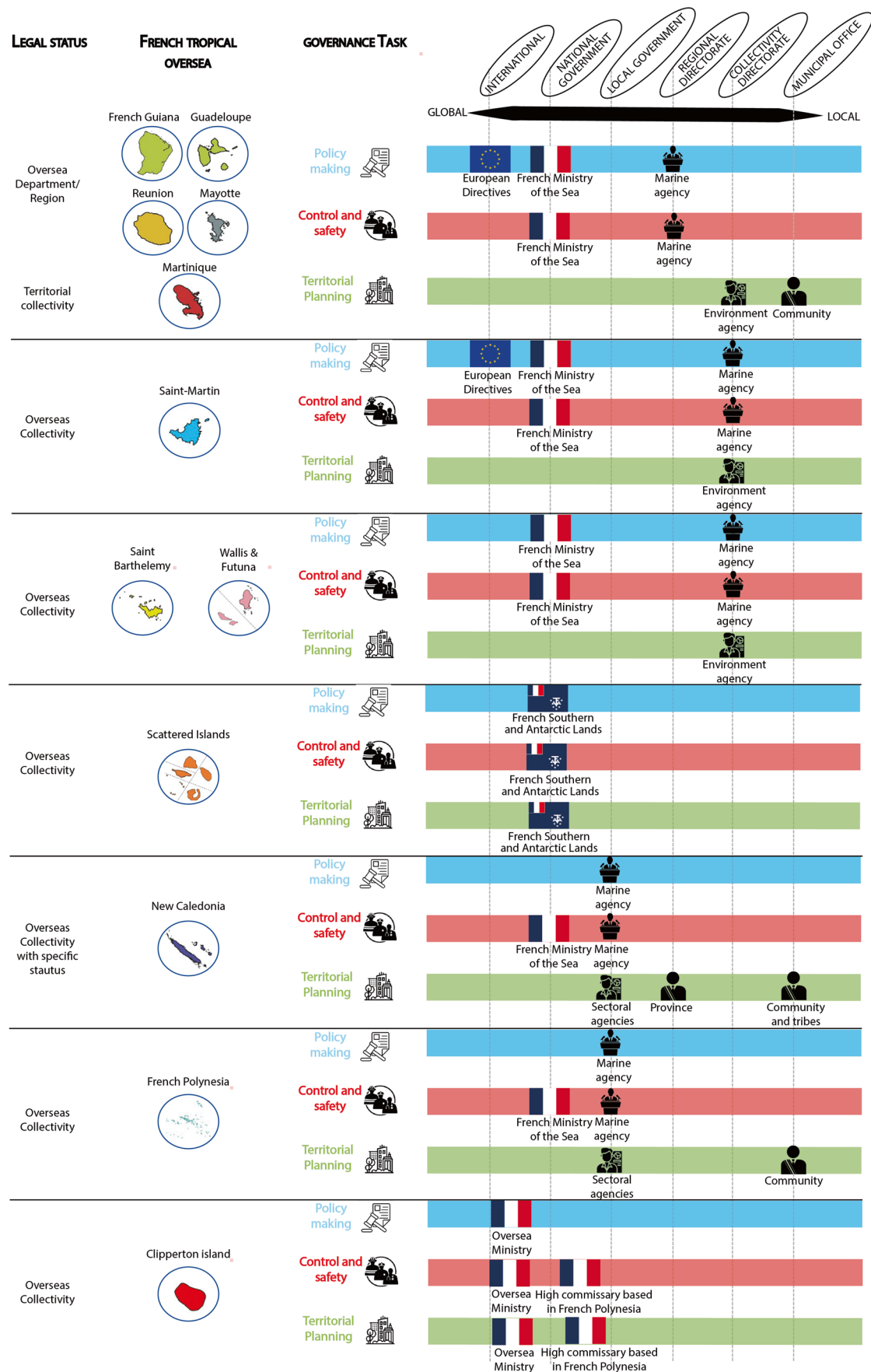


Fig. 10.28 Governance systems of coral reef socio-ecosystems in French tropical overseas. Diagrams represent the hierarchy and jurisdictions of different governing bodies in relation to the three tasks of

policy-making, public safety, and territorial planning. Note that the uninhabited atoll of Clipperton is governed by France through a delegation based in French Polynesia

contrasting human histories, social and political organizations, and cultural and economic ties to natural resources. Societal challenges in these dispersed insular systems include finding a balance between local and national identities in a postcolonial era where the search for democracy, local governance, and social development is reliant on ecosystem preservation for coastal protection, food security, and economic development but challenged by pressures for over-exploitation from the globalized market, a context increasingly exacerbated by environmental degradation and coral reef decline.

10.3.11 Biogeoclimatic Systems

Coral reefs interact with the Earth's geologic and climatic environments through multiple ocean-land-atmosphere interchanges whose prevalence varies with the size and characteristics of the systems (Fig. 10.29). By accreting carbonated reefs along the coasts, corals sequester oceanic carbon, modify ocean alkalinity, and produce shallow water substrate at slow yet potentially large scales (Smith 1978; Spalding et al. 2001; Jones et al. 2015; Carlot et al. 2021). The reefs reduce wave energy protecting coastlines from erosion and submersion and produce large amounts of carbonated sand that accumulates to create new habitats for many marine and terrestrial species, therefore amplifying biodiversity and associated benefits (Figs. 10.20 and 10.29c). Indeed, coral reef accretion and erosion generate conditions favorable to the establishment of diverse biological communities including seagrass and algae beds, mangroves, and the vegetation covering lagoonal islets, all of which contribute additional sets of ecological functions and ecosystem services such as habitat creation, carbon sequestration, and attenuation of wave and wind energy (Moberg and Folke 1999; McIvor et al. 2012; Guannel et al. 2016; Andréfouet et al. 2021; Carlot et al. 2023; Heudier et al. 2023). Among French tropical overseas, the contribution of coral reef accretion to the coastal systems' emerged land and lagoonal systems is most prominent in Scatter Islands, Clipperton, French Polynesia, Wallis and Futuna, Mayotte, Guadeloupe, and New Caledonia (Fig. 10.29c).

Coral reefs also interact with the local climate. By producing large stretches of white sand beaches and clear and shallow underwater habitats, coral reefs modify the local albedo, or how much solar radiation is sent back to the atmosphere, with a direct impact on surface temperature (Hays et al. 2001; McGowan et al. 2019). Coral reefs and associated ecosystems may influence local atmospheric conditions through heat and moisture exchanges and affect local meteorology such as cloud cover and rainfall (McGowan et al. 2022). Coral reefs are a source of dimethyl sulfide, an important aerosol involved in cloud formation, though its contribu-

tion to the local and regional aerosol burdens might be low compared to human sources (Yuan et al. 2022; Fiddes et al. 2022). Human societies living off the reef also contribute to local changes in albedo and wind through deforestation, urbanization, and various heat sources (Jin et al. 2019; Ouyang et al. 2022). The relative importance of coral reefs to the local climate might therefore vary from one system to another, depending on local characteristics of land-to-reef ratio, climatic environment, and human emissions of heat, gas, and particles. This includes direct emissions of heat for energy production and use in diverse sectors such as transport and industries, changes in albedo through land-use change including deforestation and urbanization, and emissions of greenhouse gas such as CO₂ and methane, and aerosols (Yuan et al. 2022). This diversity of coral reef biogeoclimatic systems is well illustrated across French tropical overseas (Fig. 10.29), providing a rich study system to investigate how coral reef systems interact with local and regional climate nowadays and into the future. This research avenue may help deepen understanding of mechanisms determining coral reef vulnerability to climate change, identification of potential adaptation and mitigation solutions, and predictions of thermal stress induced coral bleaching under future climatic conditions.

In the objective of socio-environmental sustainability, decarbonation of island emissions remains a real challenge, as many tropical overseas rely heavily on importations for food, material, energy, and economic activities (e.g., tourism), all of which come at a high cost in terms of carbon emissions (Kuo and Chen 2009). Among French tropical overseas, New Caledonia, whose economy is based on the mining industry, has the highest energy consumption and carbon emissions (Fig. 10.29a), with >75% of energy consumption associated with mineral extraction, purification, and export, mostly of nickel and cobalt (Losfeld et al. 2015). It is also the most distant tropical overseas from metropolitan France (Fig. 10.4), amplifying import-export-associated emissions. Despite ample access to solar, aeolian, and hydraulic energy, New Caledonia has a low proportion of renewable energy, though transition to green energy is a local priority and more supporting infrastructure has started to emerge around the archipelago over the recent years. In descending order of emissions, Reunion, Guadeloupe, Martinique, French Polynesia, and Guiana follow human population abundances (Fig. 10.30). Per capita emissions are lowest in Mayotte, which recently transitioned into a French overseas department and exhibits relatively low rates of urbanization (Figs. 10.25 and 10.28; Ninon 2007), and highest in New Caledonia with its mining industry, the two places standing out from the CO₂ emission to human population relationship (Fig. 10.30). Guadeloupe, Reunion, and Martinique are leading the transition to sustainable energy (Fig. 10.29a), with rapid changes over recent years. While

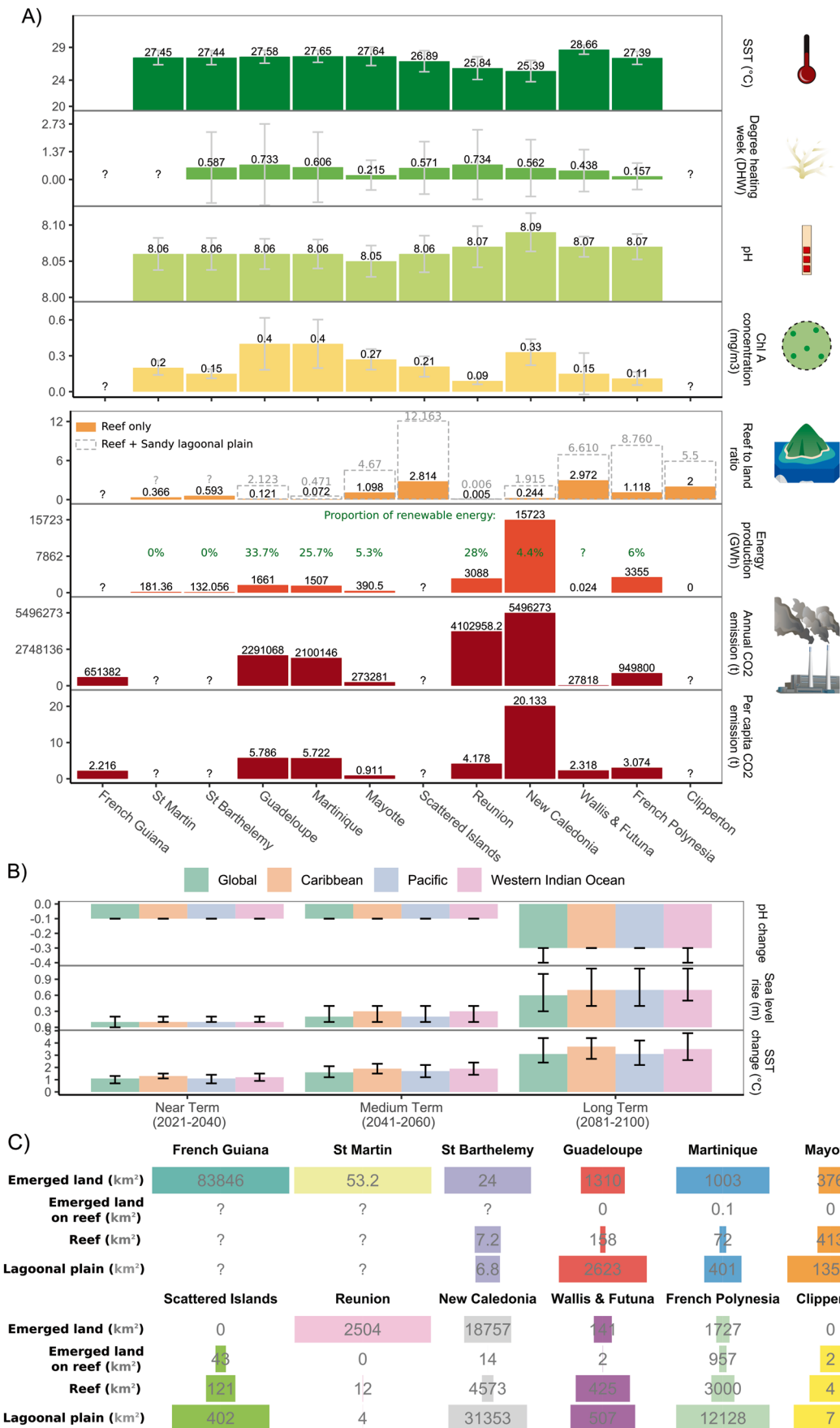


Fig. 10.29 Variability in coral reef biogeoclimatic features among French tropical overseas. (a) current characteristics (2021 data from Recif.epfl.ch, Andrefouet et al. 2008, www.worldometers.info, <https://www.iedom.fr>). (b) Predicted changes according to IPCC following the

SSP5-8.5 (business-as-usual) scenario (data from <https://interactive-atlas.ipcc.ch>). (c) Surface areas of reef, lagoonal plain, and emerged land per region. (Data from Andrefouët et al. 2008)

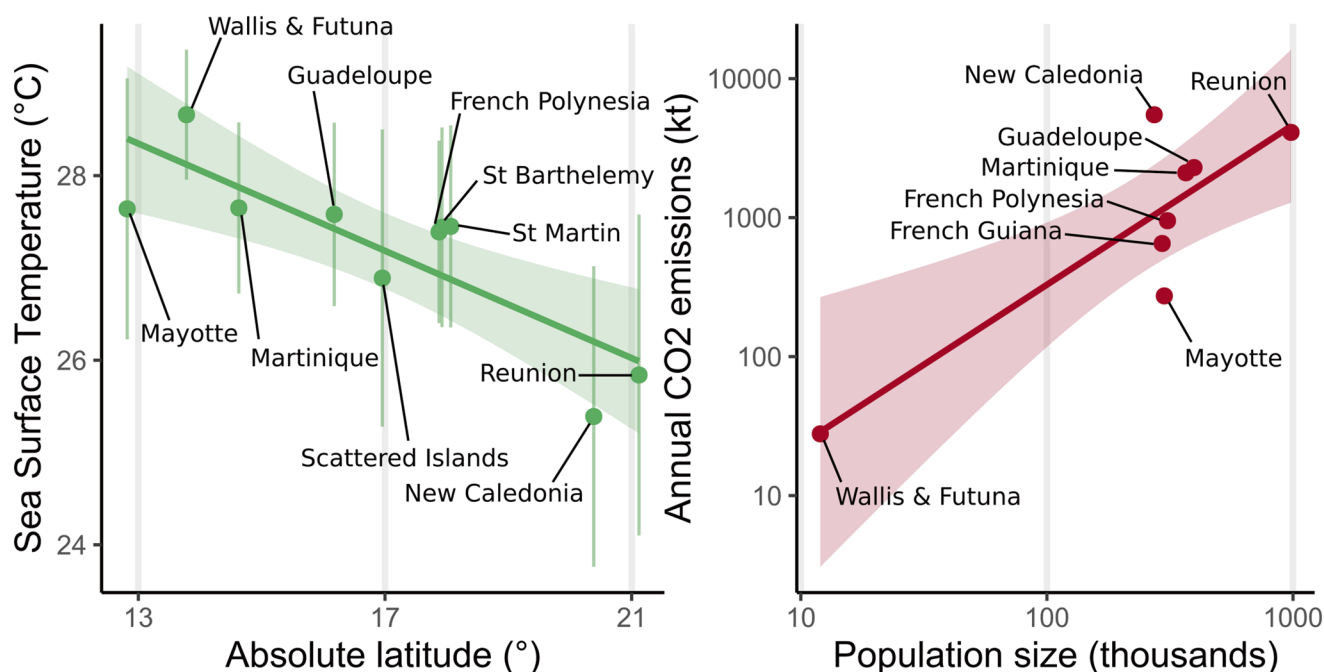


Fig. 10.30 Relationships between sea temperature (mean $\pm$ range) and latitude and CO₂ emissions and human demography across French tropical overseas

coral reef systems around the globe are exposed to different temperature regimes in relation to their latitudinal distributions (Fig. 10.30), the Intergovernmental Panel on Climate Change (IPCC) projections predict higher temperatures, sea-level rise, and lower pH, with a higher exposure for Caribbean reefs (Fig. 10.29b) that adds to their already higher vulnerability to coral decline and ecological shifts (Figs. 10.21b and 10.23; Hoegh-Guldberg et al. 2017; Kuempel et al. 2022). In the current battle for ecological and climate sustainability, tropical islands are key protagonists as both major contributors and victims of environmental decline and have a decisive role to play (Hernández-Delgado 2015).

10.3.12 Overview of Coral Reef Biodiversity Metrics Across French Tropical Overseas

Coral reef systems across French tropical overseas differ in many aspects, as expressed by the disciplinary metrics used to assess biodiversity at the multiple scales of biological and ecological organization covered in this chapter, though data remains incomplete and unbalanced (Figs. 10.5–10.30). A multidimensional representation along the various ecological gradients with available data enables visualizing the degrees of similarity and magnitudes of variation between the different systems (Fig. 10.31). This representation distinguishes along a primary axis New Caledonia, with the largest coral reef system and highest rates of species richness and

habitat diversity, from the other French overseas that fall into three distinct groups along a secondary axis. On one side of this axis lies the densely populated and touristic systems with a status of overseas department of Martinique, Guadeloupe, and Reunion, contrasting with the other side of less densely populated systems of French Polynesia and Wallis and Futuna in the South Pacific and the uninhabited systems of Clipperton and Scattered Islands, and between the two extremes is the grouping of Saint Martin, Saint Barthelemy, Mayotte, and French Guiana. Along this secondary axis, the less densely populated systems are also characterized by stronger ties to the reef through higher rates of coastal protection and fish catch and higher ecosystem health as reflected by ocean health and coral bleaching indices than the more densely populated localities. While every coral reef system is unique, this multidimensional representation underscores how much New Caledonia differs from other systems, standing as a singular hotspot for coral reef biodiversity. A deeper exploration of coral reef biodiversity is necessary to further our understanding of biodiversity hotspots and their preservation, in French tropical overseas and globally.

10.3.13 Knowledge Gaps

Our synthesis identifies a generally positive correlation between the bioecological scale of organization of coral reef life forms and the level of knowledge available (Figs. 10.32

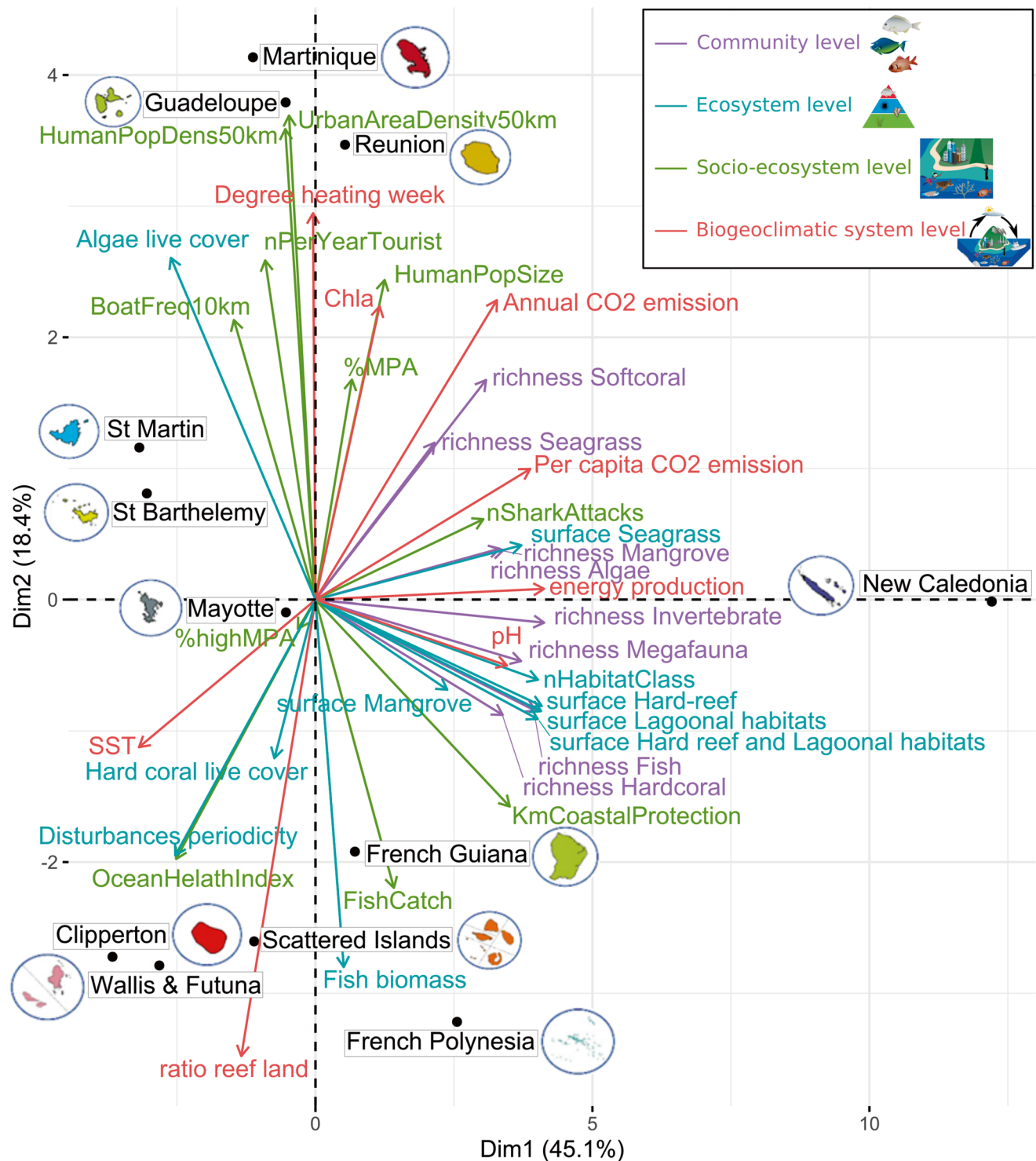


Fig. 10.31 Comparisons of coral reef systems across French tropical overseas. Principal component analysis including all biodiversity metrics considered in this study at the community, ecosystem, socio-ecosystem, and biogeoclimatic system levels of organization. Note that the distributions of the overseas systems and biodiversity variables are calculated in different spaces. The juxtaposition of the two provides

information on the relative position of the overseas along the variables rather than an absolute position. Missing values were estimated using R's missMDA package tools (Husson and Josse 2020). The lower scales of genes, molecules, cells, organs, organisms, and populations are not included due to limitations in data availability

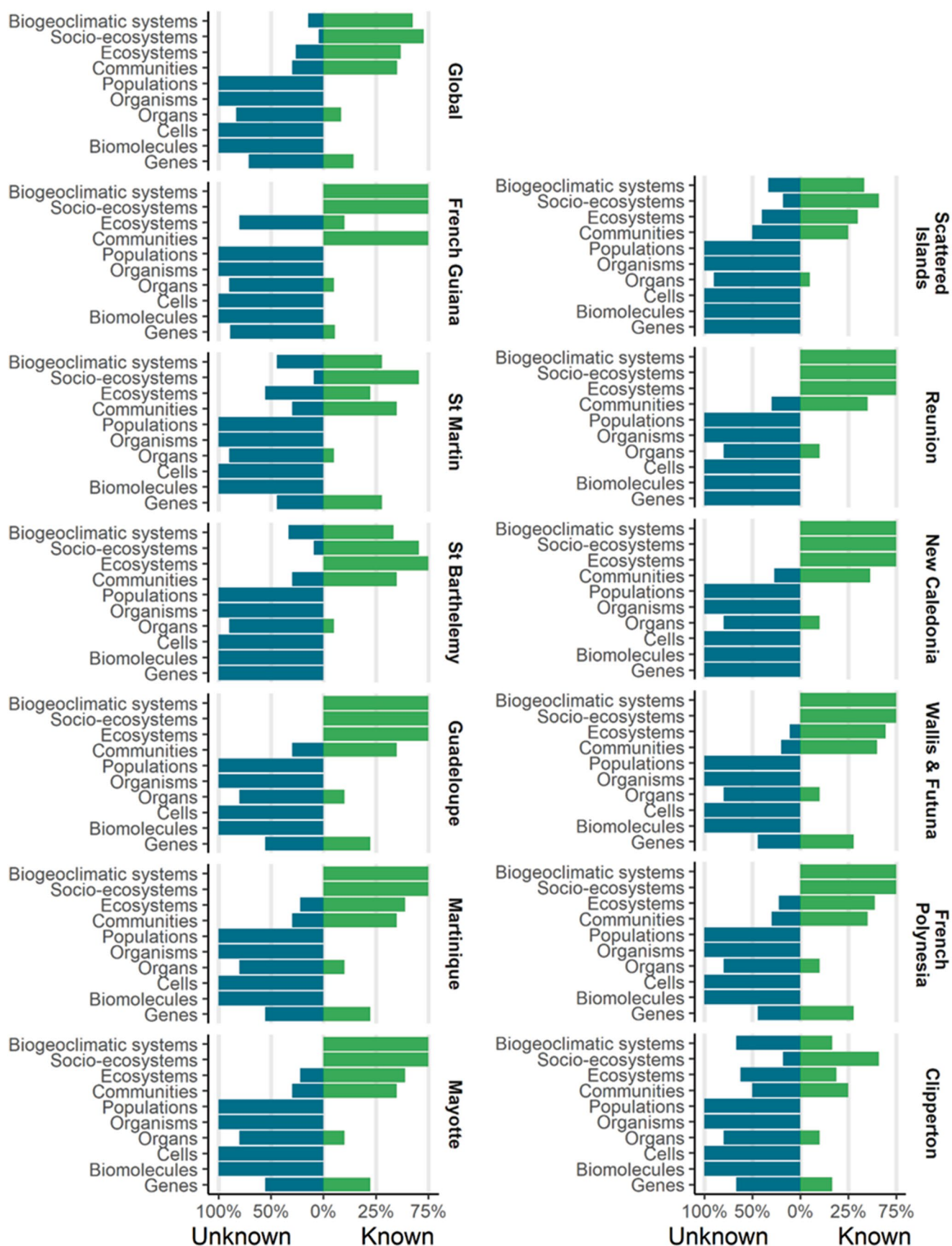


Fig. 10.32 Summarized state of knowledge on coral reef biodiversity by scale of biological and ecological organization and across French tropical overseas. Proportions of knowledge and knowledge gaps are

estimated based on data completeness for the different metrics presented in Figs. 10.5–10.30, which is in part influenced by data accessibility for the purpose of the present study

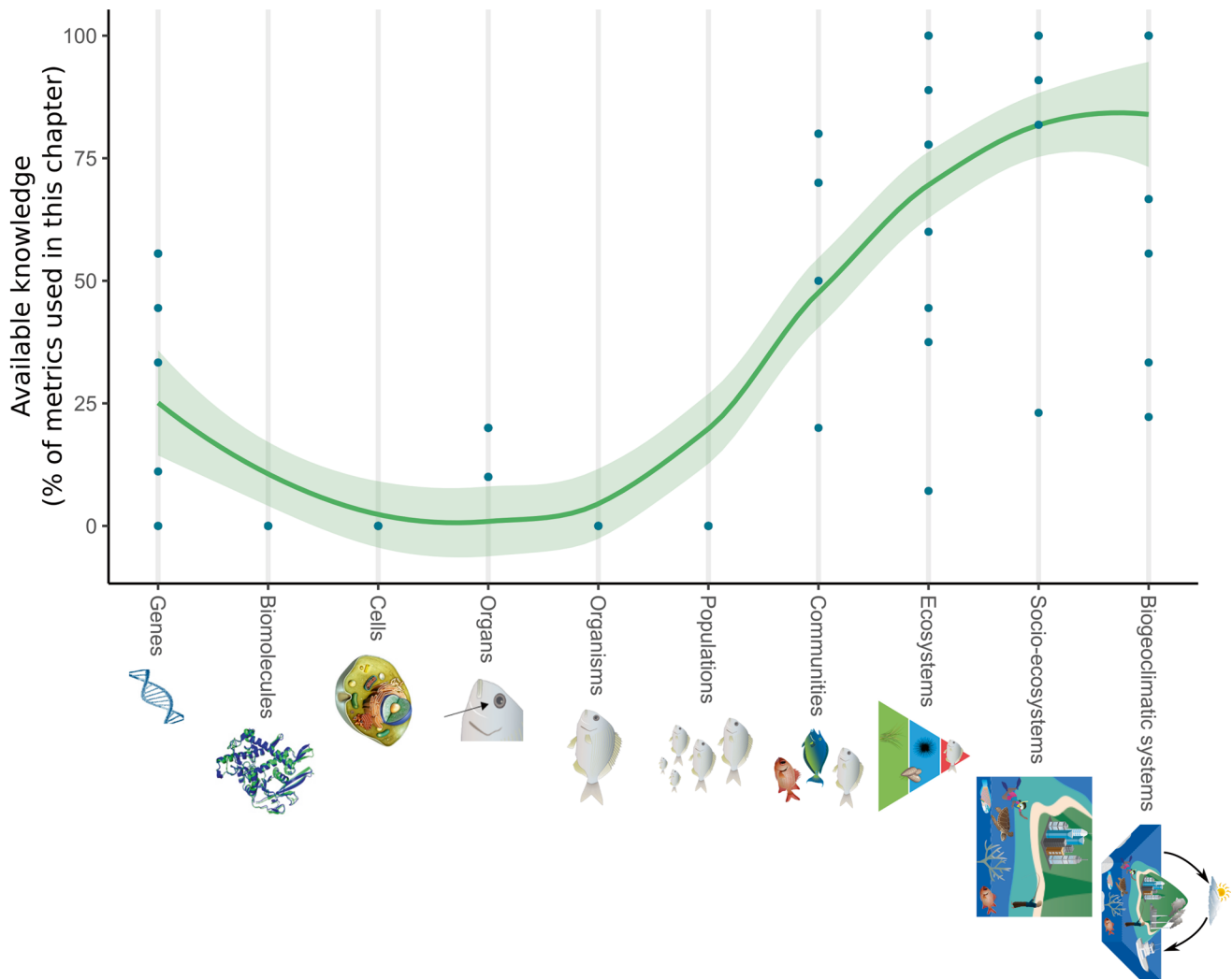


Fig. 10.33 Relationship between the state of knowledge (% of acquired data) and scale of biological and ecological organization, based on Fig. 10.32. Percentage of knowledge is estimated based on

data completeness for the different metrics presented in Figs. 10.5–10.30, which is in part influenced by data accessibility for the purpose of the present study

and 10.33), which accords with the young age of scientific disciplines and limitations in exploring biodiversity at smaller spatial scales, although genetic and molecular approaches are becoming more accessible. Similarly, little data is available for small and cryptic organisms such as bacteria, viruses, and fungi, while ecologically key and emblematic macroorganisms such as reef-building corals and fishes have been more studied. Global databases play a central role in synthesizing and making such knowledge available, though are still lacking for many biological groups and disciplines. Coral reef biodiversity metrics are also unbalanced in space as reflected among French tropical overseas, although such shortcomings are also observed in other types of ecosystems where knowledge and conservation are highly skewed (Guerra et al. 2020; Maxwell et al. 2020). Little is known on cryptic and mesophotic habitats, which are considered potential refuges for corals in a warmer climate and

whose exploration is only starting, including the recently discovered Great Amazonian Reef, parts of which lie in French Guinea waters (Moura et al. 2016; Francini-Filho et al. 2018; Pérez-Rosales et al. 2021b; Pérez-Rosales et al. 2022). There are still major knowledge gaps in most if not all metrics of biodiversity, and some estimations come with significant uncertainties, including recent questioning on species delineation and the speed of acclimation versus adaptation processes (Galtier 2019; Gibert et al. 2019). Overall, most of our knowledge relates to the state of coral reef biodiversity and its distribution as measured at different scales, whereas our understanding of driving mechanisms controlling biodiversity levels across scales and their dynamics remains yet too limited to enable predictions and therefore more proactive management strategies for biodiversity resiliency in the face of environmental changes (Rogers et al. 2015; Donovan et al. 2023). Nevertheless, some coral reef

sites stand out as world references for exploring coral reef biodiversity and its drivers Thirukanthan et al. 2023. This includes portions of the Great Barrier Reef in Australia, such as Lizard Island (<https://australian.museum/>), the island of Moorea in French Polynesia, which is arguably the most studied reef system on the planet, thanks to two international field research stations acting as hubs for coral reef studies (www.criobe.pf, www.moorea.berkeley.edu) and coral reefs near Noumea in New Caledonia that have benefited from locally based scientific attention since the 1940s (www.ird.fr/nouvelle-caledonie).

10.3.14 Conclusions

Coral reef biodiversity expands in a multitude of dimensions associated with the various scientific disciplines and metrics used to characterize the variability of life forms across scales of biological and ecological organization. While biodiversity metrics are known to differ among regions, declining with distance from the center of marine biodiversity in Southeast Asia, our synthesis highlights how they also vary with the size of coral reef systems and the extent of habitats and diversity of ecological niches they provide. The exploration of coral reef biodiversity is a challenging endeavor that concentrates the efforts of an active global research community, as many knowledge gaps remain with significant unbalance between scientific disciplines and regions, alongside the decline in biodiversity levels, with life forms disappearing before they are characterized. In the face of the current biodiversity crisis, our knowledge of coral reef biodiversity appears quite superficial compared to the in-depth understanding needed to anticipate, detect, and counter ecological declines. This entails new research avenues, particularly transdisciplinary approaches to bridge our understanding of biological, ecological, and biogeoclimatic processes across scales of bioecological organization, endeavors that remain largely insufficient to comprehend the mechanisms behind biodiversity production and maintenance and safeguard their future (Jones et al. 2015; Smallegange et al. 2017; Carturan et al. 2020; Condie et al. 2021; Ouédraogo et al. 2021; Van Woesik et al. 2022; Carlot et al. 2023; Ouédraogo et al. 2023). Unanswered questions critical to human survival throughout the twenty-first century pertain to the carrying capacity of ecological systems and the effectiveness of societal paths toward sustainability. Due to their unique biodiversity and associated level of scientific attention, coral reef systems can be key to addressing these questions. In the global landscape of coral reef biodiversity, French tropical overseas are major players in this realm, thanks to their unique distribution, coverage, and a robust management and research network supported by the public system (Cocquempot et al. 2019). This unique combination provides a large set of data-rich systems that allow exploration of how

biodiversity takes form at different scales of bioecological organization and interacts with human and climatic environments. While coral reef biodiversity has received increased national and international attention, restrictions in scientific research funding remain a primary impediment to advance understanding and hence conservation of biodiversity in coral reefs and globally (Huang and Huang 2018; Thirukanthan et al. 2023).

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