Marine conservation in a changing climate and for deep ecosystems

Juliette Jacquemont

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Luke Tornabene, Chair

Joachim Claudet

Tim Essington

Phil Levin

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Abstract

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Juliette Jacquemont

Chair of the Supervisory Committee:

Luke Tornabene

Aquatic and Fishery Sciences

Human uses of the ocean are intensifying, diversifying, and spatially expanding to respond to the ever-growing food, energy, and material demand of humanity. In this context, marine protected areas (MPAs) have been increasingly promoted as a tool to mitigate impacts from extractive activities and promote sustainable uses of marine resources. However, while the ecological benefits of highly protected coastal MPAs are well-established, many controversies remain on whether these benefits will perdure under future climatic conditions, and whether MPAs are relevant tools to protect deep offshore ecosystems. This dissertation aims at addressing these uncertainties by (1) clarifying the climate benefits that MPAs can provide, (2) assessing the conservation status across depth zones of the ocean, and (3) advancing the ecological knowledge of deep-reef ecosystems to better inform their conservation. In chapter 1, I conduct a meta-analysis and demonstrate that MPAs with high levels of protection can significantly enhance multiple climate mitigation and adaptation pathways including carbon sequestration, coastal protection, species richness, and fishers' catch and income. In chapter 2, I found that conservation efforts are unevenly distributed among depths and tend to be biased towards areas with the lowest fishing efforts. In chapter 3 and 4, I evaluate the taxonomic and functional diversity of Caribbean reef-fish communities across multiple depth zones from the surface to the deep-sea boundary (< 300 m). This dissertation highlights the importance of MPAs in supporting the resilience of socio-ecological systems to climatic pressures and sheds light on the unique diversity of deep reefs, which require dedicated conservation efforts to achieve targets of ecological representation.

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DEDICATION

I dedicate this dissertation to the Ocean and all marine life that has inspired, motivated, and fueled my past years of work and the many more to come.

GENERAL INTRODUCTION

Striking a sustainable management of natural resources is one of humanity's existential challenges in the 21st century (Pörtner et al., 2023). On land like in the ocean, many natural resources are being extracted at a rhythm exceeding their regeneration rates (Jackson et al., 2001; Jouffray et al., 2020). Concomitantly, many ecosystems supporting these resources are collapsing due to environmental and anthropogenic pressures including climate change, habitat loss, and pollution (Atwood et al., 2017; Bellwood et al., 2004; Rilov, 2016). In the ocean, the technical difficulty of surveying marine resources and managing human uses has led to an important lag in the development of marine management and policy sciences compared to terrestrial sectors. Poorly managed human uses have resulted among other impacts in overfishing and the subsequent collapse of major fisheries (Worm et al., 2009). Today, human uses of the ocean are further diversifying, intensifying, and expanding toward deeper and further offshore areas (Jouffray et al., 2020), with only limited visibility on their impacts on marine ecosystems (Cordes & Levin, 2018; Halpern et al., 2019). Given the high reliance of humanity on marine resources for food security, culture, energy, and material, it is paramount to ensure that marine uses are managed in a way that can perdure for generations to come.

Among management options to achieve a sustainable use of marine resources, marine protected areas (MPAs) have been demonstrated as the most effective tool to support the recovery of ecosystems impacted by direct human pressures, in particular fisheries (Costello & Ballantine, 2015; Grorud-Colvert et al., 2021). MPAs are spatially defined, permanent areas that are primarily managed for the protection of marine ecosystems. MPAs that decrease extractive uses can significantly increase the biomass, abundance, and size of marine organisms (Costello, 2014; Edgar et al., 2014; Lester et al., 2009). MPAs are particularly effective when implemented in areas experiencing high fishing pressure, and when adequately designed can generate benefits to both marine ecosystems and local fishing communities through the spillover of fish beyond their borders (Di Lorenzo et al., 2020). Unfortunately, both the quantity of conservation coverage and its quality are falling short of the international commitments set by the Global Biodiversity Framework and the design and management of most MPAs do not abide with best practices emitted by the scientific community (Pike et al., 2024). While 196 countries have agreed to reach 30% of marine conservation coverage by 2030, only 8.3% of the ocean was protected as of 2025, primarily within nations' exclusive economic zones (MPAtlas, 2025). Furthermore, most MPAs only provide limited protection against extractive uses or are placed in remote areas that are not targeted by human uses in the first place, limiting conservation benefits (Claudet et al., 2021; Devillers et al., 2015).

While some ecological benefits provided by MPAs are now well established, many knowledge gaps and controversies remain on the full range of benefits that MPAs provide, the conditions under which these benefits accrue, and the associated socio-economic trade-offs

(Hilborn, 2018; Pendleton et al., 2018). Ongoing controversies include (1) the socio-economic impacts of MPAs (Ban et al., 2019); (2) the effects of MPAs on fisheries and food security (Hilborn & Kaiser, 2022; Vandeperre et al., 2011); (3) the capacity of MPAs to provide ecological benefits under climatic changes (Bates et al., 2019; Roberts et al., 2017); and (4) the efficacy of MPAs to protect pelagic and deep ecosystems (Game et al., 2009; Pons et al., 2018). Additionally, marine conservation is being faced with two temporal and spatial challenges: the increasing impacts of climate change on marine ecosystems (Pörtner et al., 2019) and the expansion of human impacts in deeper and off-shore ecosystems (Crespo et al., 2019; O'Leary et al., 2020). Both challenges fuel doubts on the future adequacy of MPAs as conservation tools (Schindler & Hilborn, 2015) because their static nature does not accommodate shifts in species range nor encompass the range of offshore species, many of which are pelagic and highly migratory (Game et al., 2009; Mee et al., 2017). While "climate-smart" MPAs, which are designed to be effective in a changing climate (e.g., by targeting refuge areas, promoting connectivity or accounting for range shifts), are becoming increasingly popular (Brito-Morales et al., 2022; Jones et al., 2016; Wilson et al., 2020), we still have a limited understanding of whether current conservation benefits can be achieved under increasing climatic pressures. The well-established ecological benefits generated by MPAs have been theorized to enhance ecological resilience through portfolio effect and enhanced connectivity, but the evidence supporting these speculations remain disparate and contradictory (Bates et al., 2019; Roberts et al., 2017).

Similarly, important knowledge gaps hinder our capacity to evaluate the types of benefits to be expected from MPAs established in deep, offshore areas. Historically, the establishment of MPAs has mostly been limited to coastal and shallow ecosystems (Biber et al., 2022; O'Leary & Roberts, 2017). However, the international target of reaching 30% of protected ocean by 2030 now requires extending the MPA network to incorporate deeper areas. This extension is also important to match the concurrent spread of human uses in the deep ocean. Further, the UN Convention on the Law of the Sea will soon enable the management and conservation of areas beyond national jurisdiction (Brito-Morales et al., 2022; O'Leary et al., 2020), providing the legal framework to vastly expand the conservation network in the high seas. The anticipated expansion of the MPA network towards offshore ecosystems requires a better understanding of which areas most need protection and of how to design MPAs that can provide ecological benefits to deep ecosystems (Levin et al., 2018; Venegas-Li et al., 2018). Because many deep ecosystems remain data deficient, bolstering the study of the spatial and vertical distribution of diversity in these ecosystems is paramount to guide and justify conservation efforts.

Topical deep reefs figure amongst these deep ecosystems that remain poorly studied and poorly protected (Rocha et al., 2018; Soares et al., 2020). Deep reefs are highly diverse and taxonomically rich ecosystems that extend on coastal slopes below the well-described shallow reefs (Lesser et al., 2018; Turner et al., 2017). While they were thought to be sheltered from

human and environmental pressures, increasing evidence is demonstrating that deep reefs are also affected by climatic pressures, disease outbreaks, and human extractive uses, including fisheries (Appeldoorn et al., 2016; Bo et al., 2014; Ho et al., 2020). However, these ecosystems remain poorly described, with a limited understanding of their biodiversity patterns and ecosystem processes (Radice et al., 2024). These knowledge gaps constitute one of the barriers currently impeding the adequate inclusion of deep reefs in conservation and management plans. However, thanks to their proximity to the coast and their relative ease of access compared to deep-sea ecosystems, an increasing number of new technologies are allowing the observation of deep reefs, representing an opportunity to advance our knowledge and support the management of these ecosystems (Robertson et al., 2022). In chapter 3 and 4, I provide an analysis of the taxonomic and functional diversity of deep-reef fish communities, as well as their community structure across depth, to build the baseline knowledge required to inform marine spatial planning.

My dissertation addresses two challenges and knowledge gaps in the field of marine conservation: the unknown capacity of protected areas to support socio-ecological systems under climate change, and how to adequately incorporate deep ecosystems into the conservation network. In chapter 1, I examine the debated capacity of MPAs to provide climate benefits by identifying pathways through which MPAs could support the resilience of socio-ecological systems and performing a systematic review followed by a meta-analysis of studies documenting each of these pathways. In chapter 2, I assess the protection status of the main ecological depth zones across the ocean's ecoregions and determine which depth zones require the most additional conservation effort based on current protection coverage, levels of protection, and global distribution of fishing pressure. In chapter 3 and 4, I focus on a deep ecosystem that is currently underprotected, understudied, but under high human pressure: deep reefs. The aim of these chapters will be to advance our understanding of the taxonomic (chapter 3) and functional (chapter 4) vertical zonation of reef-fish communities in order to establish baseline knowledge to inform future management and conservation plans.

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CHAPTER 1
Ocean conservation boosts climate change mitigation and adaptation

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1.1. Abstract

Marine protected areas (MPAs) are increasingly being promoted as an ocean-based climate solution. Yet such claims remain controversial due to the diffuse and poorly synthesized literature on climate benefits of MPAs. To address this knowledge gap, we conducted a systematic literature review of 22,403 publications spanning 241 MPAs and analyzed these across 16 ecological and social pathways through which MPAs could contribute to climate change mitigation and adaptation. Our meta-analysis demonstrates that marine conservation can significantly enhance carbon sequestration, coastal protection, biodiversity and reproductive capacity of marine organisms, as well as fishers' catch and income. Most of these benefits are only achieved in fully or highly protected areas and increase with MPA age. Although MPAs alone cannot offset all climate change impacts, they are a useful tool for climate change mitigation and adaptation of social-ecological systems.

1.2. Introduction

Climate change has started to undermine human well-being and planetary health, generating a sense of urgency to identify effective mitigation and adaptation strategies(Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change., 2022). Recent years have seen a growing focus on the ocean's central role for the climate(Pörtner et al., 2019) as well as an increase in associated advocacy efforts. This is reflected, among other things, in the increasing inclusion of ocean issues in Nationally Determined Contributions, for both climate mitigation and adaptation(Gallo et al., 2017).

Considerable consensus exists on the cascading impacts of climate change on marine ecosystems and coastal communities(Gattuso et al., 2015; Hoegh-Guldberg & Bruno, 2010; Pörtner et al., 2019; Thiault et al., 2019), but no such consensus exists on ocean-based climate solutions(Gattuso et al., 2018). Most notably, while the potential of ocean conservation tools

such as marine protected areas (MPAs) is widely recognized to deliver multiple positive ecological and social outcomes(Grorud-Colvert et al., 2021; Reimer et al., 2020), their ability to contribute to the resilience of marine social-ecological systems to climate change or to carbon sequestration remains highly controversial (Bates et al., 2019; Epstein et al., 2022; Hilborn, 2018; C. M. Roberts et al., 2017). While dogmatism drives part of these disagreements (Pendleton et al., 2018), the underlying scientific challenge lies in the diverse and diffuse body of research that allows to formulate a range of hypotheses on whether or not marine conservation can serve as a climate solution. Some argue that the increases in abundance, biomass and biodiversity of fished populations occurring in MPAs(Giakoumi et al., 2017; Lester et al., 2009; Zupan et al., 2018) promote other ecological outcomes such as reproductive output, genetic diversity or ecosystem stability(C. M. Roberts et al., 2017), ultimately contributing to the adaptive potential of marine ecosystems to climate change(Bernhardt & Leslie, 2013; Miller et al., 2018; O'Leary et al., 2017).

However, few studies have directly tested the effects of MPAs on climate change adaptative potential, and the existing literature shows contrasting results(Freedman et al., 2020; Mellin et al., 2016). Notably, a great amount of literature has shown that MPAs failed at protecting coral reefs from bleaching during heat waves(Bruno et al., 2019). In some instances, coral losses have even been shown to be greater in MPAs than in unprotected area. This phenomenon, referred to as "the protection paradox"(Bates et al., 2019) has fueled much of the opposition in advocating MPAs as a tool for climate adaptation.

The effects of marine conservation on social adaptive potential are another contentious topic, as millions of livelihoods directly depend on fisheries, for both income and food security. While MPAs have been shown to provide benefits to fisheries thanks to the spillover of fish from protected to fished areas(Di Lorenzo et al., 2020), controversy remains on the overall costs and benefits to fishing communities(Ban et al., 2019; J. Cinner & Huchery, 2014; Hilborn, 2016). Because coastal populations are among the most vulnerable to climate change(Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change., 2022; Pörtner et al., 2019) it is paramount to identify solutions that will not further negatively impact their resilience(J. E. Cinner et al., 2018; Mora et al., 2013). However, no synthesis of the literature examining how MPAs impact social adaptive potential exists, casting doubts on whether marine conservation can be used as a holistic tool that benefits both marine ecosystems and coastal communities(J. E. Cinner et al., 2020).

Debate has also centered on the ability of MPAs to provide climate mitigation benefits, notably through increased carbon sequestration from rebuilt fish populations or from undisturbed sediments from trawling bans(Epstein et al., 2022; Mariani et al., 2020). Achieving clarity on how ocean conservation contributes to ecological adaptation, social adaptation and climate

change mitigation, is urgently needed to ensure that effective ocean-based strategies are adopted in climate change policies.

To address these knowledge gaps, we identified the potential pathways through which MPAs could contribute to climate change mitigation and adaptation (hereafter referred to as "climate pathways"). A layered typology was used to classify these climate pathways: first along mitigation and adaptation dimensions, and then distinguishing among ecological and social dimensions of adaptation. We then carried out a systematic literature review and summarized the results of all empirical studies documenting MPA outcomes on these climate pathways using both vote-counting and a meta-analytical approach. Vote-counting, i.e., calculating the fraction of studies reporting positive, negative or neutral outcomes, allows to synthesize results from quantitative and qualitative studies and to overcome publication biases associated with meta-analysis. For these reasons, it is commonly used in social science(Ban et al., 2019; Mascia et al., 2010) but also in ecology(Leung et al., 2022; Wittmann & Pörtner, 2013). When sufficient quantitative data was available to perform meta-analysis, we also quantified the direction, magnitude and uncertainty of MPA outcomes on climate pathways. As previous analyses have shown that high levels of protection are required to achieve ecological (Zupan et al., 2018) and social (Turnbull et al., 2021) outcomes, we also investigated whether this was a necessary condition for MPAs to produce climate mitigation and adaptation benefits.

Our literature review found that marine conservation enhances most ecological and social climate pathways. Furthermore, meta-analyses showed that MPAs significantly increase carbon sequestration, coastal protection, biodiversity and reproductive capacity of marine organisms, as well as fishers' catch and income. However, these benefits were only achieved under high levels of protection. Altogether, our study provides evidence that MPAs constitute an effective solution for climate change mitigation and adaptation of the intertwined components of social-ecological systems.

1.3. **Methods**

All original code and datasets are publicly available on Zenodo repository under the DOI 10.5281/zenodo.7108799.

1.3.1. Identification of pathways

Pathways through which MPAs could contribute to climate change mitigation or adaptation were identified from the literature. Reviews on ecological and social adaptive capacity of marine systems were screened and components of marine climate change mitigation and adaptation listed therein were attributed to climate pathways. Five reviews were retained (Ban et al., 2019; Bates et al., 2019; Bernhardt & Leslie, 2013; J. E. Cinner et al., 2018; C. M. Roberts et al., 2017) from which a total of 16 pathways were identified as detailed in Table S1. A description of each pathway identified (definition, indicator, unit) is detailed in Table S2. Definition of social adaptation pathways were adapted from (J. E. Cinner et al., 2018).

1.3.2. Systematic literature review search strategy

To investigate the 16 pathways identified in section 1, nine independent systematic searches of published peer-reviewed literature were performed on Web of Science. Social adaptive pathways were reviewed through a unique systematic search because most social studies tackled several social pathways, making it more effective to review articles for all social pathways at once. Following the same logic, the pathways "body condition", "phenotypic plasticity", "resistance" and "recovery" were reviewed jointly, as well as "connectivity" and "reproductive potential". All other pathways were reviewed individually.

To make sure no important article was missed, the database obtained through our systematic literature searches was complemented with studies included in previous systematic reviews relevant to one of our pathways. The following systematic reviews were used to complete our database:

- for social pathways: (Ban et al., 2019);
- for Carbon sequestration: (Epstein et al., 2022; O'Connor et al., 2020; Sasmito et al., 2019);
- for resistance and recovery: (Bruno et al., 2019).

Additional articles identified from expert knowledge or from citations in reviewed publications were also added to our database.

All systematic reviews were performed using Web of Science, with no time limitation and using the "Topic" (titles, abstracts and keywords) search section. The dates at which the searches were performed are detailed in the Data S1 (accessible through the provided zenodo link). All search strings were composed of two parts: a part describing the system of interest, and a part describing the climate pathway. The full search string used for each systematic review can be found in Data S1. Search strings were validated by making sure a set of five pre-selected studies that matched our search criteria were found.

For adaptation pathways, the system of interest was limited to marine protected areas (MPAs), and the search string included all the different designations used to refer to MPAs in the literature: ((“locally managed marine area*”) OR (“locally-managed marine area*”) OR (“community-based marine area*”) OR (“marine community-based area*”) OR (“fisher* closure*”) OR (“marine closure*”) OR (“marine restricted area*”) OR (“restricted marine area*”) OR (“taboos”) OR (“tabus”) OR (“rahui”) OR ("marine protected area*") OR ("marine reserve*") OR ("marine conservation area*") OR ("marine sanctuar*") OR ("marine conserved area*") OR ("marine conserved territor*") OR ("ocean conservation area*") OR ("marine community-based conservation area*")).

For mitigation pathways and coastal protection, the system of interest was enlarged to preserved habitats, because mangroves and marshes benefit from a variety of conservation measures that

act similarly to MPAs by regulating natural resource extraction. To allow for a maximum of results to be found, the search string broadly included the names of the habitats of interest (see Data S1), and the articles were subsequently selected if they compared preserved habitats with degraded controls (see section 2.3).

1.3.3. Screening criteria for the vote-counting approach

Screening of articles was performed using a three-stage process: screening of titles, screening of abstracts and screening of full texts. Some criteria were common to all systematic reviews, while others were specific to pathways. Common screening criteria were the following:

- the article provided primary data collected on the field or in a lab (models, reviews and synthesis were excluded, as well as studies using datasets already presented in previous studies);
- the system studied was a marine or coastal habitat (freshwater systems were excluded);
- the study compared an MPA site with a non-MPA site (or a preserved/restored habitat with a degraded habitat in the case of mitigation pathways and coastal protection), using a before-after or a control-impact design (before-after-control-impact designs were extracted when available);
- studies with pseudo-replication were excluded.

In the case of studies comparing MPAs with control sites (all studies documenting adaptation pathways except coastal protection), screening criteria were the following:

- the control site must be outside of the MPA (comparisons between no-take zones and buffer zones or partially protected areas were excluded);
- the MPA must be a permanent closure (seasonal fishery closures were excluded).

Screening criteria specific to each pathway are detailed in Table S2.

Title and abstract screening were conservative to avoid excluding any relevant studies and were used to phase out those studies that were clearly irrelevant to our search. Selected titles on Web of Science were exported in an Excel file with all their relative (including abstracts). Abstracts of the selected articles were then screened using the abstract screener interface provided by the {metagear} package in R Core Team (2021)(R Core Team, 2024). This package allows to screen through abstracts without showing authors nor the journal's title, limiting sources of bias in the selection process. Articles selected after abstract screening were downloaded and their text fully read to assess whether they were relevant to our search criteria.

1.3.4. Selection of indicators for each pathway

A list of indicators used to describe pathways was identified from the studies that met all screening criteria. When different indicators informed on a same aspect of a pathway, they were grouped together (e.g., larval density and egg density were grouped under reproductive output). When different indicators informed on different aspects of a pathway, they were kept distinct (e.g., reproductive output and recruitment for the "reproduction" pathway). The list of indicators selected for each pathway is detailed in Table S2. For clarity of figures and content, a maximum of two indicators per pathways were presented in the main article. Indicators presented in the main article were chosen to represent contrasting MPA outcomes (e.g., a positive and a negative outcome within the same pathway).

1.3.5. Number of values extracted per study

In the following cases, several values were extracted from a same article:

- when different MPAs were studied;
- when different ecological groups (fish, fished invertebrates, corals, algae, seagrass…) were studied;
- when different stakeholder groups (fishery, tourism, recreational and coastal community) were studied;
- when MPA zones with different levels of protection were studied.

In all other cases, values were averaged between categories (e.g., different species of a same taxon, different religions within a community…) in order to avoid over-representing studies. When timeseries of values were presented for a given MPA, only the most recent data point was kept as the MPA "after" value, and the data point the closest to before MPA establishment was kept as the MPA "before" value.

1.3.6. Qualitative data extracted from screened articles

For each value extracted, the following information was also extracted:

- design of the study: before-after (BA), control-impact (CI) or BACI. For social studies, the category "perception" when MPA outcomes were based on interviews and stakeholders' perceptions;
- MPA name, MPA size (km^2) and MPA age (year) at the time of data collection. MPA age was counted from the moment when the MPA was enforced rather than announced to account for years during which marine ecosystems were effectively protected. When MPAs underwent several stages of extension, we counted MPA age from when the latest extension performed was carried out. When MPA features were not reported in the publication, we used information from the MPA atlas (https://mpatlas.org/);

- the level of protection of the zone studied by the MPA and when present, the size of the fully protected area within the MPA studied (km^2). Levels of protection were determined according to the Regulation Based Classification System for MPAs (Horta e Costa et al., 2016). In addition to information provided in the study, complementary searches were performed using the MPA atlas and the official management declarations of MPAs to determine the level of protection;
- continent, oceanic region, climate of the study location;
- ecosystem, taxon and species studied;
- type of governance and of stakeholder studied for social pathways;
- pathway, indicator, unit, type of error provided in the study.

One spatial point was mapped for each data point used in vote counting and meta-analysis. Spatial points were located at the centroid of the protected area, as found in the MPA atlas (https://mpatlas.org/). Mapping was carried out using {sf} package to manipulate vectors, {maps} to create the background layer and {tidyr} to manipulate datasets. The projection used was Mollweide.

1.3.7. Direction of MPA outcomes reported in vote-counting

For each article meeting our search criteria, the direction reported by the article (i.e., how marine protection influenced the outcomes of the pathway) was extracted. Direction of outcomes were either positive, negative, neutral or ambiguous. “Ambiguous” was used when contradicting trends were reported by the article, and when the article could not conclude on how the MPA affected the pathway. Increases of positive indicators (e.g., participation, alternative livelihoods, catch…) were coded as positive (resp. negative for decreases) while increases of negative indicators (conflict, costs, mortality, coefficient of variation) were coded as negative (resp. positive for decreases).

When results were quantitative and were associated with an error, the direction “neutral” was attributed if the 95 % confidence interval overlapped zero. When results were qualitative or when no error was associated with the results, the direction of the article was determined using the authors’ interpretation of the results in the article’s text.In social studies, the directions of outcomes were often given as percentages, in which case the prevalent category was chosen for the global direction of the study (e.g. 45% positive, 25% neutral and 35% negative was reported as positive). When two outcomes’ proportions were closer than 5% to each other (e.g., 48% negative and 52% positive), “ambiguous” was attributed.

1.3.8. Additional screening criteria for the meta-analyses

Among studies that met our search criteria for vote-counting, we identified those which provided standard statistical data required to perform a meta-analysis, i.e. mean, error and sample size.

Studies providing median values instead of means were excluded. We subsequently identified the most common unit to measure a given indicator in the selected studies and excluded all studies that used units that were not comparable. Several indicators were kept for a same pathway when they informed on different aspect of that pathway (e.g. species richness and Shannon index for biodiversity). The list of indicators kept for each pathway is detailed in Table S2. A meta-analysis was only performed if more than three articles met our criteria for a given indicator.

1.3.9. Quantitative data extraction and preparation

Quantitative results were extracted from the main text, tables and figures of articles and from supplementary material. Mean values and errors were extracted from figures using the online application WebPlotDigitizer Version 4.0 (Rohatgi 2018). Data extraction of the 16 pathways was carried out by three of the co-authors of this study. Data extraction of five studies was first carried out by all co-authors to make sure that the methodology was acquired by all. All data extracted by a co-author was double-checked by another co-author to reduce extraction or calculation mistakes.

All types of errors (standard errors, variance, confidence intervals) were converted into standard deviations (SD). Mean values and variance were calculated when results were presented across categories irrelevant to our study (see 3.1), and sample size were added. The same was done when a publication presented multiple control sites for a unique MPA site. The variance of mean values $s^2_{aggregated}$ was calculated using the following formula:

$$s^2_{aggregated} = \frac{1}{\mathrm{k}^2} \cdot \sum s_i^2$$

with s_i the variance associated with the mean value i being averaged and k the total number of values being averages.

1.3.10. Calculation of effect size

All MPA outcomes (except in two cases, see below) were modelled as the natural logarithm response ratio of the indicator measured inside the MPA and outside the MPA (Hedges et al., 1999). For each study *i*, the MPA effect size ln RR_i were calculated as the log ratio difference of the mean value of the indicator inside ($\bar{X}_{MPA,i}$) and outside ($\bar{X}_{control,i}$) the MPA (control-impact design), or after ($\bar{X}_{after,i}$) and before ($\bar{X}_{before,i}$) MPA establishment (BA design) :

$$\ln RR_i = \ln\left(\frac{\bar{X}_{MPA,i}}{\bar{X}_{control,i}}\right) \text{ for control-impact designs}$$

$$\ln RR_i = \ln(\frac{\bar{X}_{after\ MPA,i}}{\bar{X}_{before\ MPA,i}}) \text{ for before-after designs}$$

In the case of before-after-control-impact design, we calculated the effect size as the log ratio of the ratio of the mean indicator value after MPA establishment inside ($\bar{X}_{after\ MPA,i}$) and outside ($\bar{X}_{after\ control,i}$) MPAs, and before MPA establishment inside ($\bar{X}_{before\ MPA,i}$) and outside ($\bar{X}_{before\ control,i}$) MPAs:

$$\ln RR_i = \ln(\frac{\bar{X}_{after\ MPA,i} \Big/ \bar{X}_{before\ MPA,i}}{\bar{X}_{after\ control,i} \Big/ \bar{X}_{before\ \ control,i}})$$

Positive ln RR_i indicated that the pathway investigated had a higher mean value in the MPA than in the control site. Effect sizes were calculated so that a higher mean value was equivalent to a positive MPA outcome. As a result, the effect size used for the stability pathway was calculated by taking the natural logarithm of the opposite of the ratios detailed above. This is because the indicator used to measure stability (coefficient of variation) is inversely proportional to stability i.e., the greater the coefficient of variation, the lower the stability.

The within-study variance v_i associated with each effect sizes was calculated as:

$$v_i = \frac{s^2_{MPA,i}}{n_{MPA,i} * \bar{X}^2_{MPA,i}} + \frac{s^2_{control,i}}{n_{control,i} * \bar{X}^2_{control,i}} \text{ for control-impact designs,}$$

where $s^2_{control,i}$ and $s^2_{MPA,i}$ are the variances of $\bar{X}_{control,i}$ and $\bar{X}_{MPA,i}$ respectively and where $n_{control,i}$ and $n_{MPA,i}$ are the associated sample sizes;

$$v_i = \frac{s^2_{before\ MPA,i}}{n_{before\ MPA,i} * \bar{X}^2_{before\ MPA,i}} + \frac{s^2_{after\ MPA,i}}{n_{after\ MPA,i} * \bar{X}^2_{after\ MPA,i}} \text{ for before after designs}$$

where $s^2_{before\ MPA,i}$ and $s^2_{after,i}$ are the variances of $\bar{X}_{before\ MPA,i}$ and $\bar{X}_{after\ MPA,i}$ respectively and where $n_{before\ MPA,i}$ and $n_{after\ MPA,i}$ are the associated sample sizes;

$$v_i = \frac{s^2_{before\ control,i}}{n_{before\ control,i} * \bar{X}^2_{before\ control,i}} + \frac{s^2_{before\ MPA,i}}{n_{before\ MPA,i} * \bar{X}^2_{before\ MPA,i}} + \frac{s^2_{after\ control,i}}{n_{after\ control,i} * \bar{X}^2_{after\ control,i}} + \frac{s^2_{before\ MPA,i}}{n_{before\ MPA,i} * \bar{X}^2_{before\ MPA,i}}$$ for BACI designs

where $s^2_{before\ MPA,i}$, $s^2_{after,i}$, $s^2_{before\ control,i}$ and $s^2_{after\ control,i}$ are the variances of $\bar{X}_{before\ MPA,i}$, $\bar{X}_{after\ MPA,i}$, $\bar{X}_{before\ control,i}$ and $\bar{X}_{after\ control,i}$respectively and where $n_{before\ MPA,i}$, $n_{after\ MPA,i}$, $n_{before\ control,i}$ and $n_{after\ control,i}$ are the associated sample sizes.

The effect size used for sediment accretion (coastal protection indicator), and pH buffering were not calculated as a log ratio but as an Euclidean difference. This was done because values of accretion were sometimes positive for the MPA and negative for the control (because of erosion), which did not allow to calculate log ratios, and because variations in pH are best measured through differences. As a result, the MPA effect size d_i and variance v_i for sediment accretion and pH buffering was calculated as:

$$d_i = \bar{X}_{MPA,i} - \bar{X}_{control,i}$$

$$v_i = s^2_{control,i} + s^2_{MPA,i}$$

1.3.11. Parametric data analysis

We used a weighted random-effects model to quantify the effect of MPAs on each indicator. Effect sizes were weighted accounting for both the within- and among-study variance components (Hedges & Vevea, 1998). Models were fitted using the {metafor}(Viechtbauer, 2019) package, under R Core Team (2021)(R Core Team, 2024). Model heterogeneity, residual heterogeneity, degrees of freedom and p-values associated to each model tested are detailed in Table S4. MPAs were considered to have a significant effect of an indicator when the 95% confidence interval calculated by the model did not overlap zero.

1.3.12. Sensitivity analysis

To test the robustness of our meta-analysis results, we carried out a sensitivity analysis to detect : (1) the presence of a publication bias and of outliers using visual observation of funnel plots (Page et al., 2021) (Fig S5.1 to S5.6), (2) the sensitivity of our results to publication bias using the Rosenthal's fail-safe number (N_{fs})(Sampaio et al., 2021), (3) whether a different outcome could be obtained when correcting for publication bias using Duval and Tweedie's Trim and Fill test(Duval & Tweedie, 2000; Shi & Lin, 2019) and (4) the impact of outlier removal on our

results. For meta-analysis which did not have a significant result in the first place (Shannon index, recruitment and recovery), only the Trim and Fill test was performed.

Rosenthal fail-safe number. The Rosenthal's fail-safe number is an estimation of the number of additional non-significant effect size required for a significant meta-analysis result to become non-significant. This allows to check the sensitivity of results to uncaptured studies. This risk is estimated to be high if N_{fs} is below the 5n+10 with n the number of data points in the meta-analysis(Sampaio et al., 2021). This was the case for only one meta-analysis result (resistance), which was the only meta-analysis showing a negative effect of MPAs on resilience attributes (Table S4).

Trim and Fill test. Nine out of 12 meta-analyses showed robust results to the trim and fill test (Table S4). The trim and fill test detected two potentially unstable meta-analysis results: C sequestration by sediments and sediment accretion by blue carbon ecosystems.

Impact of outliers on result. Outlying effect sizes were identified through the visual observation of funnel plots(Page et al., 2021) (Fig S5.1 to S5.6). Additionally, the weight attributed to each effect size by the random-effects models was checked using forest plots (Fig S5.1 to S5.6). This was done to make sure no data point was overrepresented by a much higher weight than those of the other data points. This was not the case for any of our meta-analyses. The studies corresponding to outlying points were scrutinized for factors that could explain the extreme values found. Because no flaw or marked differences in experimental design of these studies were found no points were excluded from our meta-analyses. The one-by-one removal of outliers did not affect any of our meta-analysis results except for the resistance indicator, which became non-significant (Table S4).

1.3.13. Non-parametric data analysis

The indicators associated with genetic diversity and variability (respectively allelic richness and coefficient of variation) were not associated with errors in the literature because of how these indicators are calculated. In order to provide quantitative results from those indicators, we performed non-parametric analyses using boot-strapping. Our boot-strapping analysis was weighted using the sample size associated with each value. MPAs were considered having a significant effect on an indicator when the 95% confidence interval calculated through boot-strapping (n=1000 iterations) did not overlap zero.

1.3.14. Influence of moderators

Influence of moderators were investigated for pathways for which MPAs had a significant positive effect. Heterogeneity tests were run to assess how features (MPA level of protection, size (log-transformed), age, presence of a fully protected area, habitat) could mediate MPA outcomes on climate pathways (Supp. Table 4). All analyses were carried out in R using the {metafor} package(Viechtbauer, 2019).

MPAs of poor and moderate protection levels were grouped into "low level" of protection because sample sizes were too small to evaluate their effect separately. As a result, the effect of level of protection were assessed for full, high and low protection.

1.3.15. Carbon sequestration from fish values

The Carbon sequestration pathway was investigated using key words related to "carbon storage" or "carbon sequestration", which returned very few results for fish. However, C storage in living fish biomass is directly proportional to fish biomass, which has been extensively measured in MPA research. As those studies were not found through our dedicated literature search for C sequestration and many synthetic studies and meta-analyses have already been performed to quantify the effect of MPAs on fish biomass, we based the value of this effect size on previous meta-analysis

The effect of MPAs on fish biomass was calculated from three previous meta-analysis (Edgar et al., 2014; Lester et al., 2009; Zupan et al., 2018). Those three meta-analyses were chosen because they used completely distinct data sets, they are among the most cited publications for effects of MPAs on fish biomass and together, they represent all levels of protection existing in MPAs and cover all oceanic regions of the world. For the effect of level of protection on fish biomass, we used values given in (Lester et al., 2009) for the effect of full protection, and values given in (Zupan et al., 2018) for the effects of low and high protection.

1.3.16. Capacity of habitats to provide climate benefits.

Values of baseline capacity of habitats to provide C sequestration and coastal protection and values of global habitat extent were based on the most recent and extensive available published reviews. Values and the reference of the study from which the values were extracted are detailed in Table S4.

Additionally, we performed a systematic search and meta-analysis following the methodology presented in section 3 and 4 to estimate the amount of C stored in macroalgae and the capacity of mangroves, seagrass and macroalgae to provide acidity buffering. This was done because we found no reviews that provided these values. The search string and date of the systematic search, as well as the indicators selected were the same as those specified for the C sequestration and acidity buffering pathway (Data S1). Studies included in the meta-analysis on pH buffering capacity of marine habitats and on C storage capacity of macroalgae can be found in Data S3 and Data S4 respectively (accessible through the provided zenodo link).

1.3.17. Resistance, recovery and adaptation potential values

Observed resistance and recovery were calculated through meta-analysis, and the methodology used to screen and select relevant empirical studies was as detailed through section 3 and 4. The

search string and date of the systematic search, as well as the indicators selected are detailed in Data S1.

Expected adaptation potential was calculated as the mean value of all effect size contributing to ecological adaptation i.e., allelic richness (genetic diversity), species richness and Shannon index (biodiversity), temporal stability (stability), reproductive output and recruitment (reproduction). The confidence interval was calculated by boot-strapping, using n=1000 iterations.

1.4. **Results and discussion**

1.4.1. MPA mitigation and adaptation pathways

Sixteen pathways through which MPAs could contribute to climate change mitigation and adaptation were identified by drawing on reviews of social and ecological outcomes of MPAs (Ban et al., 2019; Bates et al., 2019; Bernhardt & Leslie, 2013; J. E. Cinner et al., 2018; C. M. Roberts et al., 2017) (Table S1). Two climate pathways contributed to climate mitigation (carbon sequestration and local acidity buffering) and 14 to climate adaptation (Fig. 1). Social adaptation pathways were derived from the five pillars of social adaptive capacity (J. E. Cinner et al., 2018): assets, flexibility, agency, learning and social organization, to which was added food security (J. E. Cinner et al., 2020). Ecological pathways were derived from climate adaptation pathways described in (Bates et al., 2019; Bernhardt & Leslie, 2013; C. M. Roberts et al., 2017): connectivity, phenotypic plasticity, genetic diversity, biodiversity, stability, reproductive output, body condition and coastal protection. Up to two indicators were selected to measure each pathway based on the most common indicators used in the reviewed studies. Additional indicators were also investigated when they allowed to quantify aspects of the studied pathways not yet captured by the first two indicators (Table S2 and Fig. S4). The definition of each pathway and the units used to measure each indicator are detailed in Table S2. For two pathways (C sequestration and coastal protection), we further included all studies comparing exploited and preserved marine areas, even when not officially labelled as MPAs. This was done because the literature documenting the effect of preservation initiatives, comparable to MPAs, is abundant, while almost no study directly documenting MPAs is available.

The systematic literature review on MPA effects on climate pathways generated a total of 22,403 publications of which 378 were included in vote counting, providing insights from 241 different MPAs. Publications were unevenly distributed among continents (Fig. 1B-D), with most ecological adaptation pathways studied in Europe and most mitigation and social adaptation pathways studied in Asia (Supp. Fig.2). We found empirical evidence documenting the effects of MPAs on all climate pathways except for acidity buffering, connectivity and phenotypic plasticity (Fig. 1). Eight climate pathways had sufficient quantitative data (n>3) to perform a meta-analysis.

1.4.2. Marine conservation contributes to Carbon sequestration

We investigated the effects of marine conservation on the Carbon (C) sequestration capacity of six marine C sinks: three Blue Carbon ecosystems (mangrove, tidal marshes and seagrass), which have already been recognized by the IPCC for C accounting schemes (Groupe d'experts intergouvernemental sur l'évolution du climat, 2014), as well as sediments, macroalgae and fish(Krause-Jensen et al., 2018; Mariani et al., 2020). C sequestration was defined as organic C stored for over 100 years(Griscom et al., 2017). Significant increases in C sequestration were found in preserved or restored seagrass (lnRR=0.76 ± 0.34) and mangrove (lnRR=0.75 ± 0.14) in comparison to similar areas undergoing human pressures (e.g. thinning, anchoring, conversion to plantations). Similarly, untrawled sediments sequestered significantly more C than areas exposed to trawling (lnRR=0.13 ± 0.10). Conservation had no effect on the C sequestered by tidal marshes (Fig. 2D), mostly because the conversion of unprotected marsh into agricultural land increased the C sequestered in plant biomass and in the soil (W. Yang et al., 2019). Partial (e.g., thinning, anchoring) or full (e.g., clear-cutting, excavating) degradation of mangroves and seagrass both resulted in similar decreases of sequestered C, indicating that even low levels of human impact result in important C emissions (Fig. S6). No studies documented the effect of protection on the quantity of sequestered C originating from fish or macroalgae biomass. However, many studies have shown that MPAs significantly increase fish biomass (lnRR=1.10 ± 0.58)(Lester et al., 2009), which can serve as a proxy for C sequestration since a portion of that biomass undergoes exportation and is subsequently sequestered in the deep sea(Saba et al., 2021). This is supported by several studies that calculated large impacts of fisheries on C sequestration from fish biomass removal (Mariani et al., 2020; S. L. Martin et al., 2016). However, this remains an indirect measurement of C sequestration, and further research is needed to quantify the exportation rates of organic C from fish biomass towards sediments(Stafford et al., 2022). Although macroalgae are increasingly being advocated as significant actors in marine C sequestration(Krause-Jensen et al., 2018; Ortega et al., 2019), major knowledge gaps remain on how marine conservation affects their living biomass and thus their contribution to C sequestration.

While the effect of MPAs on local acidity buffering was not documented by any study, our meta-analysis revealed that seagrass increased mean local pH, and that mangrove and macroalgae decreased it (Fig. 3). Benefits to the adaptive potential of marine organisms could arise from exposure to greater pH fluctuations that occur in vegetated habitats that has been shown to increase tolerance to acidification (Cyronak et al., 2018). More research is required to support this hypothesis and to assess whether the conservation of vegetated habitats could benefit pH buffering or acidity tolerance.

1.4.3. Contribution of MPAs to ecological adaptation

We found that MPAs contribute to ecological adaptation by increasing biodiversity levels, reproductive output and coastal protection compared to unprotected sites (Fig. 2C). Species

richness was higher inside MPAs (lnRR=0.20 ± 0.10) in agreement with previous regional (Giakoumi et al., 2017) and global(Claudet et al., 2008) meta-analyses but Shannon index was unchanged between protected and unprotected sites (lnRR=0.06 ± 0.06). Increased species richness could play a central role in climate adaptation because more species increases the odds that ecosystem functions are maintained even after a stressor eliminates certain species (Duffy et al., 2016), a concept referred to as the insurance hypothesis (Yachi & Loreau, 1999). Effects of MPAs on the reproductive output of marine organisms (measured as increased larval densities and egg production) had the greatest magnitude of all studied pathways (lnRR=1.21 ± 0.96). This likely results from larger, older and more abundant individuals in MPAs, leading to an increased production of offspring (Hixon et al., 2014). By contrast, recruitment rates showed no significant increase, which could be explained by the higher predation rates on recruits experienced in MPAs (Galzin et al., 2000). Reproductive capacity is an important attribute of adaptation because it is linked to faster rates of population recovery (Micheli et al., 2012) and increased larval dispersal distance, which in turn can promote populations' connectivity and ability to colonize new habitats (Hixon et al., 2014).

Preservation of mangroves and tidal marshes enhanced coastal protection through soil accretion rates of an additional 1.38 ± 0.88 cm $year^{-1}$ when compared to degraded habitats. Coral reefs and seagrass can also contribute to coastal protection through wave attenuation (Fig. 3), but no studies have assessed whether wave attenuation is enhanced when habitats are within an MPA. However, wave attenuation is linked to a habitat's structural complexity and vegetation density (Ferrario et al., 2014; Shepard et al., 2011), which suggests that habitats protected from physical disturbance would perform better than degraded habitats. We found that MPAs increased ecosystem stability although quantitative evidence remains too low to draw general conclusions (lnRR=0.10 (-0.03, 0.63), n=5). MPAs had no effect on genetic diversity (measured as allelic richness, expected heterozygosity and observed heterozygosity; Fig. 2C and Fig. S7). This is consistent with the one previous regional meta-analysis (Wennerström et al., 2017) that also found no effect of MPAs on genetic diversity.

Body condition could only be assessed through vote-counting, and studies mostly reported a neutral effect of MPAs (Fig. 2B). Connectivity and phenotypic plasticity were not addressed by any studies. Greater larval and egg densities in MPAs do indicate an increased potential for dispersal, but whether this potential effectively translates into increased connectivity with adjacent areas remains to be evidenced, using indicators such as fixation index (Hadi et al., 2020). The ability of MPAs to enhance connectivity constitutes a major knowledge gap, as connectivity is one of the most important pathways for adaptation to climate change, by allowing recolonization of disturbed habitats, gene exchanges, and climatic migrations (Carr et al., 2017).

1.4.4. Contribution of MPAs to social adaptation

Among social adaptation pathways, food security and assets displayed sufficient quantitative data to perform meta-analyses. MPAs significantly increased food security (lnRR =0.43 ± 0.21, Fig. 2C) measured using catch per unit effort (CPUE). Increase in CPUE arise from the replenishing of fish populations in MPAs which can subsequently spillover into fishing grounds, benefiting to local fisheries (Di Lorenzo et al., 2020). Increase in CPUE occurred when comparing fishing inside and outside MPAs, in the case of partially protected areas, and when comparing fishing near and far from MPAs (Fig. S8). In both cases, we only observed increases in CPUE when the MPA included or was a fully protected area i.e., a protected area where no fishing is allowed (Fig. 2F). Our results oppose those of a regional meta-analysis (Vandeperre et al., 2011), which found a negative impact of MPAs on the CPUE of Southern European fisheries. We suggest that our results, built on a higher number of studies and a wider geographical scale, overcome the specificities of this previous meta-analysis and better reflect the effects of MPAs on fisheries. This result is further backed-up by the observed increase in fishers' income in the presence of a fully protected area (lnRR=0.35 ± 0.29). Increased fishers' income demonstrates that MPAs can offset costs generated by the displacement of fishing grounds. Increases in CPUE and income support the long-running controversy that MPAs can enhance the livelihood of fishers, which in turn contributes to building social adaptive capacity to climate change through increased food security and assets.

MPAs had a majority of positive outcomes across all social adaptive pathways (i.e., 8 indicators out of 11) with the exception of social organization (Fig. 2B and Supp. Figs. 3-4). In addition to CPUE and income benefits, the most positive social adaptive outcomes of MPAs were increases in environmental awareness (95% of cases), participation (57% of cases), and alternative livelihood (48% of cases). These findings are consistent with previous systematic reviews (Ban et al., 2019; Mascia et al., 2010). The three indicators for which we found negative outcomes of MPAs were user-rights, conflict and costs (used to measure agency, social organization and assets pathways, respectively). In 65% of cases, users-rights were negatively affected by access and extraction restrictions imposed by MPA regulation, hence reducing local people's agency (J. Cinner & Huchery, 2014; van de Geer et al., 2013). Increases in conflicts (59% of cases) arose from changes in the spatial use of marine areas, potentially leading to tensions between different activity sectors, e.g., tourism operators and fishers (Y.-C. Yang et al., 2013). However, MPAs increased social cohesion (56% of cases), likely resulting from a shared conservation vision, and sense of purpose between stakeholders (Gollan & Barclay, 2020). Such discrepancy of MPA outcomes on conflict and cohesion suggests that impacts of MPAs on social organization are strongly context-dependent.

1.4.5. Conditions under which MPAs deliver climate benefits

We found sufficient data to investigate the effect of the level of protection, age and size of MPAs on four climate pathways (C sequestration, biodiversity, CPUE and income).

Across all four pathways, only full and high levels of protection resulted in mitigation or adaptation benefits (Fig. 2E). In contrast, low levels of protection generated no benefits. Furthermore, increases in species richness and in fishers' income only occurred for fully protected areas, where no fishing is allowed. Increases in CPUE and in C sequestration were also achieved by highly protected areas, where low-impact fishing is allowed. However, this was only the case if a fully protected area was also present in the MPA considered.

All four climate pathways were positively correlated with MPA age (Fig. S9, Table S5). This is explained by the time required for exploited fish stocks to rebuild and subsequently benefit adjacent fisheries. Similarly, C sequestration was positively correlated with the number of years since restoration of mangrove and seagrass. CPUE was positively correlated with MPA size (Fig. S10), which can result from a greater proportion of mobile fish having their home ranges included in the MPA (Villegas-Ríos et al., 2021). Level of protection, age and size have already been established as important drivers and enabling conditions for MPAs to deliver positive ecological outcomes (Edgar et al., 2014; Zupan et al., 2018). Our results show that this is also the case for climate mitigation and adaptation benefits.

In addition to size, age and protection level, the magnitude of climate benefits achieved through protection depends on the marine habitat considered. Indeed, the characteristics of each marine habitat influence their ability to contribute to climate pathways and their spatial extent determines their maximum potential contribution to climate change adaptation and mitigation (Table S6). This is particularly true for the C sequestration, coastal protection and acidity buffering pathways, which derive from ecosystem services delivered by specific habitats. Habitats with high C sequestration potential but low spatial extent (e.g., mangrove and seagrass, Fig. 3) translate into a high mitigation potential per surface area, but into a low mitigation potential at global scale. Conversely, fish and sediments have lower mitigation potential per surface area but can play an important role in global climate mitigation because of their vast extent. More research on sediments, and new or updated IPCC guidelines for including sediments and other marine carbon pools into national greenhouse gas accounting, would help making MPAs more actionable in climate change mitigation and including them into Nationally Determined Contributions (NDCs).

1.4.6. From adaptation pathways to resilience

To test whether the enhanced ecological pathways found in this study effectively translate into increased climate adaptation, we performed two complementary meta-analyses quantifying the effect of MPAs on the resistance and recovery of marine organisms to climatic stressors. Our systematic literature review identified 19 papers that focused exclusively on warm-water coral species. We found that MPAs had a negative effect on the resistance of corals ($lnRR = -0.38 \pm 0.36$) and no effect on their recovery ($lnRR = 0.04 \pm 0.23$) to climatic stressors (Fig. 4), which is consistent with previous findings (Bruno et al., 2019) and referred to as the "protection paradox" (Bates et al., 2019). In contrast, we found a significantly positive effect of MPAs on expected

ecological adaptation (lnRR= 0.31 (0.03-0.87)), calculated from all the data points included in resilience-related pathways (stability, biodiversity, genetic diversity and reproduction). The gap between the expected adaptation benefits that should emerge from enhanced ecological pathways and the observed absence of improvement in resistance and recovery of marine organisms could result from (1) the fact that the adaptation pathways we measured are inappropriate or too indirect to inform on adaptation capacity or (2) differences in the studied system between recovery/resistance studies and adaptation pathways studies. The latter hypothesis likely plays an important role in this gap, as all studies on recovery and resistance focused on corals whereas most studies documenting adaptation pathways focused on fished species. Additionally, not only is the literature on conservation outcomes on resilience biased towards coral species, but it has also been shown to be further biased towards specific oceanic regions(Roff & Mumby, 2012). Furthermore, the ability of MPAs to enhance ecological adaptation results mostly from the alleviation of fishing pressure, which represents a minor threat to corals in comparison to temperature rise and acidification (Hoegh-Guldberg et al., 2017). In contrast, fishing pressure is currently the main threat to fished species, which is why fully protected areas were observed to enhance several adaptation pathways. As a result, the "protection paradox" observed for corals cannot be generalized to other taxa, and dedicated studies should be performed to test how MPAs affect the climatic resilience of fished species. Although evidence remains scarce, both theoretical (Cheung et al., 2017; Hopf et al., 2019) and empirical (Emslie et al., 2015; Mellin et al., 2016) research suggests positive effects of MPAs on the resilience of fish populations. Further research is required to test whether the enhanced adaptation pathways reported in this study effectively translate into enhanced resilience of fished species.

1.4.7. Climate-smart MPA designs

A growing body of literature has focused on the design characteristics of "climate-smart" MPA features, aimed at maintaining current conservation benefits under future climatic conditions. Recommendations have included MPA networks that account for future patterns of connectivity under changing oceanic currents, spatially dynamic MPAs that follow species migrations, or the protection of climatic refuges such as upwelling sites (Tittensor et al., 2019; Wilson et al., 2020). Although these elements are certainly worth considering when designing an MPA, a recurring theme in our results is that MPAs must be highly or fully protected to provide a broad range of benefits, including positive climate change mitigation and adaptation outcomes. The clear signal that level of protection should take precedence in MPA design is in stark contrast to the current paradigm of ocean protection globally, with the proportion of fully and highly protected MPAs worldwide plummeting as countries have rushed to meet conservation commitments (Claudet et al., 2021). Ensuring high protection levels in existing marine protected area should be the priority to secure climate benefits to coastal social-ecological systems.

1.4.8. MPA governance

The diverse effects of MPAs on social organization and agency of coastal communities underscore that governance is a fundamental factor in determining whether MPAs will enhance or impede social adaptation. Indeed, the outcomes of several social adaptation pathways, such as agency and learning, result from how local stakeholders are included throughout MPA establishment and management (J. Cinner & Huchery, 2014; Weeks & Jupiter, 2013). The involvement of stakeholders through co-management allows to identify people's needs and to minimize negative social impacts, e.g., by developing alternative livelihoods options or conflict resolution tools (Christie et al., 2017). Positive perceptions of governance by local stakeholders has also been shown to increase support and compliance with MPA regulations (Chaigneau & Brown, 2016), which in turn allows for ecological benefits to accrue (Di Franco et al., 2016). This results in a positive feed-back loop whereby perceived ecological benefits act as a further incentive for communities to support MPAs (Di Franco et al., 2020), and allow for food security and asset benefits to accrue. To promote social adaptive capacity, there is benefit for MPA managers to thoroughly consult and inform local communities about MPAs' goals and rules (Bennett & Dearden, 2014), to involve local communities in MPA management and decision-making (Voyer et al., 2015), to identify potential negative social outcomes of MPAs and find solutions to avoid, reduce or compensate for them (Voyer et al., 2014), and to monitor MPA social outcomes and adjust MPA governance accordingly (Weeks & Jupiter, 2013).

1.4.9. What role for ocean-based solutions in climate policy?

Understanding the benefits and potential of effective ocean conservation has taken on particular urgency in international policy. Appealing narratives of ocean conservation have found resonance within civil society as well as governments, resulting in calls to protect 30% of the ocean by 2030 and expectations of an imminent 30% target from the Convention on Biological Diversity. Simultaneously, "blue carbon" projects have become an attractive prospect for the private sector, with a 50-fold growth in the blue carbon offset market projected by 2030 (Macreadie et al., 2021). If carefully navigated, such targets and trajectories represent a window of opportunity to underscore the benefits of ocean conservation for nature, the climate and human well-being. Likewise, an incautious or non-inclusive approach could lead to largescale dispossession of local communities from the landscapes and seascapes that sustain them (Cisneros-Montemayor et al., 2022), while poorly implemented protected areas could fail to deliver expected benefits, thereby undermining perceptions of MPAs as an ocean-based climate solution.

Our synthesis provides empirical evidence that MPAs contribute to climate change mitigation and adaptation, particularly when fully protected, making them a key tool for achieving the goals of the UN Sustainable Development Agenda and the Paris Climate Agreement. Multiple opportunities now exist to leverage this scientific basis to guide both public policy and private sector initiatives. First, there is considerable scope to expand the consideration and recognition of MPAs in national climate strategies, including Nationally Determined Contributions (NDCs)

and Adaptation Communications (Lecerf et al., 2021). Such efforts would be aided by further allocation of resources to accelerate the expansion of IPCC-recognized blue carbon strategies to include marine sediments, enabling reliable accounting for mitigation benefits of MPAs with trawling restriction (Groupe d'experts intergouvernemental sur l'évolution du climat, 2014). Second, as 64% of the ocean falls outside of national jurisdictions, it is also fundamental that ongoing negotiations on a treaty for the high seas are successfully concluded and enable the designation of area-based management tools such as MPAs. Finally, the sense of urgency to act and scale-up innovative solutions should be welcomed but not at the expense of recognized best practices regarding inclusive MPA governance and high to full levels of protection.

1.5. **Acknowledgements**

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1.6. **Figures**

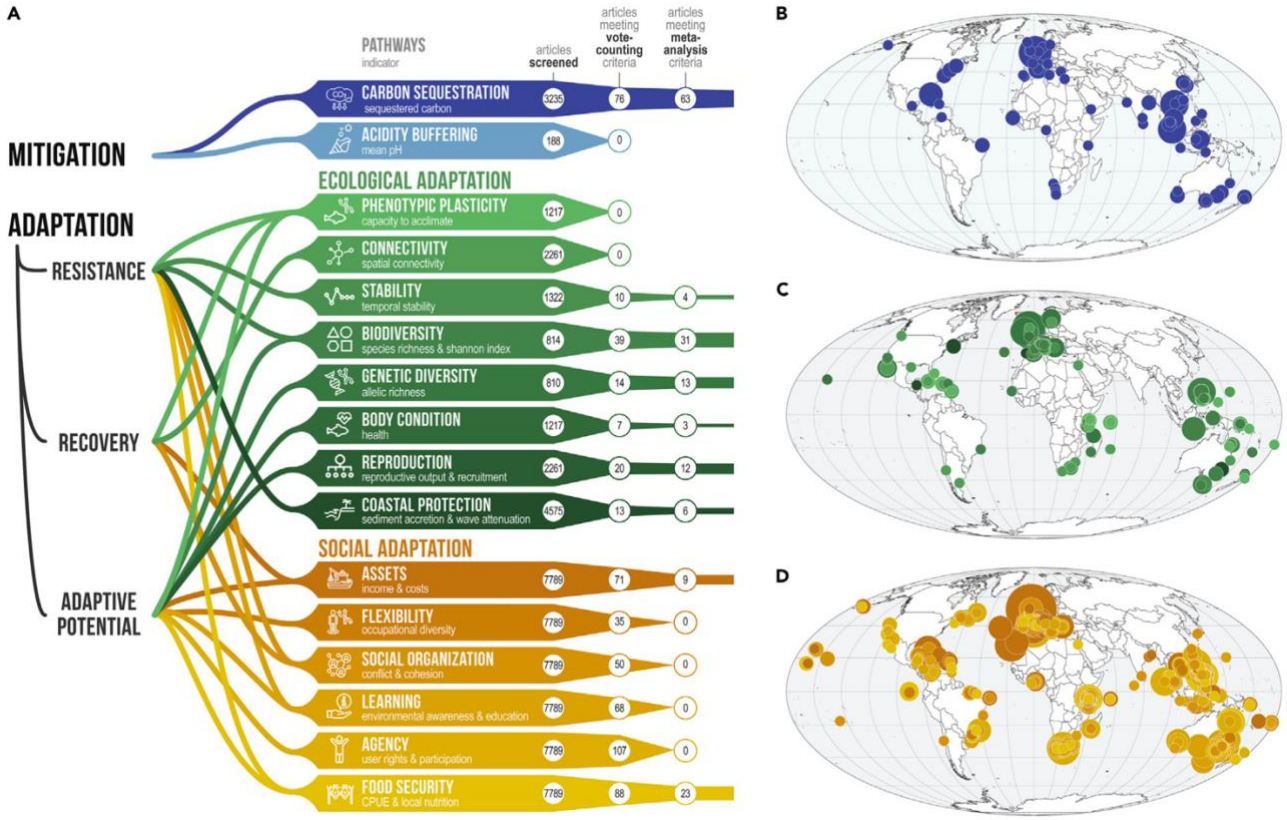

Figure. 1.1. Pathways through which marine protected areas can contribute to climate change mitigation or adaptation, with quantitative and spatial assessment of available information. (A) List of the climate pathways identified and their associated indicators. Blue, green and orange color themes highlight the classification of pathways among mitigation, ecological adaptation and social adaptation categories, respectively. Social and ecological adaptation pathways are shown linked to one or more components of adaptation (i.e., resistance, recovery and adaptive potential) to which they contribute. The number of articles found through our search query and the number of articles that met the selection criteria for vote counting and meta-analysis are indicated for each pathway. The width of bars is proportional to the number of studies selected at each step. CPUE stands for catch per unit effort. **(B-D)** Location of study sites documenting pathways of climate mitigation (B), ecological adaptation (C) and social adaptation (D). The size of dots is proportional to the number of studies at a given location for a given pathway.

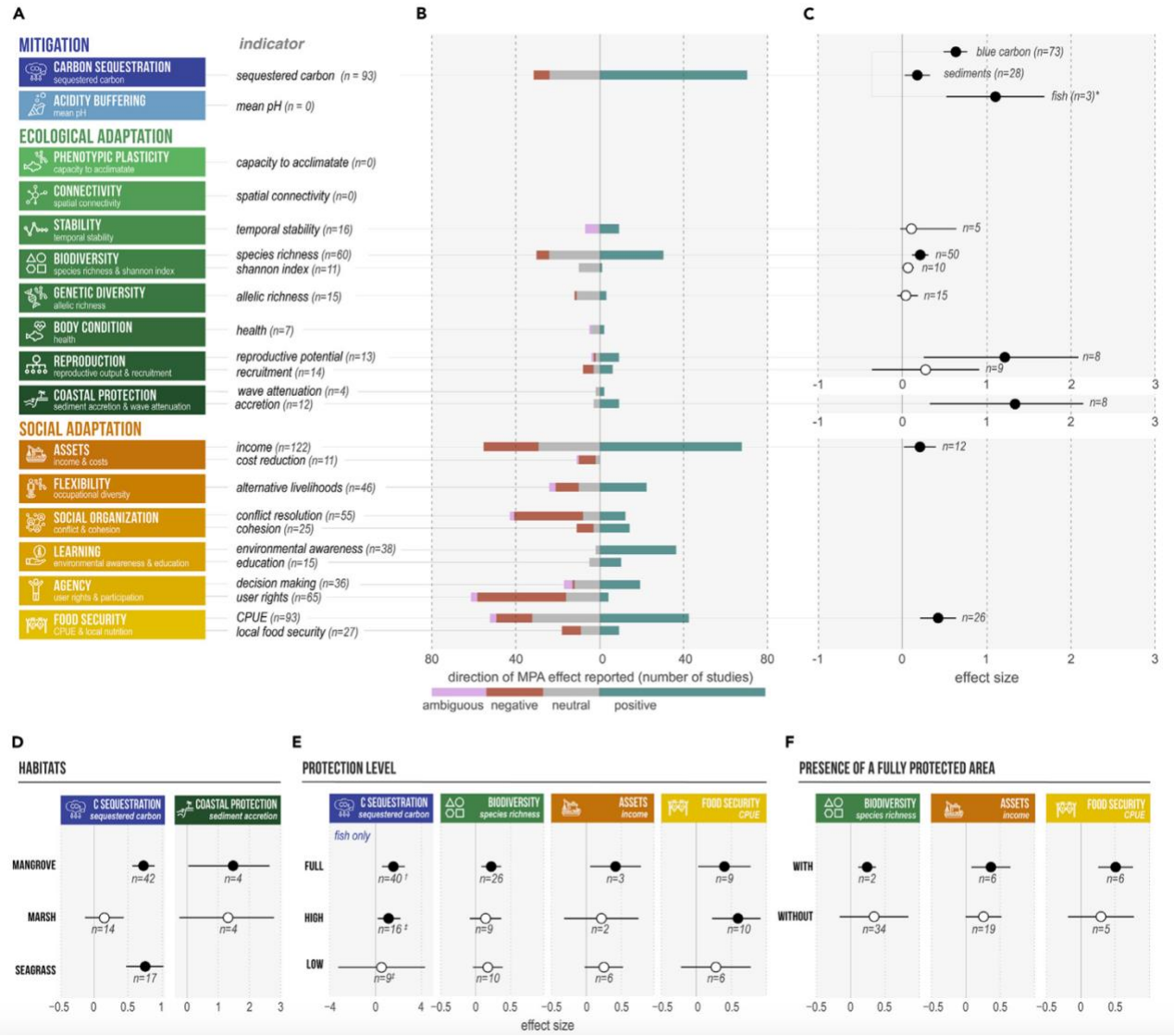

Figure 1.2. Effects of marine protected areas (MPAs) on climate change mitigation and adaptation pathways. Direction of reported MPA effects (A) from studies included in the vote-counting analysis (B) and magnitude of outcomes from studies included in the meta-analysis (C). In (B), the x-axis indicates the cumulative number of studies reporting positive outcomes (right side of the bar plot, green) and ambiguous, negative or neutral outcomes (left side of the bar plot). In (C), x-axis indicates the log-transformed ratio of indicators between MPAs and control site. In the case of coastal protection, the effect size was calculated as the Euclidian difference between MPAs and controls, hence the separate scale provided. Values are presented as mean values ± 95% CI. Black dots indicate effect sizes that do not overlap zero and white dots those that overlap zero. *In the case of carbon sequestration from fish biomass, the effect size was calculated from three previous meta-analyses, representing data from many more individual studies. Sample size of vote-counting and meta-analysis results are indicated by n values. CPUE stands for catch per unit effort. Effect of habitat type (D),

protection level (E) and presence of a fully protected area (F) on the capacity of MPAs to provide climate benefits. Colors, sample size and x-axis have the same meaning as in (C). † Effects of full protection on carbon sequestration (fish biomass only) are reported from Lester et al., (2009). ‡ Effects of high and low protection on carbon sequestration (fish biomass only) are reported from Zupan et al., (2018).

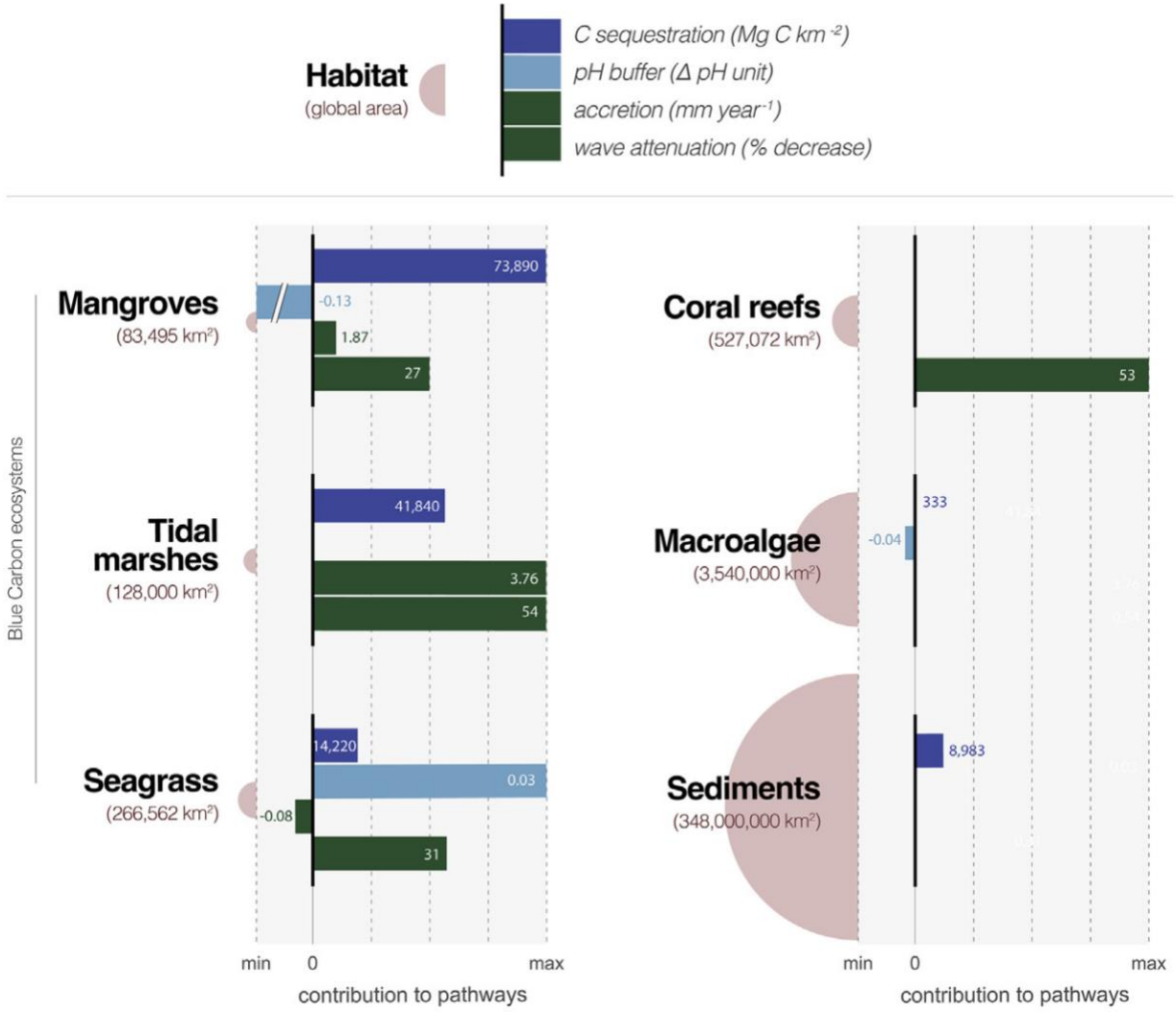

Figure 1.3. Contribution of marine habitats to climate pathways. Values in barplots indicate the capacity of marine habitats to contribute to carbon sequestration (Mg C km^{-2}), coastal protection (accretion in mm $year^{-1}$ and wave attenuation in % wave decrease) and acidity buffering (Δ pH unit). Height of barplots represent the relative capacity of habitats to contribute to a given indicator compared to the maximum value reached by a habitat. For pH buffering, negative values mean that the habitat decreases average local pH. The spatial extent of habitats is indicated under each habitat's name and is represented by a half-sphere area log-proportional to its global spatial area.

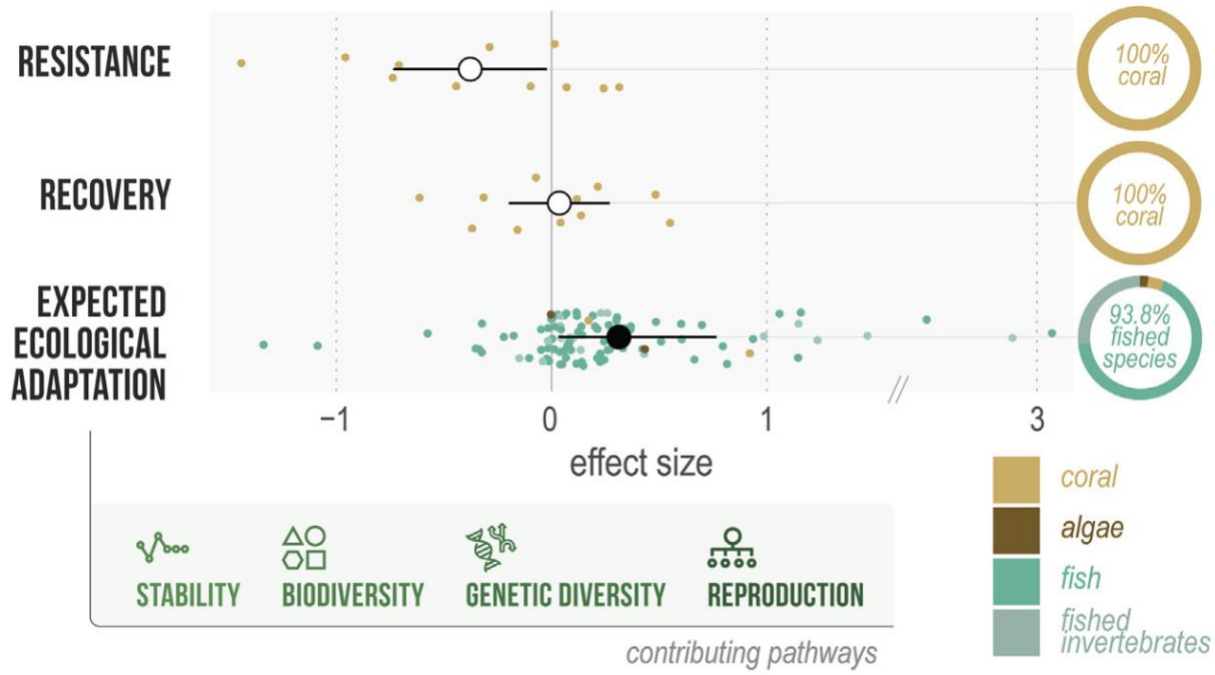

Figure 1.4. Disentangling confounding factors of the protection paradox. Effect sizes were calculated as natural log-ratios of MPA and control conditions for resistance, recovery and expected ecological adaptation of marine organisms. Values represent mean ± 95% CI. Black effect sizes indicate CIs that do not overlap zero, white effect sizes indicate CIs that do overlap zero. Colored dots represent individual effect sizes calculated from each publication that were included in the overall effect size represented. Colors of dots represent the taxa of organisms studied in each publication. Donuts diagrams on the right represent the distribution of individual effect sizes among corals, algae, fish and fished invertebrates. Contributing pathways indicate the pathways of which mean values were aggregated to obtain the effect size of expected ecological adaptation.

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CHAPTER 2

3D ocean assessments reveal that fisheries reach deep but marine protection remains shallow

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2.1. Abstract

The wave of new global conservation targets, the conclusion of the High Seas Treaty negotiations, and the expansion of extractive use into the deep sea call for a paradigm shift in ocean conservation. The current reductionist 2D representation of the ocean to set targets and measure impacts will fail at achieving effective biodiversity conservation. Here, we develop a framework that overlays depth realms onto marine ecoregions to conduct the first three-dimensional spatial analysis of global marine conservation achievements and fisheries footprint. Our novel approach reveals conservation gaps of mesophotic, rariphotic, and abyssal depths and an underrepresentation of high protection levels across all depths. In contrast, the 3D footprint of fisheries covers all depths, with benthic fishing occurring down to the lower bathyal and mesopelagic fishing peaking in areas overlying abyssal depths. Additionally, conservation efforts are biased towards areas where the lowest fishing pressures occur, compromising the effectiveness of the marine conservation network. These spatial mismatches emphasize the need to shift towards 3D thinking to achieve ocean sustainability.

2.2. Introduction

Global conservation efforts are about to significantly expand as the United Nations (UN) Convention on Biological Diversity (CBD)'s Kunming-Montreal Global Biodiversity Framework (GBF) has set the course to cover 30% of land and ocean with area-based conservation tools by 2030 (Ramaj, 2022). Additionally, the GBF recognizes that both protected areas and other effective area-based conservation measures (OECMs) can contribute towards area-based conservation targets. OECMs are geographically defined areas that, unlike protected areas, do not have biodiversity conservation as a primary objective, but still achieve biodiversity benefits from their management (Claudet et al., 2022). Additionally, a legally binding instrument under the UN Convention on the Law of the Sea to protect and sustainably use marine biological diversity in areas beyond national jurisdiction (BBNJ), otherwise known as the High Seas Treaty, has just been concluded. These agreements bring considerable opportunities for marine conservation by increasing coverage targets, vastly extending areas that can be conserved, and by diversifying the types of governance regimes and sectors that can contribute to area-based conservation. However, they also create new challenges for conservation planning, such as designing area-based conservation tools suited for off-shore, deep and vertically complex areas (Costello & Chaudhary, 2017; L. A. Levin et al., 2022), as well as mindfully incorporating OECMs that are often vertically zoned in the conservation network (Claudet et al., 2022). Realizing the potential of these agreements requires a shift from a reductionist two-dimensional (2D) representation of the ocean to a three-dimensional (3D) representation of ecosystems, human use, and impacts (Danovaro et al., 2014; L. A. Levin et al., 2023; N. Levin et al., 2018). This shift is essential to avoid compounding on the weaknesses of the current conservation network, which already fails at achieving ecological representation (Maxwell et al., 2020), high levels of protection (Claudet et al., 2020), and at abating human impacts (Devillers et al., 2015).

The ocean is inherently three-dimensional. Unlike on land, life in the ocean spans over a considerable vertical range from the surface to the seafloor, with an average depth of 3,800 m. However, apart from recent model-based prioritization studies (Brito-Morales et al., 2022; Doxa et al., 2022; Venegas-Li et al., 2018), assessments of human use (Halpern et al., 2015; Kroodsma et al., 2018) and of conservation achievements (Jantke et al., 2018; Maxwell et al., 2020) remain two-dimensional. Although the vertical stratification of marine life and human use has long been recognized, multiple factors have led to the persistence of 2D representations. The historical predominance of terrestrial conservation and of land-use management have shaped marine conservation and marine spatial planning, with human use and UN CBD conservation targets mostly allocated in 2D. This approach has remained mostly unchallenged because human activities, scientific research and conservation have historically been constrained to shallow marine environments where vertical structure is simple (Webb et al., 2010). Besides, the fragmented nature of ocean governance, with multiple sector- and area-specific regimes, hampers a holistic three-dimensional management of the ocean(Ardito et al., 2023).

Distinct scientific groups have previously raised awareness on the fact that deep marine ecosystems, such as the mesopelagic, deep reefs, and seamounts, are under increasing human

pressures and require dedicated conservation efforts (L. A. Levin et al., 2020; Mengerink et al., 2014; Rocha et al., 2018). However, a three-dimensional framework to identify conservation gaps and priority areas *across* depths is still missing. In particular, while fisheries are the main driver of marine biodiversity erosion (IPBES, 2019), global assessments of fisheries' footprint remain two-dimensional (Amoroso et al., 2018; Halpern et al., 2015; Tickler et al., 2018; Zeller et al., 2023) and fail to inform on which depths are being targeted (Morato et al., 2006; Villasante et al., 2012; Watson & Morato, 2013). This represents a critical knowledge gap to inform fisheries management and marine conservation because the sensitivity of ecosystems to fishing pressure varies greatly with depth (J. Clarke et al., 2015). Global 2D mapping of marine cumulative impacts (Halpern et al., 2008, 2015) have been instrumental in guiding marine policies by demonstrating the extent and acceleration of the human footprint on the ocean. There is now a need for 3D mapping of the human footprint across space and depth to guide global conservation policy.

Here, we develop a novel mapping framework by overlaying benthic and pelagic depth realms, which captures main ecological units across depths, onto commonly used 2D marine ecoregions (Spalding et al., 2007, 2012). Using this mapping framework, we assess for the first time the 3D ecological representativeness of the global ocean conservation network and conduct the first global assessment of the depth distribution of fishing effort. We then test whether marine protected areas (MPAs) and OECMs are appropriately sited to provide protection to areas under highest fishing pressure across both space and depth. Based on our results, we identify conservation gaps, conservation priorities, and provide recommendations on how to account for specificities linked to the three-dimensionality of the ocean in the global conservation agenda.

2.3. Methods

All datasets used in this study are available in open access at the websites of the institutions detailed in the methods. All original codes used for this study are publicly available on the Zenodo repository under the DOI 10.5281/zenodo.10246615.

2.3.1. Definition of three-dimensional marine realms

We obtained a 3D zonation of the ocean by overlaying a 2D zonation of marine ecoregions (e.g. Temperate Northern Atlantic, Tropical Eastern Pacific) with a depth zonation of the main benthic and pelagic realms (e.g. epipelagic, mesopelagic). To define a 2D zonation of marine ecoregions (latitude and longitude), we used the global map of pelagic and coastal realms as described in Spalding et al. (2012, 2007)(Spalding et al., 2007, 2012). Realms (hereafter ecoregions) provide the largest spatial unit with coherent biota at high taxonomic levels resulting from shared environmental conditions and evolutionary history (Spalding et al., 2007). This makes ecoregions relevant units to assess biodiversity representation. Ecoregions are divided into 11 coastal ecoregions and four "pelagic" ecoregions (Fig. S1). Coastal ecoregions extend to 200 nautical miles (370 km) offshore or to the 200-m isobath where the later occurs further. As such, coastal ecoregions cover all waters shallower than 200 m, but also areas of bathyal and abyssal

depths when the later occur within 200 nautical miles from shore. “Pelagic” ecoregions cover off-shelf pelagic waters, including waters beyond national jurisdiction. Because all ecoregions actually include both pelagic and benthic ecosystems, we referred to “pelagic” ecoregions as “off-shore” ecoregions hereafter to avoid confusion with the distinction between the benthos versus the water column. We used the ecoregions vector layer from the UN-WCMC Ocean Data Viewer (The Nature Conservancy, 2012) with a precision of 0.01 degrees.
We defined the zonation of benthic depth realms based on the description of ecological depth zones in the literature (Baldwin et al., 2018; Carney, 2005; Stefanoudis et al., 2019, Priede et al. 2017), as follows: the euphotic (0-30 m), upper mesophotic (30-60 m), lower mesophotic (60-150 m), rariphotic (150-300 m), upper bathyal (300-1000 m), lower bathyal (1000-3500 m), abyssal (3500-6000 m) and hadal (below 6000 m). Similarly, we defined the pelagic depth realms as follows: epipelagic (0-200 m), mesopelagic (200-1000 m), bathypelagic (1000-3500 m), abyssopelagic (3500-6000 m), and hadopelagic (below 6000 m).

2.3.2. Three-dimensional distribution of MPAs and OECMs

We used the World Database on Protected Areas (WDPA (UNEP-WCMC and IUCN, 2022)), the most comprehensive source for protected areas data, to build our global map of MPAs (Thomas et al., 2014). Similarly, we used the World Database on Other Effective Conservation Measures (UNEP-WCMC and IUCN, 2022) to build our global map of OECMs. We followed the methodology recommended in Thomas et al., (2014)(Thomas et al., 2014) to process the WDPA vector layer in a way that generates reliable information on the area and protection level of MPAs. Only MPAs for which spatial boundaries were known were included in the analysis. Although circular buffers have been used in the past to include MPAs for which size but not shape is known (e.g., Spalding et al. 2008), we chose not to do so to avoid false information on bathymetric coverage of MPAs (Visconti et al., 2013). Terrestrial parts of MPAs were excluded by clipping MPA boundaries with a terrestrial land vector (Natural Earth version 5.1.1, 10m resolution). The MPA vector layer was simplified to a resolution of 0.01 degree to save memory consumption and computation time.

To account for the MPAs level of protection (Grorud-Colvert et al., 2021) we used the management categories defined by the International Union for Conservation of Nature (IUCN) (Stolton et al., 2013) from the WDPA (Table S1). Although the IUCN categories and levels of protection as defined by the MPA guide do not have perfect correspondence (Horta e Costa et al., 2016), the IUCN management categories reflect a gradient from exclusive biodiversity protection (Ia) to integrated human use and extraction (VI), which we used here as a proxy for levels of protection. IUCN categories reported as “Not Applicable”, “Not Reported” or “Not Assigned” were merged into a unique level of protection categorized as “Unknown”.
MPAs resulting from different designation processes can spatially overlap. To avoid double-counting MPA coverage that protect the same area, we only kept the designation providing the highest level of protection for a given area. To do so, we created a unique vector layer for each IUCN level of protection by extracting the corresponding polygons from the original vector layer

and merging all polygons. We then subtracted the vector layer of the highest level of protection (Ia) from the vector layer of the second highest level of protection (Ib). We then merged vector layers Ia and Ib and subtracted it from the vector layer of the following highest level of protection (II), and so on. Finally, we merged the vector layers obtained, resulting in non-overlapping MPA polygons of the highest levels of protection for a given area

We used bathymetric data from the GEBCO raster layer (GEBCO Compilation Group, 2020) to assess the depth distribution of protection coverage. The depth distribution of MPAs and OECMs was obtained by extracting values from the bathymetric raster in each polygon of the MPA layer and summing the area of cells corresponding to the same depth realm.
This layer used a polar projection (EPSG:4326) and thus the area covered by each cell size varied with latitude. The area of each raster cell was calculated using the following formula:

$$\text{cell area} = \text{cell height} * \text{cell width} \qquad (1)$$

The height of a cell is constant and equal to:

$$pixel\ height = resolution\ in\ degrees * minutes\ per\ degree * \ meters\ per\ minute$$

with resolution in degrees = 0.004166; minutes per degree = 60' and meters per minute = 1852m. This gives a cell height of 463m.

The width of a cell is equal to:

$$\text{cell width} = \frac{\text{earth perimeter (latitude)}}{\text{nb of cells}} \qquad (2)$$

with nb of cells = 86,400.

The perimeter of the Earth at a given latitude was calculated as:

$$\text{earth perimeter (latitude)} = 2\pi R * \cos\left(\text{latitude} * \frac{\pi}{180}\right) \qquad (3)$$

with *R*=6,378 km.

To verify our calculations, we performed a second cell size calculation using the cellSize() function from {terra} and compared the matrix of values obtained from both methods. Results were identical and we chose to keep our formula-based calculation method because of shorter processing time.

The depth realms protected by MPAs or OECMs were determined by the bathymetry of protected cells. The benthic depth realm protected by an MPA or OECM cell corresponds to the bathymetry of that cell, and the pelagic depth realms protected correspond to all realms occurring between the surface and the seafloor. For example, if a protected cell had a bathymetry of 3000m, it was assumed to be protecting the upper bathyal (benthic realm) and the epipelagic, mesopelagic and bathypelagic (pelagic realms).

We calculated the proportion of benthic protection existing for each benthic realm *i* as follow:

$$\%\ \text{benthic proctected}_i = \frac{\text{benthic area protected}_i}{\text{total benthic area}_i} * 100 \qquad (4)$$

We performed the same calculation for pelagic depth zones.

2.3.3. Three-dimensional distribution of fishing pressure

For the fishing data, we used the most recent (2.0) version of fleet daily fishing activity (Kroodsma et al., 2018) from Global Fishing Watch (GFW) at the highest available resolution (0.01 degree). GFW collects data from publicly available automatic identification system (AIS) and vessel monitoring systems operated by governments. While only 2% of all fishing vessels carry AIS (mostly large, commercial vessels), those vessels are responsible for 50% of the fishing in economic exclusive zones (EEZ) and 80% of the fishing in the high seas (Kroodsma et al., 2018). This dataset was chosen over the FAO global fishing catch dataset because fishing pressure on marine ecosystems is better captured by fishing effort (hours km^{-2}) metric than catch (ton km^{-2}) data. We analyzed fishing data from the three most recent years available on the GFW on the 20th May 2022: 2018 to 2020. We found a strong correlation between the number of fishing hours by gear type and bathymetry across these three years (tau=0.96, p-value < 10^{-16}) demonstrating that results were stable across years. In our figures, we represented values from the 2019 dataset. The inter-annual variability is represented as a 95% confidence interval in Figure 4. Files tracking the intensity (fishing hours $cell^{-1}$) and location (latitude and longitude) of daily fleet activities in 2019 were combined into a dataset of 205,656,988 fishing events. Data files were converted to vector shapefiles using spatial coordinates of fishing activities (see Fig. S2) and fishing activities were then attributed to ecoregions and bathymetric ranges. Information on vessels' gear type was joined to this dataset using the Maritime Mobile Service Identity (MMSI), a unique identification number for vessels.

We assessed the distribution of fishing pressure across depth realms using two approaches: an approach that estimates the broad impacts of fishing activities across depths (hereafter "depth impacted"), and an approach that estimates the depth directly targeted by fishing activities (hereafter "depth targeted"). We considered as impacted by fishing activities all depth realms occurring in the vertical column of that activity, from the surface to the seabed. This assumption is based on empirical and model-based evidence that disrupting one part of the surface-to-seabed continuum has cascading effects on the rest of the continuum because of vertical connectivity processes. Such cascading vertical impacts have been demonstrated between ecosystems as distant as the epipelagic and abyssal benthos (Yool et al., 2013, 2017). To determine the depth realms impacted by fishing activities, we used the bathymetric value at the location of fishing activities and determined the benthic and pelagic realms present in that surface-to-seabed column. As such, only one benthic realm can be impacted by each fishing activity, but several pelagic realms can be impacted at once. We calculated the fishing pressure (hours km^{-2}) impacting each benthic depth realm by summing the total hours of fishing activities impacting that benthic depth realm divided by the spatial extent of that depth realm (Figure 2). Similarly, we calculated the fishing pressure (hours km^{-2}) in each 3D realm (Figure 4) by summing the total

hours of fishing activities impacting a given benthic depth realm within a given ecoregion and dividing it by the spatial extent of that 3D realm (km^2).

To determine the depth realms targeted by fishing activities, we relied of the depth range of fishing gears associated with each fishing activity. This method was only achievable for gear types that discriminate pelagic and benthic activities (Table S2). We considered that benthic activities targeted the benthic depth realm corresponding to the bathymetry of the fishing location. We considered that pelagic activities only had a direct impact on pelagic realms within the depth range of the fishing gear used, and within the depth range (i.e., the bathymetry) of the location fished. For example, a pelagic fishing gear with a depth range of 30-350 m operating at a location of 400 m depth was considered to target both the epipelagic (0-200 m) and mesopelagic (200-1000 m) realms, but if the same vessel operated at a location of 150 m, it was considered to only target the epipelagic. To determine the depth range of pelagic gears, we reviewed technical descriptions in published and grey literature (e.g., NOAA, MSC). We checked the information collected by consulting fisheries experts. The depth range of each fishing gear obtained from this literature review is summarized in Table S3.

Three gear types used in the GFW did not discriminate benthic and pelagic activities: "purse seines", "trawlers" and "fishing", which represented 62% of the total fishing hours registered. To increase our ability to discriminate benthic and pelagic activities, we contacted managers of the GFW database to access further details on registered trawler vessels, the gear type combining the most unspecified (pelagic vs. benthic) fishing hours. This additional data allowed us to distinguish in many instances between bottom and midwater trawlers and assign an additional 17% of the total fishing hours to benthic or pelagic activities and brought the total proportion of fishing activities for which a directly impacted depth could be determined from 38% to 55%. The remaining 45% of fishing hours were categorized as targeting an "unspecified" depth (Figure 4).

2.3.4. Definition of conservation priority profiles

Relation between protection coverage and fishing pressure was tested using a linear regression model (Pearson method) from the {ggplot} function suite 'ggpubr'.
Conservation priority profiles were defined based on the fishing pressure and protection coverage occurring within each 3D realm. Four categories of fishing pressure were defined using the quartiles of fishing pressure (hour km^{-2} $year^{-1}$) calculated in 2.3 for 3D realms. Four categories of protection coverage were defined based on the progress towards the achievement of conservation targets. This was calculated first using the CBD target of 30% of total protection coverage by 2030, and then using the target of 10% of high protection coverage by 2030 (e.g. [67]. For the first assessment, we distributed 3D realms among four categories of protection coverage: 0-10%; 10-20%, 20-30% and >30%. For the second assessment, we distributed 3D realms among four categories of IUCN Ia/Ib category coverage: 0-2.5%, 2.5-5%, 5-10% and > 10%. For

both assessments, we attributed a score to each 3D realm from 1 to 16 reflecting their position in these 4x4 categories (Figure 5A).
We then simplified these 4x4 categories into 2x2 categories using as thresholds the median value of fishing pressure and 20% of total protection (resp. 5% of Ia/Ib protection coverage), which correspond to halfway completion of global conservation targets. These four resulting categories defined different levels of conservation priority for 3D realms: "highest priority" for above median fishing and below halfway completion of conservation targets; "lowest priority" for the opposite scenario; "fills conservation gaps" for below median fishing and below halfway completion of conservation targets and "mitigates fishing pressure" for the opposite scenario.

2.3.5. Software, R packages and scripts

We carried out all vector and raster operations using the {sf} (Pebesma, 2018) and {terra} (Hijmans et al., 2022) packages under R Core Team (2021) R Core Team (2021). Figures were created using {ggplot2} (Wickham, 2009) and {tidyr} (Wickham & Henry, 2020), and edited using Illustrator ®. QGIS ® was used for the preliminary visualization of data and production of supplementary figures.

2.4. Results and Discussion

2.4.1. Uneven conservation effort across depth

Based on the vertical zonation of marine species, habitats, and environmental conditions (Baldwin et al., 2018a; Carney, 2005; Priede, 2007), we identified eight benthic and four pelagic realms that represent ecological units across depths (Figure 1).

We found that the distribution of area-based conservation (MPAs and OECMs) is uneven across depth realms (Figure 2 and S3) and ecoregions (Figure 3). The euphotic (0 to -30 m) is the best protected depth realm, combining the second largest protection coverage (15%, Figure 2B), the second largest coverage (1.2%) of Ia and Ib protected area categories of the International Union for Conservation of Nature (IUCN), which tend to more strictly regulate human use (see Table S1 for details on IUCN categories), and the most widespread protection across ecoregions (Figure 3 and S5). By contrast, the abyssal realm has the smallest extent of protection coverage (5.8%) and the smallest coverage of Ia and Ib IUCN categories (0.6%). The BBNJ treaty now provides the legislative framework to increase abyssal protection coverage, as 75% of this depth realm occurs in areas beyond national jurisdiction (Figure 2D). When considering depth realms predominantly occurring within economic exclusive zones (EEZs), lower mesophotic and rariphotic realms are the least protected globally (Figure 2B) as well as across most of the world's coastal ecoregions (extending 200 nautical miles offshore, Figure 3).

Across all depths, the majority of protection coverage falls under IUCN category VI or unknown (Figure 2B), which corresponds to the lowest levels of protection from human use (Horta e Costa et al., 2016). Most 3D realms are covered by less than 1% of Ia and Ib IUCN categories (0.7% as

a global average) and one third by less than 0.1% (Figure 3), which corresponds to the highest levels of protection. The greatest coverage of Ia and Ib IUCN categories is found in the hadal realm (3%), in the Eastern-Indo Pacific (10%) and in polar ecoregions (Arctic and Southern Ocean, 1-2%).

2.4.2. Distribution of fishing activities across space and bathymetry

We assessed the 3D distribution of fishing footprint by overlaying the spatial distribution of fishing activities reported by the Global Fishing Watch (GFW [33]) with the highest resolution bathymetric map of the ocean (GEBCO Compilation Group, 2020). We found that both fishing pressure and fishing gears are highly structured by bathymetry (Figure 2A). Areas overlying euphotic to upper bathyal depths experience above average fishing pressure dominated by trawlers, while areas overlying lower bathyal to hadal depths experience lower fishing pressure dominated by drifting longline fisheries (Figure 2A). Average fishing pressure (hour km^{-2} $year^{-1}$, Figure 2A) and total fishing effort (hours $year^{-1}$, Figure 4) are highest in the euphotic. Fishing pressure continuously decreases in areas overlying greater depths, with a sharp six-fold decrease in areas deeper than 1,500 m (upper bathyal). However, total fishing effort is as high in areas overlying abyssal depths as in areas overlying mesophotic depths. In ecoregions where average fishing pressure is the highest (Temperate Northern Atlantic and Pacific, Temperate South America), average fishing pressure remains high from areas overlying euphotic to upper bathyal depths, while in off-shore ecoregions and in some coastal ecoregions (e.g., Temperate Southern Africa, Temperate Australasia) average fishing pressure peaks in areas overlying rariphotic and bathyal depths (Figure 4).

Although bathymetry alone is insufficient to determine the depths targeted by fishing activities, it can inform on the broader depth range likely impacted by fishing activities. These indirect impacts occur through vertical connectivity processes, such as migration of organisms, top-down trophic controls or nutrient transfers (Drazen & Sutton, 2017; Irigoien et al., 2014; Scheffer et al., 2005); and through by-catch, entanglements, anchoring, fishing debris or ship collisions (Knowlton et al., 2022). Concerns are now being raised that mesopelagic fisheries could even affect carbon sequestration in deep-sea sediments by altering the ocean's biological carbon pump (Herbert-Read et al., 2022). As such, in data-poor contexts, relying on the bathymetric distribution of fishing activities can be a first entry point to assess the 3D distribution of fishing impacts.

2.4.3. Elucidating the three-dimensional distribution of fishing activities

The disaggregation level of fishing gears reported in the GFW datasets allowed us to distinguish between pelagic and benthic fisheries for 55% of the total fishing hours reported from 2018 to 2020. Depths targeted by benthic activities can be determined with accuracy as they match the bathymetry of the fishing location. For pelagic fishing activities, we determined depths targeted based on the depth range of the fishing gear reported by the GFW and the bathymetry at the fishing location (Figure 1, Table S3). We found that benthic fishing effort was greatest in the

euphotic and mesophotic (>10^7 hours year^{-1}) but remained important down to the upper bathyal (2 10^6 hours year^{-1}) and occurred down to the lower bathyal (Figure 4). Most pelagic activities occurred over lower bathyal to abyssal depths and corresponded to mid-water trawls and drifting longlines.

We found that the 3D footprint of fisheries extends across most depths in most ecoregions of the world. In particular, we found that 37% of total fishing effort overlies depths greater than 300 m and thus directly or indirectly impacts deep marine ecosystems (Figure 4). This is the result of decades of fishing down the deep as shallow and coastal fish stocks have been depleted from overfishing (Morato et al., 2006; Ortuño Crespo & Dunn, 2017; Swartz et al., 2010; Villasante et al., 2012; Watson & Morato, 2013). Unfortunately, in addition to being unprofitable if not heavily subsidized (Mariani et al., 2020; Sala et al., 2018), deep fisheries are often unsustainable (J. Clarke et al., 2015; Norse et al., 2012; C. M. Roberts, 2002), with high rates of by-catch and long-lasting impact on habitats (Althaus et al., 2009; Bailey et al., 2009). Some regions have taken action to limit the depth of fishing activities (e.g., trawling ban below 800 m in European waters), but more depth regulations are needed to ensure sustainable fishing practices (Villasante et al., 2012).

Our study is the first attempt to characterize the 3D distribution of fishing activities at the global scale and reflects the limited available knowledge to characterize the 3D fishing footprint. Importantly, about 45% of fishing activities reported in the GFW database do not discriminate pelagic and benthic activities (Figure 4). Alternatively, datasets that distinguish pelagic and benthic fishing activities, such as those produced by some Regional Fisheries Management Organizations, provide catch data pooled by large spatial units, which also prevents from determining the depth distribution of fishing activities. Systematically distinguishing between pelagic and benthic fishing and increasing the precision of the spatial information associated with catch data would constitute important steps forward to improve our understanding of the depths targeted by fisheries. Our results underestimate fishing pressure overlying euphotic to rariphotic depths because the GFW database only documents vessels with automatic identification systems, which does not capture most tropical small-scale fisheries, especially in the Caribbean, South-West Pacific and Indian Ocean where catches are systematically underreported (Amoroso et al., 2018; Zeller et al., 2023).

2.4.4. Mismatched distribution of fishing and conservation efforts

We evaluated whether conservation efforts across 3D realms is appropriately sited to mitigate fishing pressure by testing whether MPAs and OECMs are implemented in more intensely fished realms. We found that the protection coverage of 3D realms (log transformed) was negatively correlated with fishing pressure (Figure 5), indicating a large bias of ocean conservation towards least impacted areas. This negative correlation was significant when considering coverage by all MPAs and OECMs ($p=0.021$, $R^2=-0.22$), and when considering coverage by only MPAs of Ia/Ib IUCN categories ($p<0.001$, $R^2=-0.33$).

We defined four profiles of conservation priority (Figure 6b) based on the fishing pressure (below or above median) and protection coverage of 3D realms (behind or past halfway completion of 2030 targets). We found that highest conservation priority areas, i.e., with low protection coverage and high fishing pressure, mostly occur in the mesophotic, rariphotic, and upper bathyal realms across all ecoregions of the world (Figure 6A and 6B). Lowest conservation priority areas, i.e., that combine high conservation coverage and low fishing pressure, mostly occur at lower bathyal and abyssal depths in coastal ecoregions. Implementing MPAs or OECMs in such low use areas would decrease the net ecological benefits of these conservation tools. If areas of low fishing pressure still need to be targeted to minimize impacts on fisheries, then targeting 3D realms that suffer from conservation representation gaps should be the priority. Such 3D realms mostly occur in lower bathyal and abyssal depths in off-shore ecoregions and will require conservation action in the high seas (Figure 6B). Implementing and actively managing MPAs of high protection levels in any 3D realm would provide important conservation benefits, as 90% have still not reached halfway completion of 2030 CBD target and 47% cumulate low coverage with high fishing pressure (Figure 5), therefore falling under the highest priority category (Figure 6C and 6D).

Here, we restricted our 3D conservation prioritization to two variables: protection coverage and fishing pressure. While fishing pressure is considered as the main direct anthropogenic threat to marine life (IPBES, 2019), other human pressures could be considered to translate our framework into actionable recommendations towards other sectors, especially given the projected rapid expansion of offshore renewable energies, hydrocarbon drilling and deep-sea mining (Dunn et al., 2018; Jouffray et al., 2020; L. A. Levin et al., 2020). Furthermore, climate-induced shifts in species distributions (Pinsky et al., 2020) and in turn in fishing effort distribution (Cheung et al., 2010; Palacios Abrantes et al., 2022) should be accounted for to ensure that protection targets areas of high priority both now and under future climate conditions. While species and fishing effort redistribution are unlikely to alter the findings of this study given the large spatial extent of 3D ecoregions, this consideration should be reckoned by studies applying this framework at a finer spatial resolution.

2.4.5. Towards an even conservation of depth realms

Several mechanisms can explain the uneven protection of depth realms. The lack of policy tools to designate conservation areas in the high seas has resulted in the largest conservation gap of the planet, the abyssal realm. This gap will start to be addressed when the concluded High Seas treaty will be ratified and the BBNJ COP implemented. Within EEZs, the higher proximity to near-shore ecosystems and the incentive to protect areas that can generate tourism revenues (Sala et al., 2013), or the avoidance of fishing grounds have skewed conservation efforts towards the euphotic and the upper bathyal respectively at the expense of the mesophotic and rariphotic realms. These biases have led to the underprotection of unique but poorly described ecosystems (A. Martin et al., 2020; Ramirez-Llodra et al., 2010; Rocha et al., 2018) that are under increasing pressure from human use. Although out of sight, mesophotic and deep ecosystems provide spawning and

feeding grounds to valuable fish stocks (Pinheiro et al., 2021), host the largest amount of undescribed species (Webb et al., 2010), act as potential climate refugia for shallow species (Rutterford et al., 2015), and are central in the ocean carbon cycle (Bopp, 2021). Lastly, fast rates of species and habitat discovery in the mesophotic and in the deep ocean (Costello & Chaudhary, 2017) are challenging the perception that only the euphotic hosts diverse and complex communities. Collectively, these elements demand we revisit current conservation paradigms and extend conservation efforts across all depths to protect the whole range of marine biodiversity.

To address this representation gap, we propose two paradigm shifts in how conservation efforts are prioritized and measured. First, prioritization studies and measures of conservation representativeness should include criteria suited to data-poor habitats. Current methods to measure biodiversity representation rely on biodiversity features (e.g., species richness, vulnerable habitats, endangered species) that are inherently biased by the better description of shallow ecosystems, and thus will keep on disproportionately prioritizing shallow ecosystems (e.g., (Pörtner et al., 2019)). Because of the scarcity of data on deep habitats and species distributions, relying on well-described geophysical features such as depth, which is underway to be fully mapped by 2030 (Mayer et al., 2018), can be a relevant strategy to maximize biodiversity representation (Biber et al., 2022; K. E. Roberts et al., 2019). Such an approach has been demonstrated to be very effective at capturing undescribed biodiversity through incidental representation (T. C. L. Bridge et al., 2016). Additionally, depth representation can represent a climate-smart tool for adaptive conservation planning by acting as a portfolio strategy, and by guaranteeing that species undergoing depth shifts remain in well-conserved habitats (Brito-Morales et al., 2020). Second, indicators used to track the ecological representativeness of marine conservation networks should include a depth dimension in addition to commonly used 2D units, such as ecoregions (Jantke et al., 2018). The 3D ecoregion typology (depth realm x ecoregion) developed in this study could serve as the framework to set goals and track progress towards 3D ecological representativeness. The number of depth realms considered and their depth limits could be further adjusted at the regional scale to account for local ecological specificities.

In addition to the uneven distribution of conservation efforts, our analysis highlights other flaws of the conservation network that compromise its effectiveness. The correlation between low fishing pressure and high protection coverage (Figure 5) would ideally be the result of strong regulations that limit fishing pressure. However, it is rather the symptom of residual conservation by which protected areas are placed where they least interfere with human use (Devillers et al., 2015; Stevenson et al., 2020). Furthermore, we found that IUCN categories that dominate the conservation seascape (categories ≥ IV) are those that tend to correspond to lower protection levels (Horta e Costa et al., 2016), although these two classifications are not fully equivalent (Horta e Costa et al., 2017). Because high or full levels of protection (akin to Ia and Ib IUCN categories), under which extraction is forbidden or strictly regulated, provide the largest ecological, social and climate benefits (Grorud-Colvert et al., 2021; Jacquemont et al., 2022; Zupan et al., 2018), a target of 10% of high or full protection coverage has been recommended by the scientific community and is already part of the 2030 European Union Biodiversity

Strategy (EU Biodiversity Strategy for 2030, 2020). Here, we show how far we remain from this target, as high or full protection covers less than 0.7% of the ocean, is not evenly distributed across 3D realms, and is mostly implemented in areas where little fishing pressure occurs.

2.4.6. Risks of vertically zoned conservation

The proposition of stratifying conservation effort and fishing by depth (Brito-Morales et al., 2022; Grober-Dunsmore et al., 2008) has gained momentum with the increasing recognition of area-based fisheries management as OECMs, which commonly only confer protection to the benthos (Claudet et al., 2022). This assumes that impacts from human use remain compartmentalized to the depths where they occur, which overlooks numerous connectivity processes across depths. The complex energy, nutrient and population exchanges from the epipelagic to the benthos (Game et al., 2009; O'Leary & Roberts, 2018) imply that disturbing one depth realm will likely have cascading effects on any other depth of that system (Scheffer et al., 2005). This is true for shallow but also for most deep ecosystems, which almost exclusively rely on the biomass and productivity originating from epi- and mesopelagic realms (Drazen & Sutton, 2017; L. A. Levin et al., 2023). The vertical zonation of conservation tools will thus inevitably result in low levels of protection because some parts of the water column remain exploited, in turn compromising the ability to yield strong conservation benefits at any depth. Furthermore, the difficulties associated with the enforcement of varying regulations across depths would likely undermine the efficiency of vertically zoned MPAs or OECMs (O'Leary & Roberts, 2018). Finally, vertically zoned conservation might give yet another gateway for residual conservation. Indeed, it could allow to only protect depths that are not exploited for human use, whether it be the water column above mining sites, or the benthos beneath offshore windfarms. This will make the progress towards biodiversity conservation net gains even harder to measure. To avoid this loophole, we recommend (1) surface-to-seafloor protection as the standard for area-based conservation and (2) if implemented, vertically zoned MPAs and OECMs to be reported with the level of protection of the least protected depth zone.

A two-dimensional representation of the ocean could inform conservation in a world where human use was restricted to shallow ecosystems. However, with the rapid expansion of human use deeper in the ocean and further offshore (Jouffray et al., 2020) and the rise of vertically-zoned conservation tools, there is more than ever an urgent need to account for the ocean's three dimensions in conservation planning and regulation of human use. In the wake of a global push for more and better ocean conservation to reach Kunming-Montreal GBF targets, the full three-dimensional range of marine biodiversity needs to be represented in proposed conservation networks. Such considerations are extremely important for national conservation strategies, as 75% of the world's EEZs consist of deep ecosystems while concentrating the highest levels of fishing pressure. In parallel, the recent conclusion of the High Seas treaty offers a unique opportunity to build upcoming conservation efforts on a revised framework that accounts for the complex and intricately connected three-dimensional ocean space.

2.5. Acknowledgements

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2.6. Figures

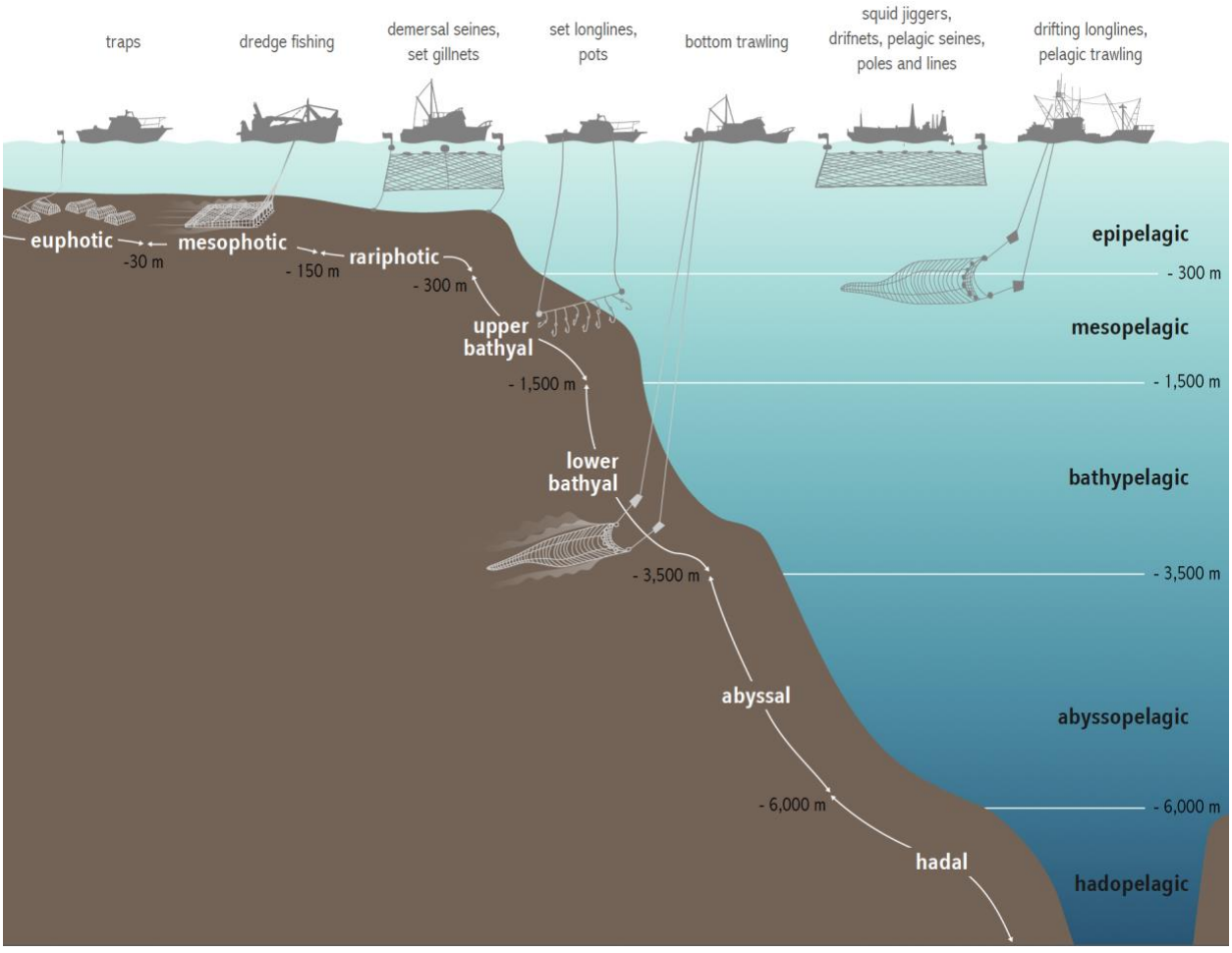

Figure 2.1. Vertical distribution of benthic realms, pelagic realms and depths targeted by fishing gear. The depth at which fishing gears are represented indicates the maximal depths at which these gears are operated. Only one type of fishing gear was depicted per depth maxima, but the same depth maxima apply to all gears listed under the same column (e.g., set longlines and pots are deployed down to the upper bathyal). The mesophotic benthic realm (-30 to -150 m)

was further subdivided into “upper mesophotic” (-30 to -60 m) and “lower mesophotic” (-60 to -150 m) in our analyses.

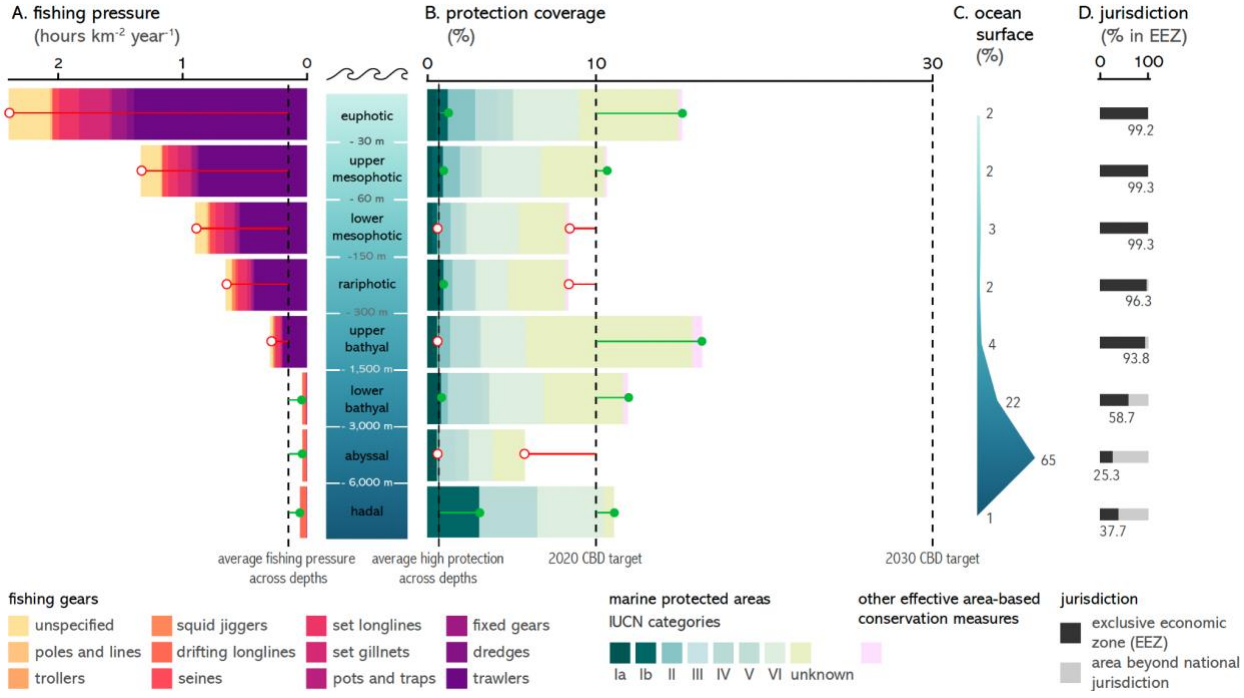

Figure 2.2. Distribution of fishing pressure and conservation efforts across depth realms. (**A**) Average fishing pressure by fishing gear across depth realms. Lollipops indicate whether fishing pressure in each depth realm is above (red lollipops) or below (green lollipops) global average fishing pressure. (**B**) Protection coverage of MPAs (by IUCN categories) and OECMs across depth realms. Lollipops indicate whether the current protection coverage of depth realms is behind (red lollipops) or ahead (green lollipops) of the average coverage of high protection and of the 2020 CBD target. (**C**) Proportion of ocean surface across depth realms. (**D**) Proportion of each depth realms falling under exclusive economic zone or areas beyond national jurisdiction. The four vertical dashed lines represent from left to right: average fishing pressure across depths, average coverage of high protection (MPAs of Ia and Ib IUCN categories) across depths, and the 2020 and 2030 CBD coverage targets.

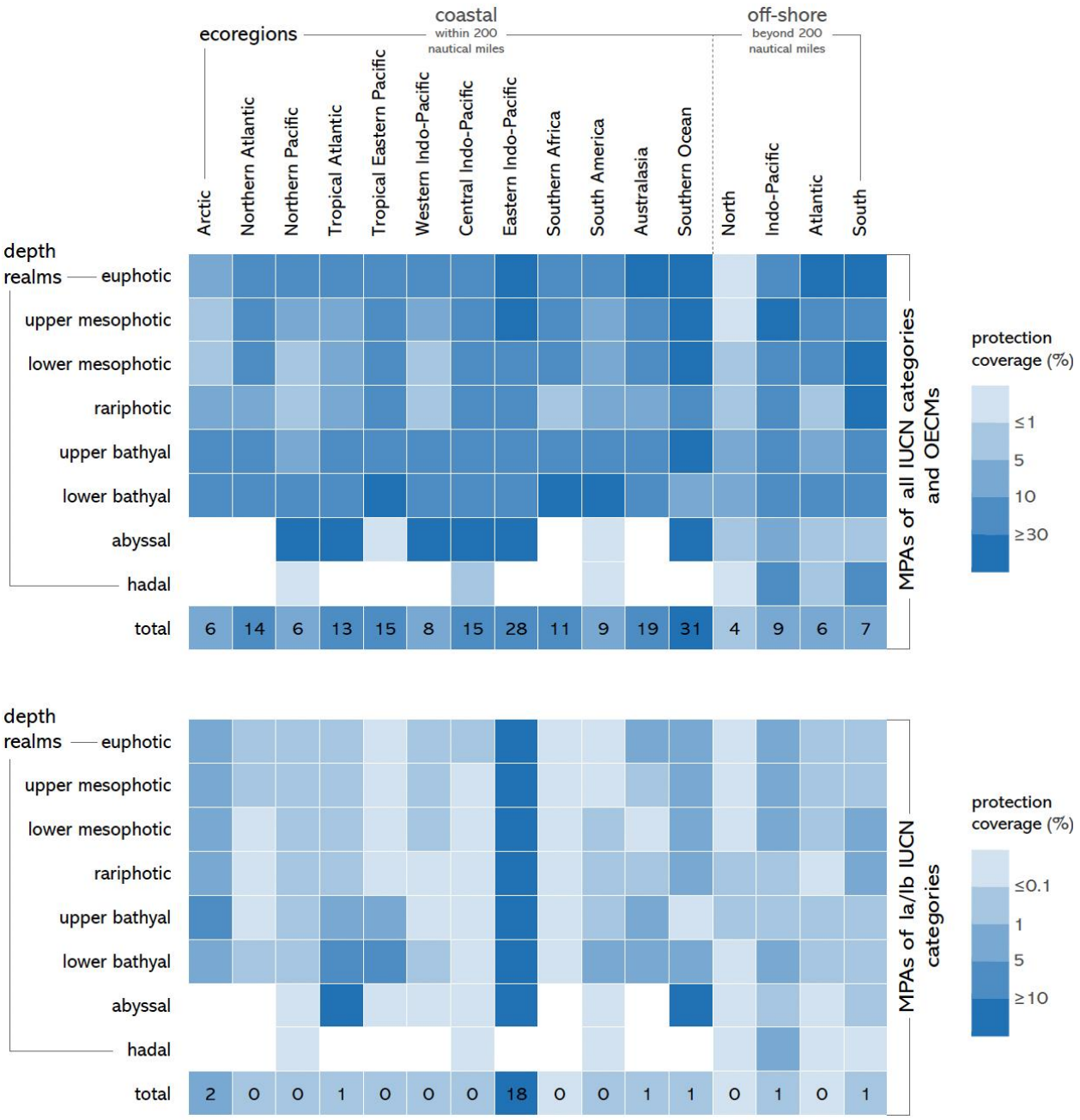

Figure 2.3. Three-dimensional distribution of marine conservation efforts. Protection coverage across depth realms per ecoregions for MPAs of all IUCN categories and OECMs (upper panel) and for MPAs of Ia/Ib IUCN categories only (lower panel). Void cells indicate depth realms that do not occur in a given ecoregion. The last row of each panel ('total') represents the total protection coverage across depths in a given ecoregion.

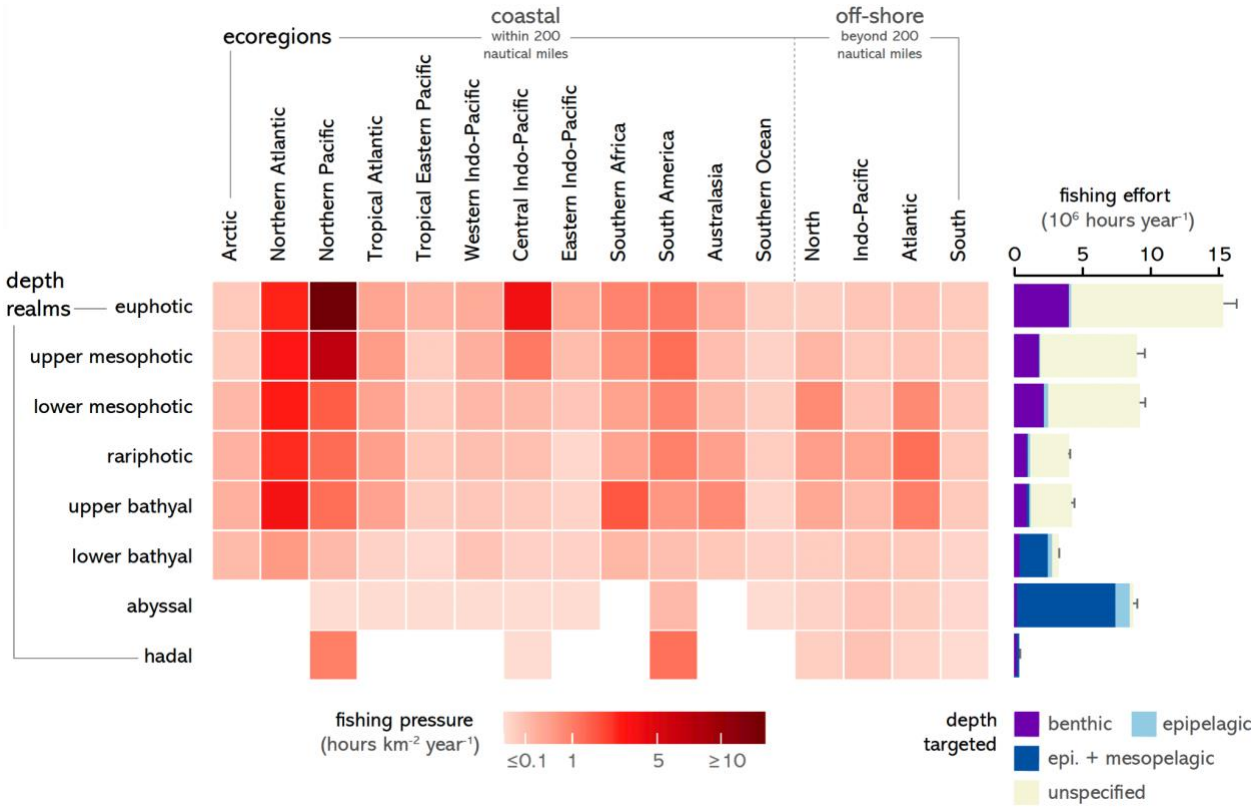

Figure 2.4. Three-dimensional distribution of fishing pressure. Average fishing pressure across depth realms and ecoregions (left panel) and absolute fishing effort per benthic and pelagic depth realms (right panel). White cells indicate depth realms that do not occur in a given ecoregion. Error bars represent 95% confidence interval from n=3 years of fishing data (2018-2020). The 'unspecified' category indicates ambiguous gear types in the Global Fishing Watch database (e.g., "trawling" without distinction between mid-water and bottom). Note that for fishing pressures over lower bathyal and abyssal waters indicated in the left panel, most fishing occurred in shallower pelagic realms (epipelagic and mesopelagic, 0-1000 m).

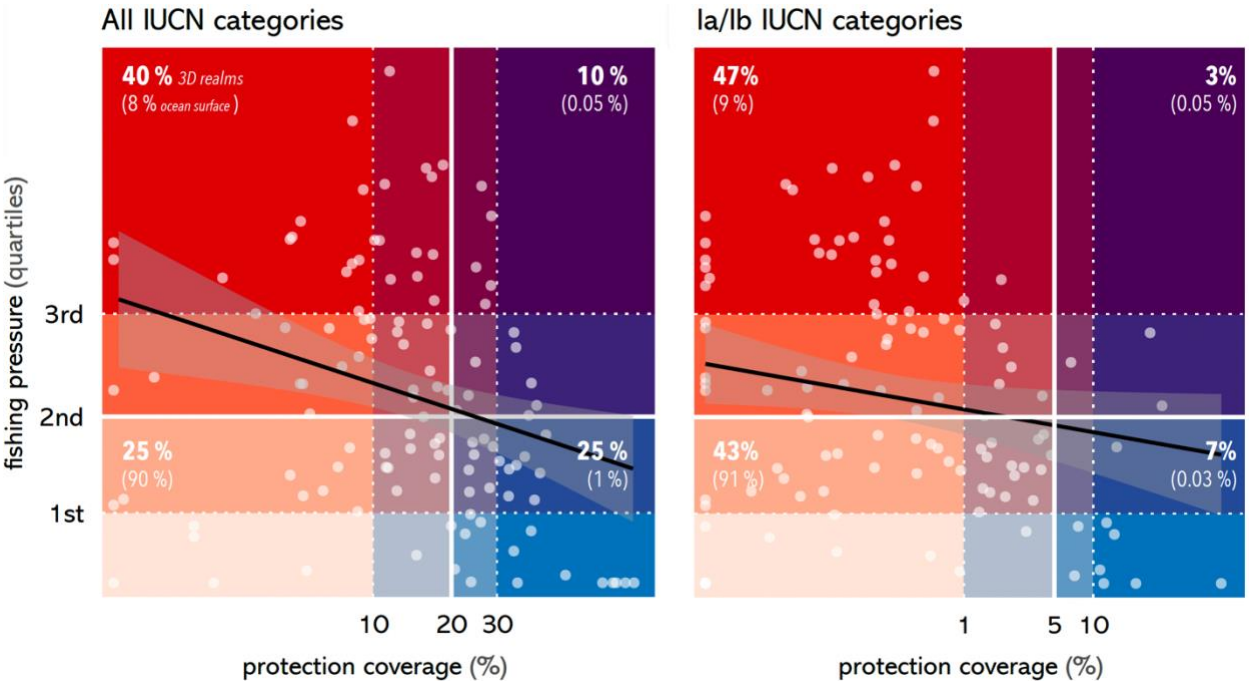

Figure 2.5. Distribution of 3D realms along fishing pressure and protection coverage gradients. Each 3D realm (depth realm per ecoregion) is represented by a dot. Fishing pressure and protection coverage axes are log transformed. Protection coverage takes into account marine protected areas (MPAs) of all International Union for Conservation of Nature (IUCN) categories and other effective area-based conservation measures (left panel), or only MPAs of Ia/Ib IUCN categories (right panel). Underlaying colors represent different categories of fishing pressure (divided by quartiles) and of protection coverage. Percentage values in bold represent the proportion of 3D realms falling into each of the four main categories (below/above median fishing pressure and behind/past halfway completion towards 2030 conservation targets). Percentage values in parentheses represent the proportion of ocean surface falling under these same categories. Regression lines indicate the linear regression model between log-transformed fishing pressure and log-transformed protection coverage, and shaded areas represent the 95% confidence interval associated with that model.

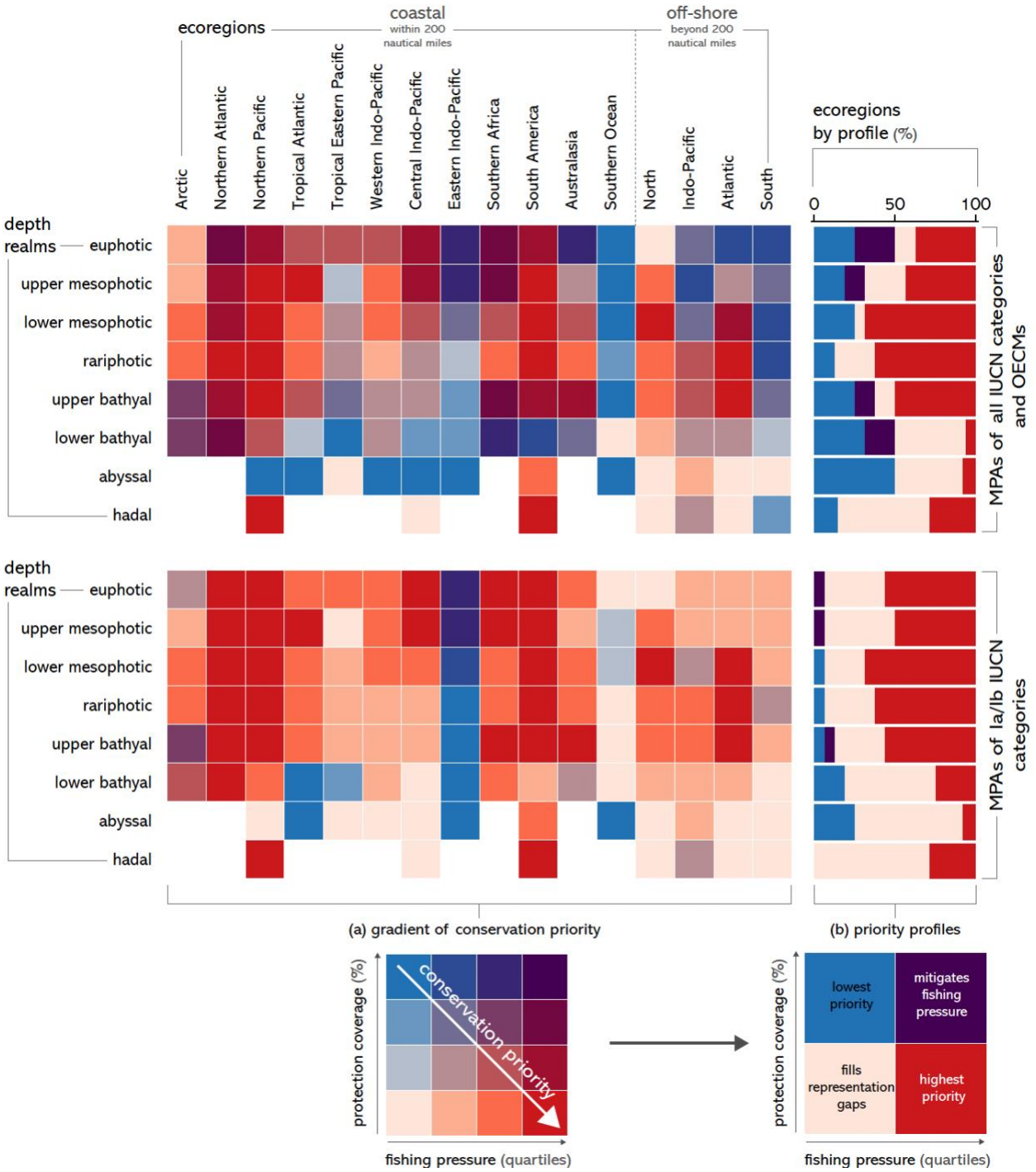

Figure 2.6. Three-dimensional distribution of conservation priority areas based on fishing pressure and protection coverage. Distribution of conservation priority areas across depths based on quartiles of fishing pressure and progress towards 2030 conservation targets for all IUCN categories and other effective area-based conservation measures (top left) or only Ia and Ib IUCN categories (bottom left). Conservation priority increases with increasing fishing pressure and decreasing protection coverage (legend a). Proportion of conservation priority

profiles across depths for all IUCN categories (top right) or only Ia and Ib IUCN categories (bottom right). Four conservation priority profiles were defined based on fishing pressure being below or above median and protection coverage being behind or past halfway completion to 2030 conservation targets (legend b).

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CHAPTER 3
Vertical structure of Caribbean deep-reef fishes from the altiphotic to deep-sea boundary

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3.1. Abstract

While recent technical breakthroughs have enabled advances in the description of reefs down to 150 m, the structure and depth zonation of deep-reef communities below 150 m remains largely unknown. Here, we present results from over 10 years of deep-reef fish surveys using human-occupied submersibles at four locations across the Caribbean Sea, constituting one of the only continuous reef-fish surveys from 10 to 480 m (1 site) and 40 to 300 m (3 sites). We identify four vertically stratified deep-reef fish communities between 40 and 300 m bordered by an altiphotic (0-10 m) and a deep-sea (300-480 m) community. We found a strong faunal break around 150 m that separates mesophotic and rariphotic zones and secondary breaks at ~70-90 m and ~180-200 m subdividing these zones into upper and lower communities. From 300 to 480 m in Roatán, we found a single fish community dominated by deep-sea families, indicating that the lower boundary of the reef-fish realm occurs at 300 m. No differences were found between communities ranging from 20 to 60 m, suggesting that fishes from the lower altiphotic and upper mesophotic form an ecological continuum. While some variability was observed across sites, the overall depth zonation and key species characterizing depth zones were consistent. Most deep-reef species observed were depth specialists restricted to a single depth zone, but many shallow-reef species extended down to mesophotic depths. Depth segregation among species of a genus was found across ten reef-fish genera and likely constitutes one of the mechanisms driving community distinctiveness and fish diversity across depths.

3.2. Introduction

Tropical and temperate reefs are amongst the best described marine ecosystems, yet their study has largely been restricted to shallow depths down to 40 m, corresponding to the traditional limits of non-technical SCUBA diving, depicting a very skewed representation of these ecosystems (Eyal et al., 2021; Rocha et al., 2018). The recent widespread adoption of closed-circuit rebreather diving coupled with the increased use of remotely operated vehicles (ROVs), baited remote underwater videos, and human-occupied submersibles has enabled a surge in the

description of reefs below 40 m, highlighting their diversity and taxonomic distinctiveness with respect to their shallow counterparts (Bell et al., 2022; Robertson et al., 2022; Turner et al., 2017). Despite these advances, our understanding of the ecology of mesophotic (40-150 m), and even more so of rariphotic (150-300 m), reef communities lags behind that of their shallow counterparts.

Most tropical reef communities surveyed across the world display decreases in fish abundance, biomass and richness with depth (Loiseau et al., 2023; Stefanoudis et al., 2019; Weijerman et al., 2019). While many shallow species have wide depth ranges that extend down to the mesophotic (Laverick et al., 2018), deep-reef fish species (below 40 m) tend to be depth-endemic and therefore are not found on shallow reefs (Baldwin et al., 2018b; Loiseau et al., 2023; Quattrini et al., 2017). The number of distinct fish communities occurring along the reef slope, as well as the depths of associated faunal breaks, varies regionally (Lesser et al., 2019) depending on temperature, light availability, and other environmental factors (Hollarsmith et al., 2020; Kahng et al., 2010; Laverick et al., 2020). Similarly, the composition of deep-reef fish assemblages at a given depth is known to vary within and between regions (Pinheiro et al., 2016, 2023). Regional gradients of reef-fish richness have been found to dampen with depth, likely a result of increased environmental constraints that lead to convergent filtering of species composition (Pinheiro et al., 2023).

Despite recent advances, several data gaps still hamper our understanding of deep-reef fish community structure and its regional variability. First, the limited number of deep-reef survey locations constitutes an important barrier to evaluating global patterns of deep-reef fish diversity and levels of deep-reef fish endemism (Kosaki et al., 2017; Pinheiro et al., 2023). The limited number of study sites also restricts regional comparisons, which are essential for identifying environmental drivers of deep-reef fish diversity patterns and, in turn, increase our capacity to predict the spatial distribution and composition of deep-reef communities (T. Bridge et al., 2012; Costa et al., 2015). Such information is necessary to reveal evolutionary and demographic processes at play on deep reefs and to adequately place and design conservation tools that protect the full range of reef diversity (Turner et al., 2019). Second, technical limitations of rebreather diving and the scarcity and cost of submersibles and ROVs have restricted most deep-reef fish studies to the upper range of deep reefs (40-120 m (Turner et al., 2017); leading to the continued discovery of new species below those depths (Baldwin et al., 2018b; Pinheiro et al., 2019; Rocha et al., 2018) even in the most heavily sampled sites (Tornabene et al., 2023). While submersible research at several locations in the tropical western Atlantic has established that deep-reef fishes extend down to at least 300 m (Baldwin et al., 2018b; Quattrini et al., 2017; Robertson et al., 2022; Stefanoudis et al., 2019), the lower depth limit of deep-reef fish distribution and their transition to deep-sea fish communities remains largely unknown.

Here, we advance the understanding of deep-reef fish community structure using one of the most extensive datasets on deep-reef fish communities, comprising observations down to 480 m collected by submersible diving at four sites in the Caribbean. Using hierarchical clustering

and similarity profile analyses, we first test whether distinct communities occur across depths, identify the depth of associated faunal breaks, and quantify the relative role of nestedness and turn-over in explaining the dissimilarity between these communities. We then evaluate the relative contribution of reef-associated vs. deep-sea families to total abundance and richness across depths, and test for depth segregation between closely-related species. Lastly, we perform a cross-site similarity analysis to test whether vertical structure and community composition are stable at the regional scale.

3.3. Methods

Datasets and R scripts used for analyses are available through the author's personal GitHub repository (https://github.com/jjacquemont/Deep.Reef.Fish.Carib).

3.3.1. *Sites*

Data collection occurred at four locations in the Caribbean (Fig. 1): two neighboring western Caribbean islands that are part of the Lesser Antilles (Bonaire and Curaçao), an eastern Caribbean island that is part of the Leeward Islands (Saint Eustatius, hereafter Statia), and a western Caribbean island off the coast of mainland Honduras (Roatán). See Supplementary Information for a more detailed description of islands' environmental and ecological specificities.

3.3.2. Data collection

All fish data were collected using human-occupied submersibles as part of the Smithsonian Deep Reef Observation Project (DROP). Fishes were identified by two trained observers (among Luke Tornabene, Ross Robertson, and Carole Baldwin) in the submersible as it slowly descended (first half of dives) or ascended (second half of dives) the reef slope. Ascents were conducted on a different trajectory than descending transects. Some fishes, with emphasis on cryptobenthic fishes, were opportunistically collected using anesthetics and a suction hose attached to the submersible, either for identification purposes or for systematic projects. See Baldwin et al., (2018) for additional details.

In **Curaçao** (site coordinates: 12.083197N, 68.899058W) fish data were collected between 2011 and 2016 for a total of > 100 submersible dives ranging from 40 to 310 m using the Curasub. Surveys covered ~ 1,000 m on both sides of the drop-off site. In **Bonaire,** fish data were collected in January 2017 during 11 submersible dives. Submersible dives were performed between Klein Bonaire Island and the South of Punt Vierkant by Belnem (drop-off coordinates: 12.094974N, 68.296635W) between 40 to 300 m depth using the Curasub. Each dive averaged 3

to 4 hours in duration and altogether covered ~ 1,000 m on both sides of the drop-off site. Depths between 40 and 150 m were systematically covered, five dives extended down to 180-230 m, and one dive reached 300 m. In **Statia,** fish data were collected in April 2017 during 12 submersible dives between 40 to 305 m depth using the Curasub. Different locations off the southwestern edge of the island were sampled using the R/V Chapman (Robertson et al., 2020), including Gallows Bay (17.474734N, 62.987370W) and Kay Bay (17.467653N, 62.978778W). Dives were conducted off the southwestern edge of the island's 200 m platform and lasted 5 to 6 hours. In **Roatán** (drop-off coordinates: 16.305557N, 86.597669W), fish data were collected between 2016 and 2018 during 17 dives from 0 to 480 m using the submersible Idabel. Each dive averaged 3 to 4 hours in duration, and altogether covered ~ 500 m on both sides of the drop-off site. *Guidelines for the Use of Fishes in Research* co-established by the American Society of Ichthyologists and Herpetologists (Use of Fishes in Research Committee (joint committee of the American Fisheries Society, the American Institute of Fishery Research Biologists, and the American Society of Ichtyologists and Herpetologists, 2014) were followed for all field-collecting activities, and fish specimens collected as part of this study were done so under Smithsonian Animal Care and Use Committee (ACUC) approval to C. C. Baldwin (ACUC #2011–07 and #2014–13). No In Vivo Experiments were conducted as part of this research.

3.3.3. Data analysis

All data analyses were performed using R version 4.4.1 (R Core Team, 2024) in R Studio.

3.3.3.1.Abundance and species richness

Fish abundance was reported as the total number of individuals observed at each 10 m depth bin from 40 to 300 m (e.g., all observations from 40 to 49 m were grouped into the 40 m depth bin) across all submersible dives at a given site. Because sampling effort t (hours spent diving) per depth bin *x* varied depending on technical and environmental factors (e.g., steepness of the slope), abundance values were normalized using coefficients denoting the relative time spent at each depth bin *x* and site *z* (Baldwin et al., 2018):

$$abundance\ normalized_{x,z} = abundance_{x,z} \times sampling\ coefficient_{x,z} \quad (1)$$

with sampling coefficient at depth *x* of site *z* being calculated as:

$$sampling\ coefficient_{x,z} = \frac{\max_x(t_{x,z})}{t_{x,z}} \quad (2)$$

Because total sampling time also varied between sites, we transformed normalized abundance values into relative abundance values when comparing data between sites (see Fig. 2):

$$relative\ abundance\ (x) = \frac{abundance\ normalized_x}{\max_{x\in[40,300]}(abundance\ normalized_x)} \times 100 \quad (3)$$

Models of abundance and species richness were fitted using generalized additive models ({mgcv} package, gam() function) accounting for depth and location (abundance ~ depth + location. We used Poisson error distributions to account for the non-normal data structure, accounting for depth and location (abundance ~ depth + location).

3.3.3.2.*Community structure.*

The depth structure of fish assemblages was examined using multivariate hierarchical clustering methods. First, we calculated the Bray-Curtis dissimilarity matrix, which accounts for species presence and their relative abundance within the community. To avoid overemphasizing the importance of rare species in our analysis, while also controlling for extremely abundant species that sometimes occur in large schools, we applied a square-root transformation to abundance data before performing cluster analyses. Additionally, depth bins for which fewer than five individuals were observed were pooled with the next deeper 10 m depth bin until a collective total of five individuals was reached. This was done to counter biases arising from the fact that there are inherently fewer similarities between communities with fewer individuals, as in (Selig et al., 2023). We used a complete-linkage clustering algorithm, which seeks to maximize distance between clusters based on the two most distant objects in each cluster, to group depth bins based on species composition. Hierarchical cluster dendrograms and nonmetric multidimensional scaling ordinations (MDS) based on Bray-Curtis distances were used to visualize community structure. The number of significantly distinct depth clusters was determined using Analysis of Similarity Profiles (SIMPROF) (K. Clarke et al., 2008) based on a complete linkage algorithm, Bray-Curtis distances, and a conservative value of alpha = 10^{-7} as in (Majewski et al., 2017; Quattrini et al., 2017). Based on main branching events in dendrograms, we pooled adjacent clusters into six depth zones: altiphotic, upper mesophotic, lower mesophotic, upper rariphotic, lower rariphotic, and "below rariphotic" (see Fig. S8). We confirmed the distinctiveness of these depth zones a posteriori using PERMANOVA (K. R. Clarke, 1993). We used a similarity percentage analysis (SIMPER) (K. R. Clarke, 1993) to determine which species contributed most to differences between adjacent depth zones. Lastly, we tested for faunal depth breaks across sites by performing a hierarchical clustering and SIMPROF analyses on depth bins across all four sites based on a Ward linkage (which forms clusters by minimizing variance within clusters), Bray-Curtis distances, and alpha-value = 10^{-7}.

3.3.3.3.*Depth segregation.*

To test whether depth is a driver of niche segregation between closely related species, we compared the depth distribution of species belonging to the same genus. This was performed for all genera for which at least two species had been observed on deep reefs, with each species represented by a minimum of ten individuals across study sites. Because the depth distribution of species from most genera tested (eight out of ten) did not follow a normal distribution (Shapiro-Wilk normality test, $p<0.05$) we performed Kruskall-Wallis tests followed by pair-wise Wilcoxon tests to assess the correlation between species and depth (depth~species). Statistical

tests were performed on original depth observations (non-transformed for sampling effort), but density curves and means represented in Fig. 7 display abundance corrected for sampling effort (as in equation 1).

3.3.3.4.*Depth affinities of fishes*.

We defined five categories of depth affinities at the species level: “altiphotic/mesophotic”, “mesophotic”, “mesophotic/rariphotic”, “rariphotic”, and “deep-sea”. A species was determined to have an affinity for a given depth zone when ≥ 75% of observations (Baldwin et al., 2018b) occurred in that zone. We classified species as belonging to the “altiphotic/mesophotic” category when ≥ 75% of observations in this study occurred at mesophotic depths, but the species was also known to commonly occur above 40 m depth (Froese & Pauly, 2023; Robertson & van Tassell, 2015). Similarly, the “deep-sea” depth affinity was attributed to species typically associated with deep-sea ecosystems, but also observed in the present study (e.g., *Synagrops spp.* , *Bathyclupea sp*. , *Epigonidae sp.*; see Table S1 for complete list). When determining in which depth zones a species was observed, we used the site-specific depth breaks from hierarchical clustering analyses (Figure 2).

We further defined four categories of depth dominance at the family level based on published fish databases (Froese & Pauly, 2023; Robertson & Tornabene, 2023; Robertson & van Tassell, 2015) and expert knowledge: “altiphotic/mesophotic”, “rariphotic”, “deep-sea”, and “depth generalists” (Table S1). We classified families as “altiphotic/mesophotic” when the depth ranges of their members were predominantly shallower than 130 m, as rariphotic when the depth ranges of their members were predominantly between 130 and 500 m, and as deep-sea affiliated when the depth ranges of their members were predominantly below 500 m. In addition to these three categories first defined by Baldwin et al., (2018), we classified families as depth generalists when their members spanned multiple depth zones, which was the case for some non-reef affiliated families (e.g., Paralichthyidae).

3.3.3.5.*Dissimilarity across depths and between sites.*

We calculated the β-diversity index β_{sor} (Diserud & Ødegaard, 2007) between depth zones to assess whether the distinctiveness of deep-reef fish communities is predominantly driven by changes in species composition (i.e., turnover) or by loss in diversity (i.e., nestedness (Baselga, 2010)):

$$\beta_{sor} = \frac{b+c}{2a+b+c} \quad (4),$$

where *a* is the number of species common to both groups (site or depth bin), *b* is the number of species that occur in the first group but not in the second, and *c* is the number of species that occur in the second group but not in the first. This index varies between 0 and 1, with 1 indicating no species in common between sites and 0 indicating identical species composition between sites.

We calculated the turnover component of dissimilarity using the Simpson dissimilarity index (β_{sim}), which calculates the amount of dissimilarity due to the presence of distinct species in both groups:

$$\beta_{sim} = \frac{min(b,c)}{a+min(b,c)} \text{ (5).}$$

β_{sim} varies between 0 and 1, with 1 denoting that no species are shared between the two groups, and 0 denoting that all species from a group correspond to a sub-sample of the species from the other group.

The nestedness component of pairwise dissimilarity, i.e., the component of dissimilarity linked to species loss rather than species turnover, is calculated by subtracting βsim from βsor:

$$\beta_{nes} = \beta_{sor} - \beta_{sim} \text{ (6).}$$

Taxonomic dissimilarity, nestedness, and turnover components were computed in R using the {betapart} package (Baselga et al., 2023).

3.4. Results

3.4.1. *Abundance and richness across depth.*

A total of 33,873 individuals representing 225 fish species were observed across depths ranging from 10 to 480 m, including 38 deep-reef species that were new to science at the time of their observation (Table S1). Rarefaction curves indicate that sampling effort was sufficient to sample most of the fish diversity in Curaçao, but that additional sampling effort would have likely resulted in additional species observed in Bonaire, Statia, and Roatán (Fig. S1). Fish abundance and species richness decreased with depth at all sites ($p < 0.001$, Fig. 2). Abundance decreased steeply below 80 m depth and plateaued at all sites at 0-10 % of initial abundance values below 200 m. The exception was Curaçao, where abundance remained at or above 10% and even increased back to ~25 % between 270 and 300 m (Fig. 2). Abundance remained stable from 300 to 480 m in Roatán, at 0-3 % of initial abundance. Total fish species richness across depth was 73 species in Curaçao, 119 species in Bonaire, 107 species in Statia, and 145 species in Roatán (see Table S1 for complete list of species at each site). At all sites, species richness decreased mostly linearly with depth from 40 to 300 m (Fig. 2). Below 260 m depth, species richness remained below 10 species at all sites, with values ranging between 8-10 species in Curacao and Roatán, and 0-2 species in Bonaire and Statia. Species richness halved again below 300 m in Roatán, and plateaued at 2-6 species between 300 and 480 m.

Vertical structure of fish communities. Similarity profile (SIMPROF) analyses based on species composition and abundance at each 10 m depth bin revealed between three (Statia) and seven (Curaçao) distinct fish community clusters between 40 and 300 m (denoted by black thick horizontal lines in Fig. 3). With the exception of the 190 m community in Roatán, which pooled with the 210-300 m communities, all clusters comprised communities from continuously ordered depth bins. Based on main branching events of hierarchical clustering dendrograms (Fig. 3) and on previous analyses of reef-fish depth zonation (Baldwin et al., 2018), SIMPROF clusters were pooled into four depth zones: upper and lower mesophotic, and upper and lower rariphotic. Depth zones formed a posteriori by pooling SIMPROF clusters displayed significantly different fish communities (PERMANOVA, p-value < 0.001), and explained between 46% (Statia) and 60% (Curaçao) of the total variance between fish communities at a given site (Fig. 3).

The upper mesophotic zone corresponded to a single cluster starting at 40 m and ending at 70-90 m in Bonaire, Curaçao, and Statia. In Roatán, two sister clusters from 20 to 100 m were considered to form the upper mesophotic. The lower mesophotic corresponded to a single cluster in Bonaire and Roatán and to two sister clusters in Curaçao, and spanned from 70-90 to 120-150 m. In Statia, a single large cluster spanned from 100 to 190 m. For comparative purposes, this cluster was divided into a lower mesophotic and upper rariphotic zone, with a depth break at 140 m corresponding to the main branching event within this cluster (Fig. 3). At all other sites, the upper rariphotic corresponded to a single cluster spanning from 120-150 to 170-210 m. Lastly, the lower rariphotic corresponded to a single cluster in Statia and Roatán, and to three adjacent clusters in Curaçao and Bonaire. Community breaks (i.e., boundaries between depth zones) occurred at similar depths in Curaçao and Bonaire: ~70-80 m, ~120-130 m, and ~170-190 m. At Statia and Roatán, community breaks were skewed towards deeper depths at 100 m, ~140-150 m, and ~190-210 m. Based on observations from Roatán, we found two additional community breaks: one separating the shallowest 10 m depth bin from the next altiphotic/upper mesophotic cluster (20-60 m), and one at 300 m separating the lower rariphotic from a deeper fish community that formed a single cluster down to 470 m (Fig. 3).

3.4.2. *Indicator species across depth zones.*

The top five most abundant fish species per site and per depth zones represented 46 to 91% of the total community abundance in that depth zone. Most abundant species changed between depth zones but were often identical across several sites (Fig. 4). Species that significantly contributed to differences in fish communities between depth zones (SIMPER analyses) were a subset of the most abundant species (Fig. 4). A decrease in the abundance of *Clepticus parrae*, *Chromis insolata,* and *Coryphopterus personatus* marked the transition between the upper and lower mesophotic; a decrease in the abundance of *Canthigaster rostrata* and *Bullisichthys carribaeus* marked the transition between the lower mesophotic and upper rariphotic; and a decrease in the abundance of *Serranus phoebe, Pronotogrammus martinicensis, Symphysanodon octoactinus, Palatogobius incendius, Palatogobius grandoculus,* and *Antilligobius nikkiae* marked the transition between the upper and lower rariphotic. In Roatán, an increase in the

abundance of *Hollardia hollardi*, *Epigonidae sp.*, *Chrionema squamentum*, *Phenascoscorpius nebrius*, and *Neoepinnula americana* marked the transition between the lower rariphotic and the next deeper community.

3.4.3. *Beta-diversity across depth zones.*

Dissimilarity (i.e., total beta-diversity) between depth zones increased with depth disparity, with the highest dissimilarity (~100 %) occurring between the upper mesophotic and the lower rariphotic (Fig. 5, Fig. S3). Dissimilarity between adjacent depth zones was ~ 50 % across depths and sites and mostly resulted from species turnover. However, higher contribution of nestedness (40 %) between the upper and lower mesophotic communities, and between the lower rariphotic and the next deeper depth zone in Roatán, suggest that species drop-out plays an important role in these faunal transitions.

3.4.4. *Depth affinities of species.*

We found that 151 out of 225 species were depth specialists with >75% of their observed abundance occurring in a specific depth zone: n=35 in the altiphotic, n=44 in the upper mesophotic, n=16 in the lower mesophotic, n=17 in the upper rariphotic, n=31 in the lower rariphotic and n=8 below the rariphotic (Fig. 6A). When considering depth-zone predominance at the family level, we found that reef-fish families dominated all depth zones in abundance and richness from the altiphotic to the lower rariphotic. This result stood true when pooling observations across sites (Fig. 6B), and when considering sites individually (Fig. S6). Species from altiphotic/mesophotic families dominated in abundance down to the upper rariphotic and in richness down to the lower rariphotic, but rariphotic taxa dominated in abundance in the lower rariphotic. Below the rariphotic (300-480 m), fish communities were dominated in abundance and richness by species from deep-sea families (e.g., Epigonidae, Triacanthodidae, Trachichthyidae; Table S6). However, when considering depth affinity at the species level (Fig. 6C), deep-sea fishes were only present in the lower rariphotic and below and represented a minority of total abundance and richness even in the 300-480 m depth zone. The altiphotic, upper mesophotic, and lower rariphotic were dominated by species from a single depth-zone affinity group (altiphotic/mesophotic and rariphotic, respectively), while the lower mesophotic and upper rariphotic were characterized by overlaps between four depth-zone affinity groups (Fig. 6C). Peaks in the richness of depth-zone affinity groups occurred at different depths among sites and tended to match site-specific depth breaks identified from hierarchical clustering (Fig. S5).

3.4.5. *Habitat segregation by depth.*

We found strong evidence for depth segregation between species of the same genus (Fig. 7). Within all ten genera tested, species was a significant factor influencing mean depth of occurrence (Wilcoxon and Kruskal-Wallis tests, p-values<0.01), and all pairwise comparisons of mean depths between species of a same genera were statistically significant (p-values<0.04,

Table S4 and S5). Depth segregation occurred both between and within depth zones. For instance, three *Lipogramma* species partitioned across the upper mesophotic, lower mesophotic and upper rariphotic, while *Azurina multilineata* and *A. cyanea* displayed depth segregation within the upper mesophotic (Fig. 7). The depth distributions of species varied across sites, reflecting in some instances the variations in depth zones' boundaries between sites (e.g., see *Palatogobius incendius*, Fig. S2).

3.4.6. *Cross-site community analysis.*

We performed a cross-site hierarchical clustering of deep-reef fish communities between 40 and 300 m using a Ward linkage algorithm (Fig. 8A). We found that the 96 fish communities corresponding to distinct sites and depth bins formed 15 significant clusters (SIMPROF based on Bray-Curtis distance, alpha = 10^{-6}). The total number of significant clusters was unchanged when adding communities observed at 10-40 m and 300-480 m in Roatán (Fig. S4). The two first levels of branching of the dendrogram (Fig. 8A) reproduced the four depth zones identified at the site-level (Fig. 3). The first level of branching corresponded to a depth break at 120-160 m depending on site, marking the transition between the mesophotic and the rariphotic. The second level of branching within the mesophotic branch (40 to 120-160 m) formed two groups with a depth break at 70-100 m depending on site, marking the transition between the lower and upper mesophotic. The second level of branching within the rariphotic branch (120-160 to 300 m) formed three groups: one group encompassing all rariphotic depths from Roatán (150-309 m), and two groups separating the lower and upper rariphotic depth zones from Curaçao, Bonaire and Statia, with a depth break at 170-190 m. The depth of community breaks found in the cross-site clustering (Fig. 8A) were similar to those found in site-specific clustering (Fig. 3).

We found that depth zone, site location, and the interaction between these two factors had a significant influence, in this order, on fish community structure (PERMANOVA, Table S7). In the upper mesophotic, hierarchical clustering indicated greater similarities between Curaçao and Bonaire on one hand, and Roatán and Statia on the other (Fig. 8A). However, in the lower mesophotic, fish communities from Bonaire and Roatán pooled separately, while Statia and Curaçao pooled together. In the upper rariphotic, communities from Curaçao, Bonaire, and Statia were pooled together while fish communities from Roatán were in a separate cluster. Beta-diversity based on the presence/absence of species confirmed that similarity between sites varied across depth, with Roatán tending to display higher dissimilarity to other sites (Fig. 8B). Cross-site beta-diversity values remained within similar ranges from the upper mesophotic to the upper rariphotic but were higher in the lower rariphotic.

3.5. Discussion

3.5.1. Vertical zonation of reef-fish communities

The present study provides an extensive analysis of the vertical structure of reef fishes based on continuous, direct visual observations of communities from 40 to 300 m depth at four sites from the Caribbean, with additional data from 10 to 480 m depth at one site. The number of

species observed per site (73-145) is within the range found by previous deep-reef fish studies in the Caribbean (e.g., 103 in Puerto Rico (Bejarano et al., 2014)). The patterns of decreased richness and abundance with depth documented in this study are consistent with trends observed in the Caribbean (Andradi-Brown et al., 2016) and other regions of the world (Loiseau et al., 2023; Stefanoudis et al., 2019). While we found that the number of distinct community clusters and their depth boundaries varied between sites (Fig. 3), we identified four main depth zones occurring at all sites: the upper mesophotic (~40-90 m), the lower mesophotic (~100-140 m), the upper rariphotic (~150-190 m), and the lower rariphotic (~ 200-300 m). This depth zonation was found both using site-specific hierarchical clustering (Fig. 3) and cross-site hierarchical clustering (Fig. 8). The only exceptions were the deep-reef fish communities from Statia for which the distinction between lower mesophotic and upper rariphotic was more ambiguous. Greater similarity between the upper and lower mesophotic on one hand, and between the upper and lower rariphotic on the other hand, was supported by the branching hierarchy of the cross-site dendrogram (Fig. 8A). Our results support a two-tier vertical zonation nomenclature for deep reefs as established in Baldwin et al., (2018), with a first level comprising two zones (the mesophotic and rariphotic) separated by a strong community break, and a secondary level separating "upper" and "lower" communities within these zones. While the 300 m lower boundary of the lower rariphotic was originally set by the depth limitations of submersibles rather than by actual ecological observations (Baldwin et al., 2018b; Stefanoudis et al., 2019), the depth break found at 300 m in Roatán between the lower rariphotic and a deeper fish community that extends down to at least 480 m now supports the ecological reality of this boundary. To the best of our knowledge, the only other study that tested the lower limit of the rariphotic identified a comparable faunal break depth at 320 m in Hawaii (Weijerman et al., 2019).

The depth of community breaks we identified match those of previous studies conducted locally, especially by Pinheiro et al., (2016) (Pinheiro et al., 2016) who documented a strong fish species turnover at 80 m in Curaçao, matching the upper to lower mesophotic transition found here. The few studies conducted outside of the Caribbean over a comparable depth range have also reported successions of three to five distinct reef-fish assemblages (Semmler et al., 2017; Weijerman et al., 2019), but differences in the number of distinct assemblages and in the depth of faunal breaks suggest important regional variability. Many more studies have investigated the vertical zonation of deep-reef communities, but most have been limited to a maximal depth of 60 to 100 m; as such, they have only captured the upper range of deep reefs (Laverick et al., 2018; Lesser et al., 2019). Conversely, some studies have extended below 300 m depth but did not describe fish communities continuously across depths, hindering depth-zonation analyses (Quattrini et al., 2017; Stefanoudis et al., 2023). As a result, our understanding of the number of depth zones and their boundaries across oceanic regions remains limited. Given that the shallowest deep-reef fish community break generally occurs around 60-100 m (Baldwin et al., 2018b; Boland et al., 2022; Semmler et al., 2017), surveys extending down to at least 150 m are necessary to adequately locate deep community breaks. In that regard, submersible surveys

combined with the use of ichthyocides or anesthetics offers unparalleled means to describe deep-reef fish communities. In particular, only submersibles allow for direct visual observation and fish collection below ~150 m, the lower limit of rebreather diving. Such sampling techniques are necessary to document cryptic species, a major component of deep-reef fish communities that cannot be readily observed using remotely operated vehicles or underwater video systems (Alzate et al., 2014; Robertson et al., 2022).

3.5.2. Shifts in fish community structure across depths

We found high and relatively constant values of dissimilarity (~ 50%) between fish communities of adjacent depth zones resulting mostly from species turnover (Fig. 5), corroborating existing evidence for the ecological uniqueness of deep-reef fish communities (Pinheiro et al., 2019; Rocha et al., 2018; Semmler et al., 2017). While previous studies have reported important taxonomic turnover between deep-reef fish communities (Pinheiro et al., 2019; Semmler et al., 2017), only one study has tested this down to rariphotic depths (Semmler et al., 2017). While (Semmler et al., 2017) reported lower rates of turnover at rariphotic than at mesophotic depths, we found the opposite trend, with the upper to lower mesophotic transition having the lowest rate of species turnover.

We found that "altiphotic/mesophotic" species contributed to ~60% of total diversity and ~80% of total abundance in the upper mesophotic (Fig. 6C). This aligns with previous studies demonstrating that a large proportion (~64%) of shallow reef fishes occur down to 60 m (Laverick et al., 2018) and suggests that mesophotic fish communities are largely composed of shallow reef fishes at the extremity of their depth distribution, especially in the upper mesophotic. The ecological continuum between altiphotic and upper mesophotic fish communities was further supported by SIMPROF analyses which identified a single cluster from 20 to 60 m in Roatán (Fig. 2). These results suggest that the upper mesophotic boundary, typically considered at around 30-40 m in the literature, might reflect conventional SCUBA limits, as well as breaks in habitat-forming communities rather than actual fish community breaks. By contrast, the high rates of rariphotic specialists in the rariphotic depth zones (Fig. 6C) combined with the important species turnover found between mesophotic and rariphotic communities (Fig. 5) confirm the ecological uniqueness of rariphotic fish communities, a depth zone only recently described by Baldwin et al., (2018). Together, these results suggest that the faunal break between the upper and lower mesophotic is numerical (i.e., decrease in abundance and loss of species) rather than compositional (i.e., species turnover), and represents a weaker faunal break than the mesophotic to rariphotic transition. We also confirm that the rariphotic zone is dominated by reef-affiliated families by showing this pattern across four sites of the Caribbean (Fig 6B), a result previously documented only in Curaçao (Baldwin et al., 2018b). Lastly, we determine that the lower boundary of the rariphotic occurs at 300 m in Roatán and corresponds to the depth limit of communities dominated by reef-affiliated fish families. From 300 to 480 m, we found a single community dominated by rariphotic specialists from deep-sea families rather than true deep-sea species.

3.5.3. *Depth specialization and segregation in reef fish taxa*

We found that the majority of fish species observed at our study sites occur predominantly within a single depth zone (Fig. 6A). Eighty-five percent of deep-reef species (i.e., excluding altiphotic and deep-sea affiliated species) were depth specialists, meaning that > 75% of their total abundance was confined to either mesophotic or rariphotic depths. Furthermore, our study documents depth segregation among ten reef-fish genera, with up to four species of a given genus occurring at distinct average depths (Fig. 7). These results demonstrate that habitat segregation by depth is an important ecological mechanism driving the zonation patterns observed on deep reefs. Moreover, depth segregation may be important in driving speciation in reef fish, or at the very least, an important factor in maintaining species boundaries. A substantial part of deep-reef fish diversity originates from speciation of shallow-reef fish having adapted to deep-reef environments (Baldwin et al., 2018b; Tornabene et al., 2016). Depth segregation has already been demonstrated on deep reefs for the family Gobiidae (Baldwin & Robertson, 2015; Tornabene et al., 2016), the genus *Lipogramma*, and the genus *Lipropoma* (Baldwin & Johnson, 2014; Baldwin & Robertson, 2014), or the genus *Bathypterois* found on seamounts (Quattrini et al., 2017). Importantly, large differences between global depth distributions and locally realized depth distribution (Fig. S9) suggests that depth segregation processes are underestimated when working with global datasets.

3.5.4. *Regional variability of deep-reef fish communities*

We found that fish communities from a given depth zone shared many characteristics across sites. The most abundant species at a given depth zone were usually found at several sites and participated in driving community distinctiveness between depth zones (Fig. 4). Some of these key species have already been identified at different Caribbean sites (Quattrini et al., 2017; Stefanoudis et al., 2019), in particular *Pronotogrammus martinicensis* and *Serranus phoebe* as indicators of rariphotic communities, and *Paranthias furcifer* as an indicator of mesophotic communities. Such indicator species could be useful to more promptly identify vertical boundaries of depth zones at new study sites, or to test whether depth boundaries at a given site are changing through time. The limited coastal extent (~1 km) sampled at each island precludes us from explaining differences in fish communities between sites through a biogeographic lens. Rather, variations in vertical zonation and in fish-community structure are likely due to local characteristics of study sites, such as irradiance, temperature, nutrient availability (Lesser et al., 2018), and habitat characteristics (Hollarsmith et al., 2020; Loiseau et al., 2023; Stefanoudis et al., 2019). Local geomorphological specificities of study sites, such as the location of reef walls and reef flats, could explain a large part of the variability in vertical zonation and community structure of deep-reef fish (Laverick et al., 2020; Reed et al., 2018). Human impacts, particularly fishing pressure and coastal development, could also explain differences observed between sites (Richardson et al., 2023). Notably, the survey site at Bonaire occurs within a marine protected area (Frade et al., 2019) while the study site in Curaçao is located in front of a resort complex

and experiences fishing and shoreline artificialization. More research is needed to document how such pressures affect deep-reef fish communities (Soares et al., 2020; Turner et al., 2019).

3.5.5. Increased endemism in the rariphotic?

The higher regional beta-diversity in the lower rariphotic revealed in this study could be due to (1) lower fish abundance, which might have amplified biases associated with incomplete sampling effort by artificially increasing differences between rariphotic communities described, (2) greater influence at rariphotic depths of local environmental variables and micro-habitats on community structure, (3) higher rates of endemism at rariphotic depths, or (4) a combination of these factors. While assessments of endemism rates at rariphotic depths are unprecedented, higher rates of endemism on mesophotic reefs than on shallow reefs have been documented by an increasing body of literature (Copus et al., 2022; Kane et al., 2014; Kosaki et al., 2017), and surveys of deep reefs across the Pacific found that deep-reef fishes tend to have smaller geographic ranges than shallow-reef fishes (Copus et al., 2022; Pyle et al., 2016). The greater environmental stability of deep reefs, in particular in relation to sea-level change associated with glacial-interglacial cycles (Ludt & Rocha, 2015), has been hypothesized to promote higher rates of endemism at depth (Copus et al., 2022), and could explain how endemism occurs on Caribbean deep reefs despite extremely low regional levels of endemism on Caribbean shallow reefs (Robertson & Cramer, 2014). While close to half (48 out of 109) of mesophotic and rariphotic species observed in this study were found at a single site, it is currently unclear whether these species are locally endemic. Extending deep-reef studies to new sites across ocean basins will help us to determine whether increased rates of endemism are indeed a characteristic of deep-reef fish communities or rather reflect decreasing sampling efforts with depth.

3.5.6. Accounting for depth in biogeographic studies

Decades of biogeographic research have attempted to divide the world's tropical reef regions into homogeneous and distinct ecological units (Robertson & Cramer, 2014; Spalding et al., 2007). The resulting classifications are based almost exclusively on the distribution of shallow-reef species and, as such, only account for ~20% of reef biodiversity. Given the growing evidence that deep-reef communities exhibit distinct diversity patterns relative to shallow reefs (Pinheiro et al., 2023) and could be influenced by different diversification mechanisms (Copus et al., 2022), we suggest that the delimitation of marine realms and ecoregions should shift from a two-dimensional (2D) to a 3D approach. Adding depth boundaries to marine ecological units would reflect that several ecologically distinct marine communities co-occur at a given location at different depths. For example, “depth zones” corresponding to distinct ecological communities, and “depth realms” corresponding to distinct taxonomic communities (e.g., reef-affiliated vs. deep-sea affiliated) could constitute two levels of subdivision of marine units across depth. At minima, we suggest that biogeographic studies revisit current classification by incorporating the rapidly evolving data on the distributional range of deep-reef and deep-sea species (Simon et al., 2016). Similarly, biogeographic theories developed to explain spatial

patterns of reef-fish diversity, such as the center of overlap, origin, and accumulation hypotheses (Briggs, 1999; Cowman & Bellwood, 2013) have also been restricted to explaining diversity patterns of shallow-reef fishes. Testing whether these theories could be transposed to explain diversity gradients across both space and depth could represent the next step for reef-fish biogeographic studies.

3.5.7. Conclusion

Continuous observations from the surface to 480 m at four sites in the Caribbean suggest that six vertically-stratified fish communities occur across these depths, including five reef-fish dominated communities down to 300 m. Vertical community zonation was comparable across sites suggesting regional stability of this pattern, although we observed variations in the dominating species and in the exact depth of community breaks, likely a result of local environmental conditions. Our results demonstrate that several ecologically distinct deep-reef fish communities occur below shallow reefs and support the growing literature calling to extend conservation actions beyond shallow ecosystems to ensure that the full succession of marine diversity benefits from protection.

3.6. Acknowledgments

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3.7. Figures

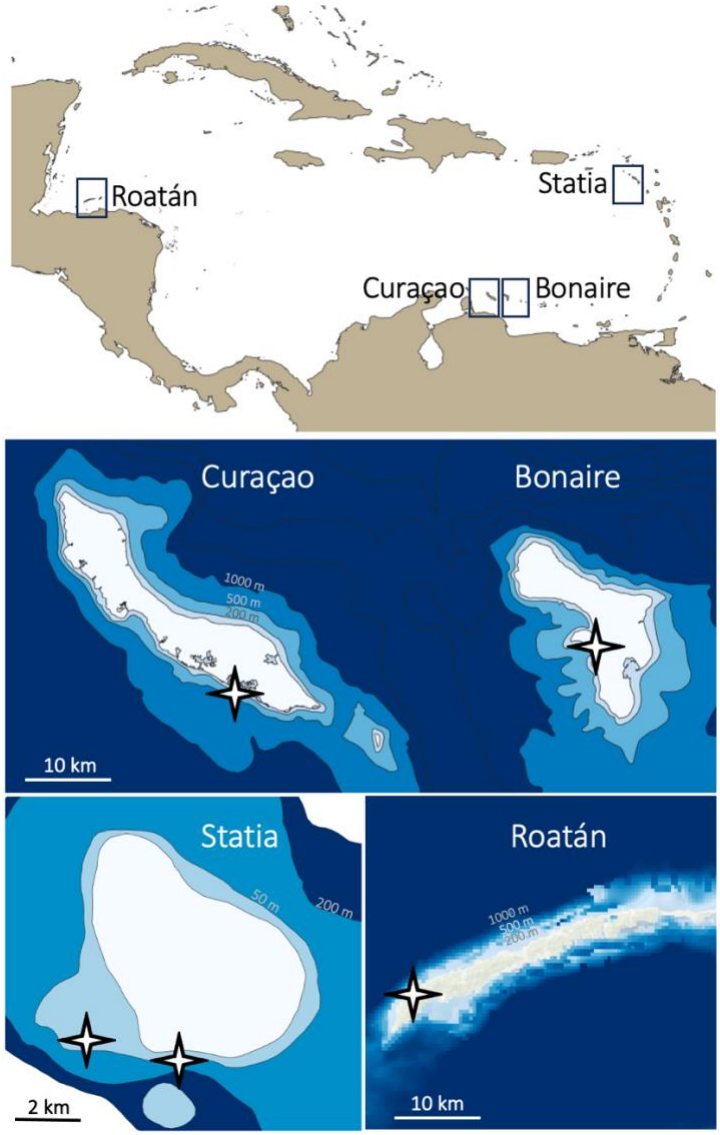

Figure 3.1. Locations of study sites. The bathymetric maps of Curaçao, Bonaire and Statia were obtained from the Dutch Caribbean Biodiversity Database, and the bathymetric map of Roatán from the General Bathymetric Chart of the Ocean. Rendering was obtained using QGIS.

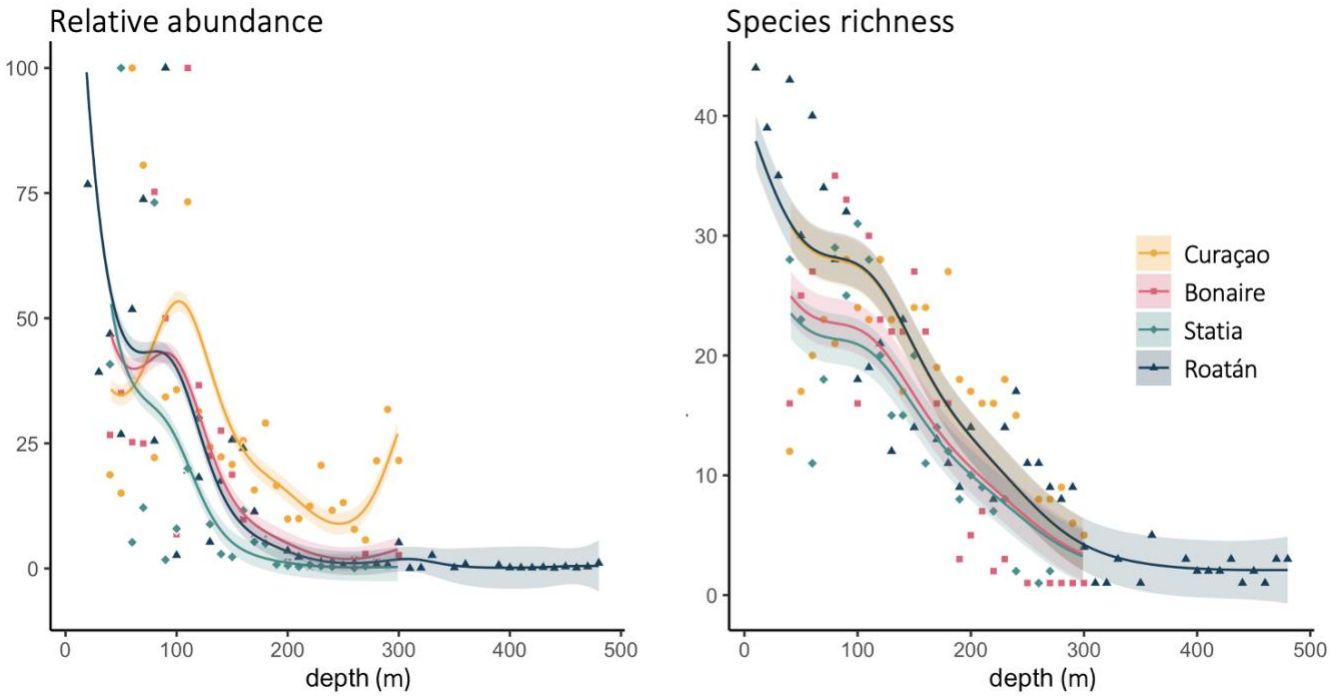

Figure 3.2. Relative abundance (left) and species richness (right) across depth at the four study sites. Relative abundances were normalized by depth-specific sampling effort and are given as a proportion of the site-specific maximal abundance. Points represent observed relative abundance and richness at each 10 m depth bin, lines represent predicted values from a generalized additive model and shaded areas represent 95% confidence intervals. Note that for depths greater than 300 m and shallower than 40 m, predictions are based on observations from Roatán alone.

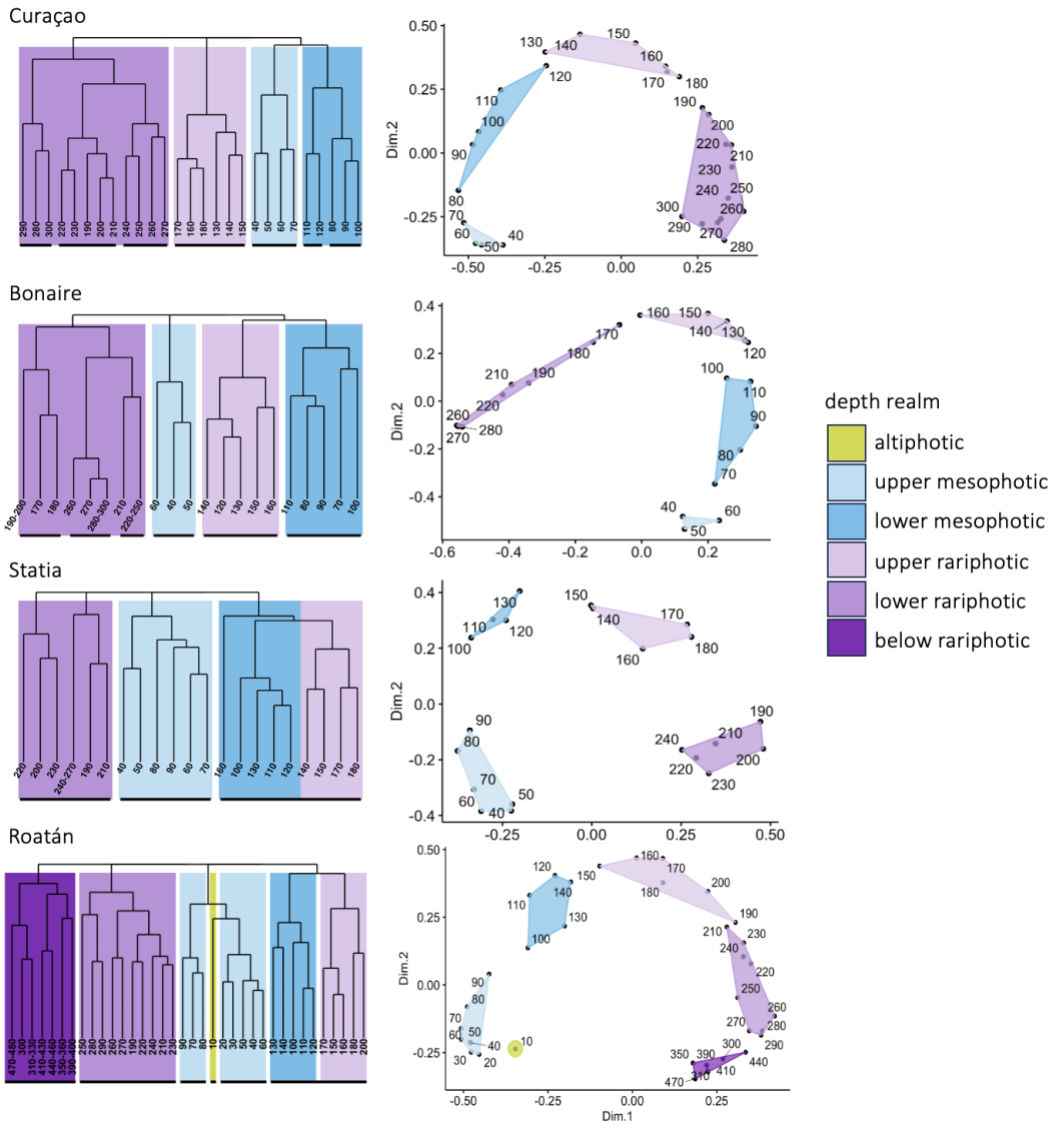

Figure 3.3. Site-specific dissimilarity analysis of reef-fish community from 40 to 300 m depth. Left panels display hierarchical clustering dendrograms, right panels display nonmetric multidimensional scaling ordination (MDS) plots derived from Bray-Curtis dissimilarity analysis. Clusters with significantly distinct composition (SIMPROF analyses) are indicated on dendrograms by thick continuous horizontal lines below depth bin values. Color scale indicates the depth zones that clusters obtained from SIMPROF analyses were pooled into. Depth-bins are labeled with the minimum depth of each 10 m depth interval (e.g., "100 m" = 100-109 m).

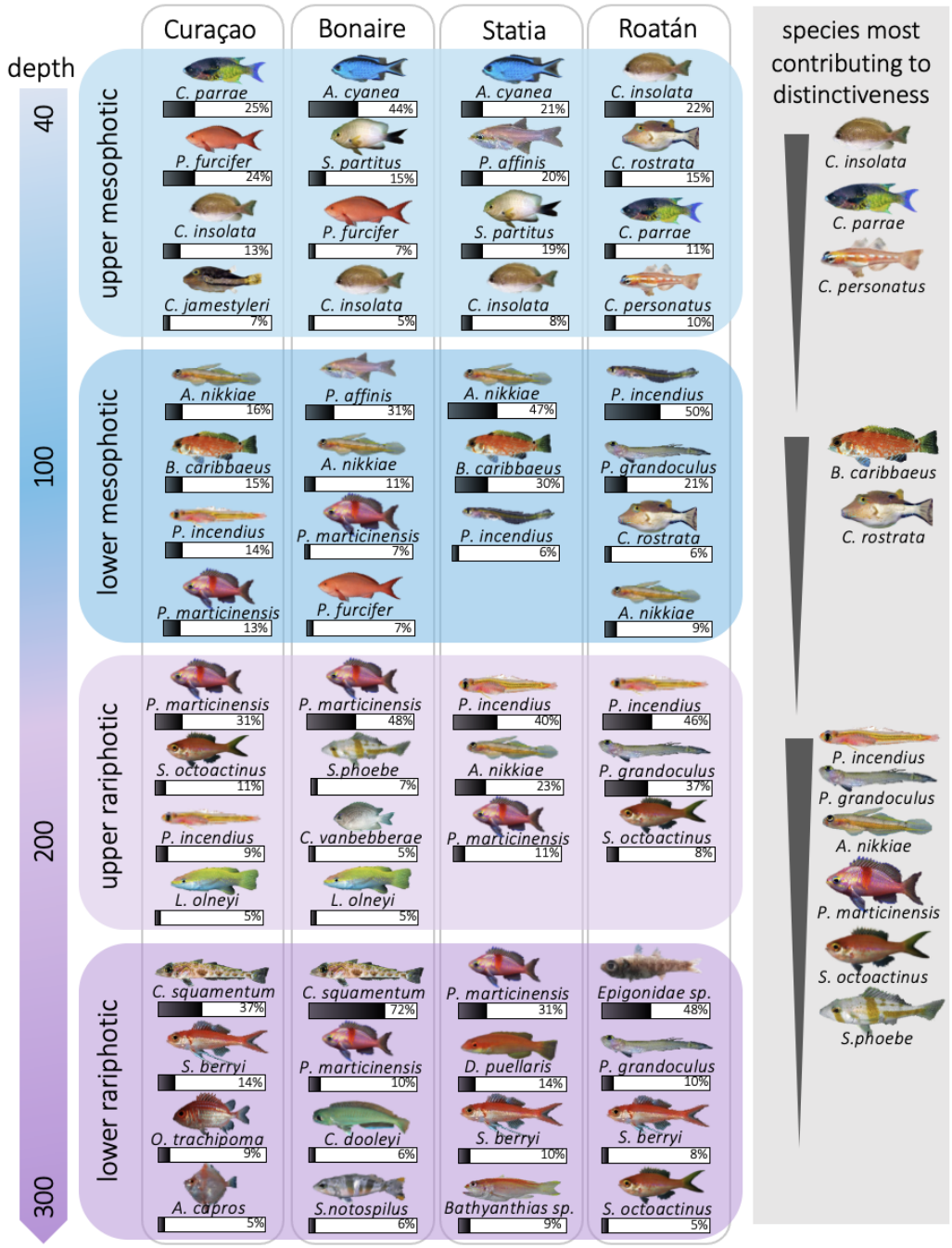

Figure 3.4. Most common species by depth zone and site. Species displayed are the top four most common species by depth zone and sites, representing at least 5% of the total abundance. The relative abundance of each species per depth zone per site is indicated in %. Species most contributing to differences between depth zones (SIMPER contribution>5% and p-value<0.05) are displayed in the right grey panel, with abundance of these species being higher in the shallower of the two depth zones. Full genus names are available in Table S1.

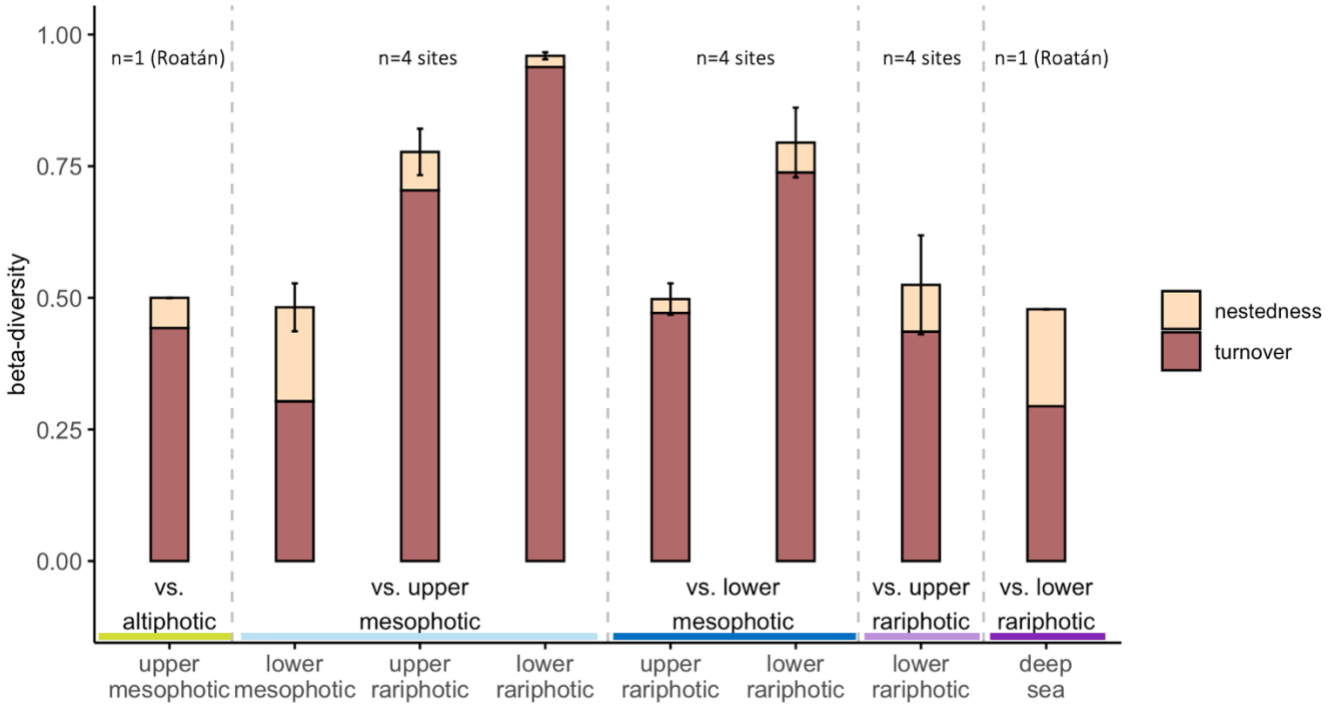

Figure 3.5. Beta diversity and its components, nestedness and turnover of reef-fish communities across depth zones. Values are shown as the average of values across the four sites, and error bars indicate standard error. "Altiphotic vs. upper mesophotic" and "lower rariphotic vs. below rariphotic" values were only available for Roatán. Coloring of bars indicate the relative contribution of nestedness (beige) and turnover (red).

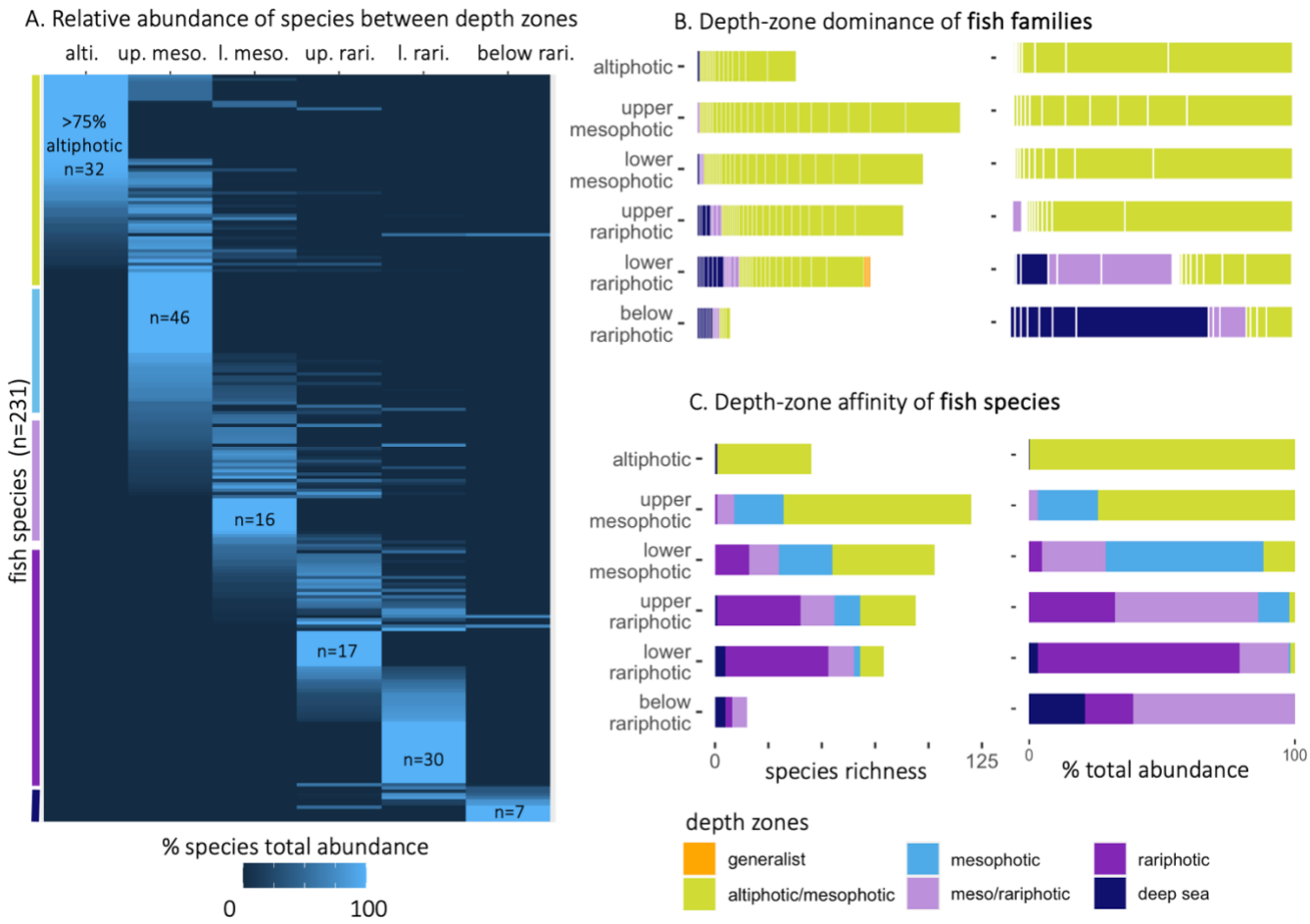

Figure 3.6. Depth affinity of reef-fish species and families across depth zones. Distribution (% total abundance) of fish species among depth zones (A). Each line displays the relative abundance of a given species across five depth zones from the "altiphotic" to "below rariphotic" (300-480 m). Vertical colored lines indicate species falling under each depth affinity category given their depth distribution. The number of depth specialists of each depth zone (>75% of total abundance in a given depth zone) is indicated on the figure ("n="). Depth-zone dominance of fish families (B) and depth-zone affinity of species (C) in each depth zone, and contribution of depth affinity groups to species richness (left panel) and abundance (right panel). White lines in barplots of panel C distinguish species from different families. Filling colors indicate the depth affinity of species, from the altiphotic to the deep sea. Results are shown pooled across the four study locations, except for altiphotic and below rariphotic zones for which data was only collected in Roatán.

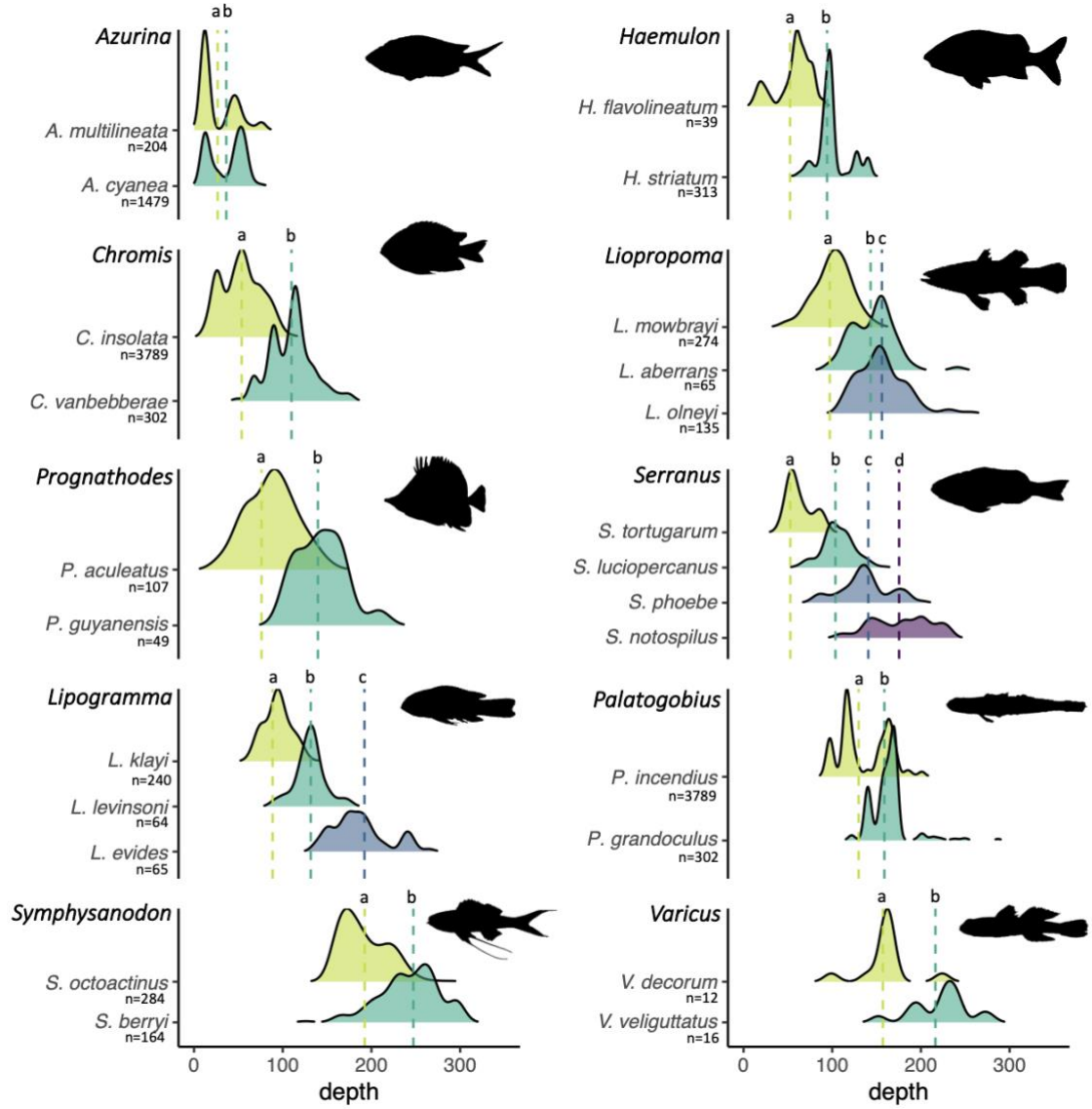

Figure 3.7. Depth segregation among congeners. Dashed vertical lines indicate the mean depth of occurrence of each species. Differently colored abundance curves represent different species within each genus. Statistically different mean depths within a genus are indicated by different letters (Table S4). A comparison of depth distributions observed at our sampling sites vs. global depth ranges is provided in Fig. S7.

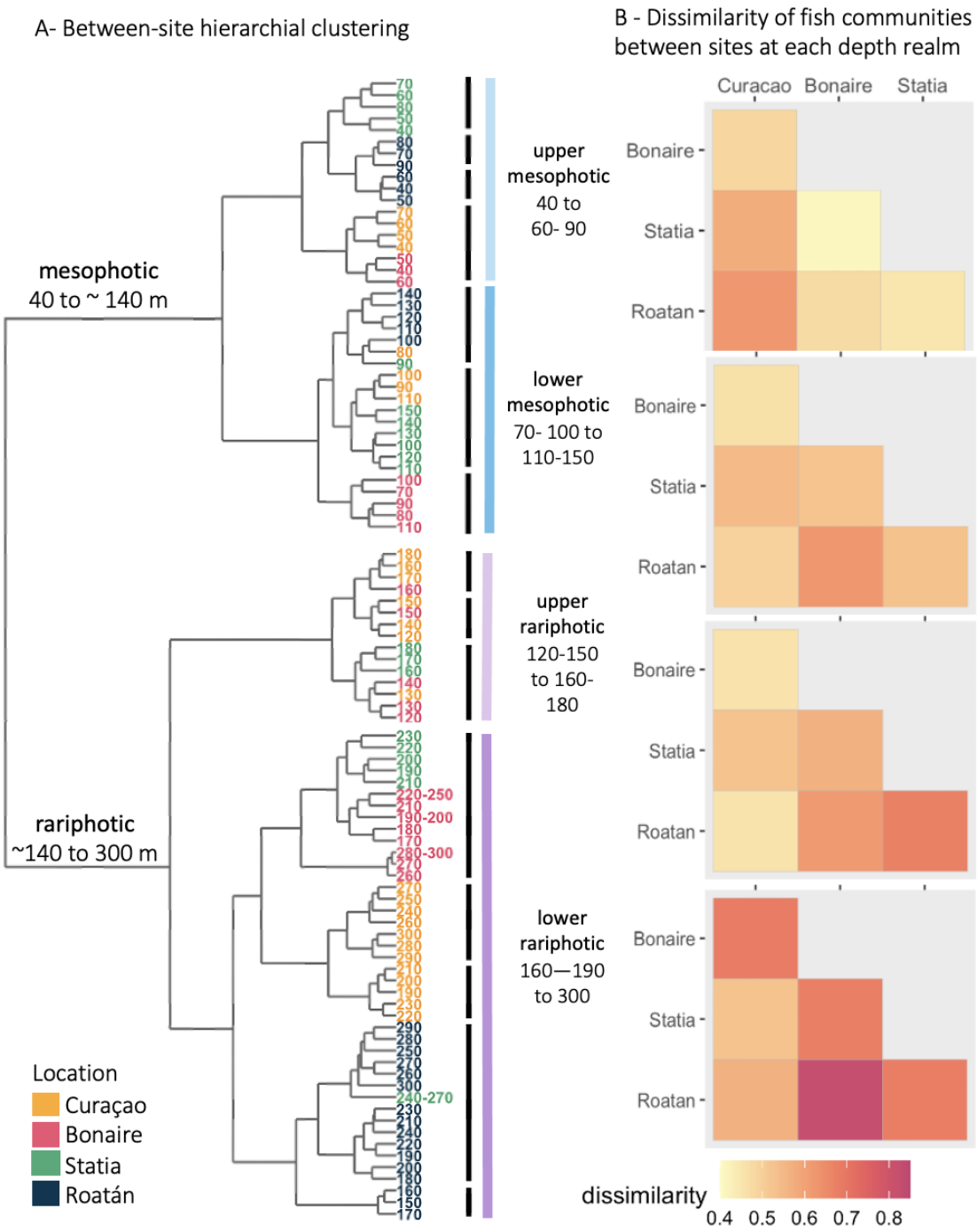

Figure 3.8. Cross-site dissimilarity analysis of deep-reef fish communities. (A) Cross-site hierarchical clustering analysis of deep-reef fish communities from 40 to 300 m. Length of branches in the dendrogram is commensurate to the dissimilarity between depth bins based on Bray-Curtis distance. Font color indicates sites. Significant clusters (SIMPROF analyses, Ward linkage) are indicated by thick black vertical lines. (B) Dissimilarity of deep reef-fish communities between sites at the four depth zones defined in this study, based on the presence/absence of fish species.

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CHAPTER 4
Environmental constraints shape trait diversity of Caribbean reef fishes across depth

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Data accessibility statement. Datasets, including a compilation of all fish observations and the compilation of traits assigned to each species, as well as R scripts used to conduct data analyses and create figures are available on Zenodo under the DOI: 10.5281/zenodo.14908247. The annotated history of R scripts are available under the public Github repository of Juliette Jacquemont (https://github.com/jjacquemont/Deep.Reef.Fish.Carib).

4.1. Abstract

Functional diversity patterns have been thoroughly described for reef fishes across geographic gradients, but the effect of depth on these patterns remains largely unknown. Using diet, life-history, and behavior traits, we evaluated the functional diversity of Caribbean reef-fish communities from the surface to 450 m depth to test if taxonomically distinct communities along the reef slope are characterized by similar or distinct ecological traits. Core ecological traits found in shallow-reef fish communities were conserved in the upper section of deep reefs (i.e., mesophotic zone) across three taxonomically distinct assemblages. By contrast, the deepest reef communities (i.e., rariphotic zone) displayed a distinct functional structure mainly driven by trait loss. Functional redundancy was highest in the deepest reef communities and was generated by intrageneric diversification and by functional convergence across multiple phylogenetic lineages. The decrease in functional richness and divergence along with an increase in functional redundancy suggest environmental filtering as the dominant evolutionary constraint shaping the functional diversity of deep-reef fishes.

4.2. Introduction

Trait-based approaches, which characterize communities through measurable species attributes, have been key tools to elucidate community assembly rules, mechanisms driving biodiversity patterns, and linkages between diversity and ecosystem functions (Díaz & Cabido, 2001; McGill et al., 2006; Tilman et al., 1997). While trait analyses were initially developed for terrestrial systems, their principles have been rapidly transferred to investigate the ecology, biogeography, and vulnerability of marine communities (Butt et al., 2022; Cheung et al., 2005; Mouillot et al., 2014). Trait-based approaches can be particularly useful to illuminate the ecological processes and assembly rules of marine communities that are difficult to access, observe, and for which traditional ecological experiments are logistically challenging. In such data-deficient contexts, functional diversity analyses based on traits have advanced understanding of evolutionary and ecological processes at play in the deep sea (Myers et al., 2021), on hydrothermal vents (Alfaro-Lucas et al., 2024), or on deep reefs (Stefanoudis et al., 2023). However, the functional ecology of deep ecosystems remains largely undocumented compared to their shallow counterparts. For instance, while dozens of studies have documented the functional ecology of shallow reef communities (Hadj-Hammou et al., 2021), only a handful have focused on deep-reefs.

Deep reefs form contiguous extensions of shallow reefs along tropical and subtropical coasts from 40 down to ca. 300 m and remained until recently largely undocumented due to the technical challenges of accessing these depths (Kahng et al., 2014; Lesser et al., 2018). The increase in deep-reef studies in the past decade has revealed their diversity and taxonomic distinctiveness (Laverick et al., 2018; Rocha et al., 2018) as well as the multiple human and environmental pressures threatening these ecosystems (Pinheiro et al., 2019; Rocha et al., 2018), underscoring the urgency to advance process-oriented knowledge to inform their management (Soares et al., 2020). However, because experimental approaches are technically difficult to conduct at depth, deep-reef studies have largely been limited to taxonomic descriptions, with limited understanding of ecosystem functioning (Radice et al., 2024). This knowledge gap is true for all deep-reef taxa including fish, the most diverse vertebrate group of the planet.

In this context, trait-based approaches appear as a valuable and untapped resource to advance our understanding of the ecological and evolutionary processes shaping deep-reef fish communities. Declines in fish richness and abundance with depth have been reported across ocean basins, along with successive taxonomic breaks defining distinct altiphotic (ca. 0-30 m), mesophotic (ca. 40-200 m), and rariphotic (ca. 200-300 m) fish communities (Baldwin et al., 2018; Jacquemont et al., 2024; Stefanoudis et al., 2023; Weijerman et al., 2019). However, apart from the repeated observation that herbivorous fishes decline with depth (Bejarano et al., 2014; Coleman et al., 2018), taxonomic breaks occurring along the reef slope have not been correlated with functional shifts. The few studies that have characterized the functional diversity of deep-reef fishes have found limited functional changes between altiphotic and mesophotic communities, mostly driven by variations in relative trait abundance (Bosch et al., 2023; Loiseau et al., 2023; Medeiros et al., 2021). While the prevailing hypothesis is that environmental

filtering, i.e., the selection of specific traits within a community due to environmental constraints, is the dominant evolutionary driver in extreme ecosystems including deep reefs, trait-based approaches have reached varying conclusions regarding its prevalence depending on the depth range and functional metrics considered (Bridge et al., 2016; Pinheiro et al., 2023; Stefanoudis et al., 2023). Lastly, many studies have discussed the potential of deep reefs to provide refuge to shallow species from disturbances (Lindfield et al., 2016; Medeiros et al., 2021), but whether deep-reef communities benefit from trait characteristics known to promote resilience, such as high redundancy or the prevalence of generalist species, has not been investigated. Lastly, the functional diversity of Caribbean deep-reef fish communities has never been evaluated, and only one functional study has studied reef communities down to rariphotic depths (Stefanoudis et al., 2023).

Here, we characterize the functional diversity of Caribbean reef fishes across their entire depth range of occurrence (0-450 m) using a dataset featuring seven traits related to life-history, behavioral, and trophic ecology. We first assess how trait composition varies across depth for individual trait categories. We then perform multi-trait analyses to test (1) whether taxonomically distinct fish communities along the reef slope are functionally distinct, and if so, which traits drive functional distinctiveness; (2) whether environmental filtering (denoted by trait loss, decreased functional space, and decreased functional divergence) or biotic competition represents the predominant evolutionary constraint on deep reefs; and (3) whether functional redundancy and evenness increase on deep reefs, which would suggest higher ecological resilience of these communities to disturbances. Lastly, we discuss how effect traits described could affect ecosystem processes on deep reefs and what response traits suggest regarding the main ecological constraints at play for deep-reef fishes.

4.3. Methods

4.3.1. Data collection

4.3.1.1. *Deep submersible transects.*

Fish data were collected from direct visual observations by trained ichthyologists using manned-submersible diving. Data were collected at four Caribbean islands (Curaçao, Bonaire, St. Eustatius, Roatán) from 10 to 480 m in Roatán, and from 40 to 300 m at the three other sites. Most data collection occurred between 2011 and 2017 as part of the Smithsonian Deep Reef Observation Project (DROP) which featured >100 submersible dives. A minimum of 11 submersible dives (each 3-6 hours long) were performed at each island, during which descending (first half of dives) and ascending (second half of dives) transects were performed on two different trajectories along the reef slope. Visual observations were complemented by opportunistic sampling of fishes using anesthetics and a suction hose attached to the submersible to document cryptobenthic fishes. See Baldwin et al., (2018) for additional details. Additional fish observations using manned submersible-diving were acquired in Curaçao in August 2024 because rarefaction curves indicated that previous sampling efforts had not fully captured deep-reef fish diversity (Jacquemont et al., 2024). Horizontal transects approximately 120 m long were

conducted at 45, 60, 80, 100, 115, 130, 150, 175, 200, 225, and 250 m. Each transect lasted around one hour.

4.3.1.2.*Shallow SCUBA transects.*

We acquired shallow fish observations (5-30 m) in Bonaire (August 2024) and in Curaçao (December 2023) to complement submersible observations that started at 40 m at these locations. Underwater visual censuses along 2 m wide x 30 m long transects at 5, 10, 20, and 30 m depth were conducted by SCUBA diving on both islands. Five to six replicates were performed for each depth and at each island, spaced out by at least 50 m. All transects were performed by two trained observers (JJ and LT) who conducted the same number of transects at each depth to avoid unbalanced observer bias across depths. Reef topography and fishes observed along the transects were filmed using a GoPro 10 mounted on a head strap to check fish identifications after dives. Survey locations were chosen to match previous submersible survey areas, i.e., east of Willemstad in Curaçao and between Bachelor's Beach and Angel City in Bonaire. In Curacao, transect lengths varied because of bottom-time constraints and challenging current conditions (see Table S.A for details on total transect length per depth). To correct for differences in transect length, abundance values were normalized by transect length.

4.3.1.3.*Fish traits.*

We compiled data on seven traits commonly evaluated in reef-fish functional studies (Loiseau et al., 2023; McLean et al., 2019; Mouillot et al., 2014): maximum body length (extra-small: < 7 cm, small: 7 – 15 cm, medium: 15-40 cm, large: 40 – 80 cm, extra-large: >80 cm), diet (macroalgae, microalgae, bony fish, detritus, ectoparasite, hard corals, mobile invertebrates, sessile invertebrates, and plankton), position in the water column (bottom, near-bottom, mid-water, near-surface), diel activity (nocturnal, diurnal, both), gregariousness (solitary, pairing, small schools: 3-20, medium schools: 20-50, large schools: > 50), mobility (sedentary, within-reef mobility, between-reef mobility, vertical mobility), and reproduction (benthic eggs, pelagic eggs, brooding, live birth). In some instances, more than one category was assigned to a given species when this best reflected the species' ecology. For example, *Sphyraena barracuda* was assigned to near-surface, mid-water, and near-bottom categories. These traits describe important aspects of fish life-history, behavior, and trophic ecology that influence and respond to ecosystem processes such as connectivity, productivity, and nutrient cycling (Villéger et al., 2017).

We assigned trait values at the species levels using the Fishes of the Greater Caribbean database (Smithsonian Tropical Research Institute, STRI; Robertson and Van Tassell 2015) to document diets, water column position, reproduction, and size at maturity. We assigned mobility, gregariousness, and diel activity traits using expert knowledge complemented by additional literature search. When species traits were not available, we used trait data from closely related species when those traits were known to be conserved at the corresponding phylogenetic scale

(e.g., members of the genus *Chromis* have similar reproductive modes; members of the family Gobiidae exhibit parental care over eggs).

4.3.2. Data analysis

All analyses were performed using R version 4.4.1 (R Core Team, 2024) in R Studio.

4.3.2.1. Variations in individual traits

To assess how individual traits varied across depth for the fish communities overall, we calculated the community weighted mean (CWM) of trait categories at each depth bin and site using the *dbFD* function from the {FD} package. Because we reclassified traits into as many binary variables as individual categories for that trait, CWMi represented the proportion of the total community abundance displaying trait *i* and was bounded between 0 and 1. We treated traits as non-ordered categories and weighted traits by abundance matrices which were square-root transformed to avoid overemphasizing the importance of rare species while controlling for extremely abundant ones. We tested the effect of depth and location on traits using General Additive Models (GAMs):

$$CMW = \alpha + s(depth) + depth{:}\,location$$

with s(x) specified as a smooth non-parametric function and depth:location the interaction between depth and location (i.e., the four islands).

We fitted CMW values using beta-regression functions and an REML method to minimize overfitting. We ran models using the {mgcv} package and visualized fits using the {marginaleffects} package.

4.3.2.2. Multidimensional trait space

To compare the breadth of ecological traits in different fish communities down the reef slope, we computed a multidimensional trait space using the six categorical traits for which we had complete data: size, diet, reproduction, position in the water column, gregariousness, and mobility. We excluded diel activity as data gaps prevented the categorization of most deep-reef species. We reclassified traits into as many binary variables as individual categories for that trait (e.g., "position in water column" was reclassified into four binary traits). This allowed us to assign multiple trait categories to a single species when this best reflected its ecology or behavior. To avoid artificially increasing the weight given to traits with more categories, we weighted each category by the inverse of the number of categories within each trait.We computed Gower dissimilarity matrices from these binary variables for each site and depth bin, and projected them in an Euclidean space using the Cailliez correction method (Cailliez, 1983). We then performed Principal Coordinates analysis (PCoA) on corrected species-species distance matrices. We calculated the associated convex hull volume based on the two first PCoA axes and projected species in this two-dimensional space according to their traits. To compare trait spaces across depth zones, we represented the trait space of six taxonomically-distinct communities across depths: altiphotic, upper mesophotic, lower mesophotic, upper rariphotic, lower

rariphotic, and below the rariphotic. We assigned site-specific depth limits for each of these depth zones based on previous work conducted on these communities by Jacquemont et al. (2024). Lastly, to assess how trait space varied between fishes from different depth affinity groups, we represented the trait space occupied by species that predominantly occur in the altiphotic/mesophotic, mesophotic, mesophotic/rariphotic, rariphotic, or in the deep sea (below 300 m). We assigned depth affinities to species as in Jacquemont et al., (2024), where the depth range capturing 75% of a species' abundance defined its depth affinity. For example, a species whose depth range extended from the altiphotic to the rariphotic zone, but with 75% of its abundance in the mesophotic zone, was coded as having a mesophotic depth affinity. By contrast, if 75% of a species' abundance straddled two depth zones (e.g., altiphotic and mesophotic), it was coded as having an altiphotic-mesophotic depth affinity.

4.3.2.3.Functional diversity metrics

We calculated functional richness, functional evenness, and functional dispersion using the {FD} package developed by Laliberté and Legendre, (2010). These metrics measure complementary and independent facets of trait diversity (Legras et al., 2018). Functional richness (FRic) measures the total space occupied by functional traits along the convex hull volume (Villéger et al., 2008). This metric does not account for relative abundance and is sensitive to trait outliers. Functional evenness and dispersion account for relative species abundance, are independent from species richness, and are much less sensitive to outliers. Functional evenness (FEve) measures the regularity of species abundance along the minimum spanning tree linking all species in the multidimensional trait space (Villéger et al., 2008). This metric is independent of the total functional volume. Functional dispersion (FDis) measures the spread of species across the trait space by calculating the mean distance of species to the center of gravity in the functional space (Laliberté & Legendre, 2010) and, as such, accounts for total functional volume.
Finally, we calculated functional redundancy following Ricotta et al., (2016) as the difference between taxonomic diversity (Simpson's index) and trait diversity (Rao's quadratic entropy) using the {SYNCSA} package. This approach accounts for species richness and species abundance in its measure of redundancy, reflecting that buffering capacity is achieved through both high numbers of species and high numbers of individuals supporting an ecological role. We used GAMs with loess-smoothers to measure the amount of variance of functional diversity metrics explained by depth.

4.3.2.4.Hierarchical clustering

To examine trait similarity between fish communities down the reef slope and identify trait breaks across depths, we conducted hierarchical clustering analyses using trait composition instead of species composition.We calculated the frequency of trait categories among all individuals found at each 10-m depth bins. This created communities composed of n=32 traits categories as opposed to n=168 trait combinations, which would have been more closely correlated to the underlying species composition (n=254). Using these communities of traits, we

calculated the Bray–Curtis dissimilarity matrix, which accounts for trait presence and relative abundance at each depth bin, using a Ward linkage (which forms clusters by minimizing variance within clusters), Bray–Curtis distances, and alpha-value = 10^{-7}. Analyses were performed with the {vegan} package. Next, we represented trait similarity between depth bins using a hierarchical cluster dendrogram where depth bins most similar in trait composition are closest in branch distance. We tested for significant differences in trait compositions using Analysis of Similarity Profiles (SIMPROF (Clarke et al., 2008)) functions from the {clustsig} package.

4.3.2.5.Sensitivity analyses

Functional diversity metrics are sensitive to the total number of traits considered and to the number of categories examined for each trait. We re-calculated the total trait space, the trait space represented in each depth zone, and re-ran hierarchical clustering after excluding successively reproductive traits, gregariousness traits, or diet traits (Fig. SL to SN). We also projected trait spaces using the first and third PCoA axes to test if results were sensitive to PCoA axes retained (Fig. SK).

4.4. Results

We observed 254 fish species between 0 and 450 m depth, representing a total of 168 distinct trait combinations. The relative abundance and the number of species supporting trait categories varied significantly with depth (Fig. 1, Fig. SB2). Across all locations, mesophotic and upper rariphotic communities (60-200 m) hosted two to four times more very small-sized fish ($p < 0.001$) than other depth zones (Fig. 1, Fig. SB) and featured the lowest proportions of large fish. Large and very large species were rare (<10%) across all depths, but their relative representation increased in the rariphotic and below (> 150 m) due to decreases in abundance of other size classes. The proportion of medium-sized species was relatively stable (~ 30 %) from shallow to rariphotic reefs but increased to 50-70% below the rariphotic (Fig. 1, Fig. SB).

Reef communities were dominated (> 80%) across depths by bottom-oriented fish (bottom and near-bottom). The proportion of bottom species increased with depth from 20% on altiphotic reefs to 80% on rariphotic reefs, while the proportion of near-bottom species decreased and mid-water species disappeared below the mesophotic ($p<0.001$, Fig. SB). The diversity of trophic strategies decreased from nine to three between altiphotic and rariphotic reefs, with only planktivores, invertivores, and carnivores present below 150 m. The transition from altiphotic to upper mesophotic reefs was characterized by an increase in planktivores and a decrease in ectoparasite cleaners, corallivores, and detritivores, which disappeared in the lower mesophotic (< 120 m). Herbivores (micro- and macroalgae feeders) declined from altiphotic to lower mesophotic reefs (20 to 5%) and disappeared in the rariphotic ($R=0.8$, $p<0.001$, Fig. SB). Trophic composition stabilized below 150 m, with piscivores, invertivores, and planktivores found in similar proportions in the rariphotic and below. Reproduction strategies involving benthic and pelagic eggs were evenly present down to the lower mesophotic, below which the

proportion of pelagic-eggs strategies increased up to 90% below the rariphotic (R=0.78, p <0.001, Fig. SB). Fish displaying brooding represented a minority at all depths but were more common in the mesophotic and upper rariphotic.

Behavioral traits (mobility, gregariousness, and activity time) were also affected by depth, with high mobility and schooling behaviors becoming extremely rare on deep reefs. Species displaying between-reef and vertical mobility represented ~20% of shallow communities, 5-10% of mesophotic and rariphotic communities, and were absent below the rariphotic (R=0.38, p<0.001). The proportion of solitary species increased from 30% in the altiphotic to 90% in the rariphotic before decreasing below the rariphotic. Species forming small and medium schools represented ~60% of fish communities in altiphotic reefs and below the rariphotic, but only ~40% in the mesophotic and ~10 % in the rariphotic. Species predominantly active at night were more common on mesophotic than on altiphotic reefs, but trends at deeper depths could not be assessed due to a lack of species data.

Functional richness (total functional space occupied) and dispersion (mean distance to centroid) decreased with depth (p<0.001, R^2=0.6) while functional evenness (mean distance between neighbor traits) increased weakly (p=0.001, R^2=0.1, Fig. 2). Richness and dispersion decreased moderately between altiphotic and mesophotic communities, steeply between lower mesophotic and upper rariphotic communities, and reached close-to-null values below the rariphotic. These patterns were mostly consistent across the four studied sites (Fig. SA). Trait redundancy was weakly and non-linearly correlated with depth (R=0.3, p<0.001) with highest values reached in the lower mesophotic and upper rariphotic (Fig. SC). The trait combination shared by most species was medium-sized, solitary, bottom predators, and was represented at all depth zones through 11 species, nine genera, and seven families (Fig. 3). Species representing medium-sized solitary bottom predators continuously increased from three in the altiphotic to seven in the rariphotic before dropping to one below the rariphotic. The second most represented trait combination (near-bottom, solitary, extra-small planktivores) was represented by n=9 species from the *Liopropoma* genus with a peak of five species occurring in the lower mesophotic and upper rariphotic.

We assessed trait similarity between fish assemblages found at every 10-m depth bin from 10 to 470 m depth using similarity profile analyses (SIMPROF) and hierarchical clustering. We found 12 distinct clusters of traits separated into four main branching events (Fig. 4). The strongest shift in trait structure occurred at 200 m, separating communities found from the altiphotic to the upper rariphotic on one hand, and from the lower rariphotic and below on the other hand. A secondary level of branching indicated trait shifts (1) between the lower mesophotic and the upper rariphotic (~ 130 m) and (2) between the lower rariphotic and below rariphotic communities (~ 300 m). These four main trait clusters were conserved when removing different traits individually from the analyses, indicating that these results reflected the overall trait

composition rather than the influence of a single trait (Fig. SL to SN). These shifts matched with shifts found when performing taxonomic clustering of fish assemblages, although exact values of depth breaks varied (Fig. 4). Shallow to mesophotic communities separated into five clusters of traits but unlike taxonomic clusters, distance between trait clusters was small and clusters did not pool consecutive depth bins.

Next, we plotted the trait space occupied by reef-fish communities to test if taxonomically distinct communities presented distinct trait spaces (Fig. 5). The two first Principal Coordinates Analysis (PCoA) axes captured 18 % of trait variation. The first axis (11% variance) was correlated to reproduction (benthic vs. pelagic eggs) and mobility (sedentary vs. reef mobility) while the second axis (8% variance) was correlated to gregariousness (solitary vs. schooling) and position in the water (bottom vs. near-bottom). Fish communities from the altiphotic to the rariphotic covered close to the entire trait space with only a small reduction in trait space with depth, indicating that extreme trait combinations were conserved across the entire reef slope (Fig. 5). By contrast, the trait space of communities below the rariphotic shrunk to around half of the total trait space. Similar patterns were found when projecting the trait space along the first and third PCoA axes (Fig. S12). By contrast, the position of communities' centroids displayed important shifts across depth zones. Centroids were ordered by increasing depth along the second PCoA axis, indicating an increase in solitary and bottom species. Centroid of communities increased along the first axis from the altiphotic to the upper rariphotic and decreased in deeper depth zones, indicating a peak in benthic egg and sedentary strategies in the lower mesophotic and upper rariphotic.

We then examined how trait space varied between depth affinity groups, which categorize species based on their predominant depth range, to test if deep-reef specialists display a more constrained trait space than depth-generalist species. Depth generalists (altiphotic/mesophotic and mesophotic/rariphotic) displayed large and overlapping functional spaces although their centroids indicated different mean trait composition (Fig. 6). By contrast, depth specialists (mesophotic, rariphotic, and deep sea) displayed narrower and non-overlapping functional spaces, which was highly reduced for deep-sea specialists. The trait space occupied by a given depth affinity group was smaller than the space occupied by the community observed in the associated depth zone, except for altiphotic communities which occupied the full functional space.

4.5. Discussion

This study examines the trait structure of Caribbean reef-fish communities from the altiphotic to the deep-sea boundary, presenting one of the first functional analyses across the entire depth range of reef-dominated systems, and the first of its kind in the Caribbean Sea. We found that depth is a strong driver of reef-fish trait diversity, with continuous declines in functional richness and divergence, accompanied by trait loss. We found high functional homogeneity across the three shallowest taxonomically distinct fish assemblages, but multiple functional breaks

separating mesophotic, rariphotic, and below-rariphotic communities, with a sharp shrinkage of the trait space below the rariphotic.

Shifts in trait composition and diversity across depth. The shallowest functional shift separated mesophotic and rariphotic communities, while shallower communities displayed similar combinations of traits despite variations in their relative abundance. This aligns with previous studies reporting changes in trait proportions in the mesophotic with limited trait loss (Bosch et al., 2023; Loiseau et al., 2023; Medeiros et al., 2021), but significant declines in the functional richness of rariphotic communities (Stefanoudis et al., 2023). In the upper section of reefs (0-120 m), we found high functional homogeneity across three taxonomically distinct fish communities: the altiphotic, upper mesophotic, and lower mesophotic. This core of shared ecological traits among taxonomically distinct reef-fish communities has previously emerged as a common feature across latitudes (McLean et al., 2021; Mouillot et al., 2014) and likely reflects the ubiquity of essential ecological roles on reefs. However, many ecological roles on mesophotic reefs were supported by lower abundances and number of species, and often by depth generalists or by species occurring at the limit of their depth range. Whether trait combinations supported by rare species occurrence still support ecologically meaningful functions on deep reefs is unclear (e.g., nutrient cycling, bioerosion, predator-prey interactions).

Hierarchical branching events indicated a functional break at the mesophotic/rariphotic boundary and between upper and lower rariphotic communities, and matched taxonomic breaks. These functional breaks suggest that although rariphotic communities are primarily composed of reef-associated families, they may fundamentally differ from shallower reefs in the variety and magnitude of their underlying ecological processes (Brandl et al., 2019). Lastly, the functional break and the sharp shrinkage of the trait space observed between rariphotic and below-rariphotic depths supports that the lower rariphotic (200 - 300 m) hosts the deepest reef community in the Caribbean, supporting taxonomic evidence of a transition from reef-associated to deep-sea associated families at this depth (Baldwin et al., 2018; Jacquemont et al., 2024; Quattrini et al., 2017; Weijerman et al., 2019). This transition remains to be documented in other ocean basins.

Environmental drivers of trait loss. Previous functional characterizations of deep-reef fishes have mostly focused on trophic guilds with an emphasis on the decline in herbivores with depth (Bridge et al., 2016; Loiseau et al., 2023; Richardson et al., 2023; Stefanoudis et al., 2023). While we also observed this trend, we found that additional trophic guilds, as well as behavioral and life-history traits, disappeared below the mesophotic. Indeed, we found that detritivores, ectoparasite cleaners, and sessile invertivores were absent in the rariphotic, likely due to the decreased coverage of associated food sources, such as corals, gorgonians, and sponges. Similarly, fewer detritus due to lower overall biomass on deep reefs could limit the presence of detritivores. Additional factors at play could include the decrease in fish density and the loss of

visual cues from low light intensity, which are both required to support ectoparasite cleaning (Caves, 2021).

The increase in benthic sedentary fishes on deep reefs could result from the decrease in habitat availability, characterized by isolated biotic and abiotic features among vast expanses of sand and rubble. In such environments where shelters are scarce and exposure to predation is high, territorial behaviors could have replaced roving demersal behaviors found on shallow reefs. Indeed, deep-reef fishes are often observed in tight association with specific features. Monospecific (e.g., *Symphysanodon spp.*) or intergeneric (e.g., pairings of *Antigonia capro*s and *Ostichthys trachypoma*) groups often aggregate around large benthic features (e.g., rocky outcrop, sunken boat), and single territorial individuals (e.g., *Serranus spp.*) are found living in association with a whip coral, a rock, or human trash (authors' observations). The decrease in habitat complexity, microhabitat variability, and habitat-forming species on deep-reefs likely contributes to the decrease in species and trait richness through a loss of specialization opportunities (Costello & Chaudhary, 2017).

Mobility and reproduction traits shape deep-reef connectivity. We observed a decrease in the proportion of fishes displaying vertical and horizontal mobility with depth, which could result in lower population connectivity and nutrient cycling (Papastamatiou et al., 2015; Slattery et al., 2011). In the mesophotic, abundant planktivorous schooling species that perform diel vertical migrations, such as *Azurina spp.*, likely play an important role in maintaining nutrient connectivity with shallow reefs. In the rariphotic, only a few large predators such as *Caranx spp.*, *Seriola spp.*, and *Pterois volitans* are known to perform vertical migrations, but their low abundance might limit their capacity to move nutrients vertically or horizontally. However, observations might have missed pelagic vertical migrators since the submersible was always facing the reef slope. Further, some fast-swimming vertical migrators might have avoided the submersible during surveys. Although potentially limited by low adult mobility, population connectivity on deep reefs could be supported by the higher proportion of reproductive strategies based on pelagic eggs, which enhance the dispersal capacity of species compared to benthic eggs. Additional factors, including environmental stability and geomorphological variability (Copus et al., 2022), determine rates of speciation and endemism on deep reefs, which remain highly debated (Jacquemont et al., 2024; Kane et al., 2014; Pyle et al., 2016).

The role of environmental filtering on deep reefs. In extreme environments such as deep ecosystems, functional diversity tends to be predominantly determined by abiotic constraints, a process referred to as environmental filtering (Myers et al., 2021). Communities under high environmental filtering typically display lower functional richness, lower functional divergence, and narrower trait space, while opposite trends characterize high interspecific competition. We found decreases in functional richness, functional dispersion, and trait space with depth, indicating that the influence of environmental filtering increased with depth. The convergent trait filtering of species across phylogenetically distant families on deep reefs and the intrageneric

diversification of some deep-reef specialists (Baldwin & Robertson, 2014; Tornabene et al., 2016) also support that deep reefs favor specific trait combinations, another indication of strong environmental filtering. However, depth partitioning amongst congeners (Jacquemont et al., 2024) indicates that resource limitations might prevent the coexistence of functionally similar species at a given depth zone, an indication of interspecific competition. Overall, findings support that environmental filtering combined with intrageneric diversification constitute strong evolutionary drivers on deep reefs (Bridge et al., 2016; Pinheiro et al., 2023). At mesophotic depths, these trends were not as pronounced, which could explain why studies limited to the upper section of deep reefs find more ambiguous results (e.g., Medeiros et al., (2021)).

From trait composition to vulnerability assessments of deep reefs. While we expected to observe a decrease in trait redundancy with depth following species loss, we found that trait redundancy was stable down to mesophotic and even increased in the rariphotic because species loss was concentrated on specific trait combinations. This process was also apparent from the increase in functional evenness with depth. Functional redundancy is thought to enhance community resilience because ecological roles supported by more species are likely to be conserved even when species are lost following a disturbance (MacArthur, 1955; McLean et al., 2019). Under this "insurance hypothesis", mesophotic and rariphotic communities could benefit from higher resilience thanks to higher trait redundancy. However, higher redundancy on deep reefs resulted from the loss of rare traits rather than from an increase in the number of species representing each trait. Similarly, higher evenness, which has also been linked to higher resistance (Oliver et al., 2015), resulted from a decrease in abundant species. Lowered abundance and trait diversity could undermine the resilience of deep reefs according to the "diversity-stability" hypothesis (Duffy et al., 2016; Isbell et al., 2015). Whether the trade-off between redundancy and diversity promotes resilience or vulnerability of deep reefs likely depends on additional factors, including trait composition and the type of pressures at play.

Trait-based approaches represent valuable tools to characterize ecological vulnerability, ecosystem processes, and evolutionary drivers, but they are now well known to quantify functional potential rather than actual ecological processes (Brandl et al., 2019). Further, the use of trait information from closely related shallow species might fail to capture the full spectrum of deep-reef trait diversity. As deep-reef ecology progresses, a finer granularity in the niches occupied by species might reveal higher levels of niche partitioning and hence lower redundancy at scales that are biologically relevant. This, combined with a better understanding of the anthropogenic and environmental pressures at play on deep reefs, will allow to better inform the conservation and management of these ecosystems. In the meantime, the growing pool of evidence supporting that deep-reef communities harbor unique taxonomic and functional diversity supports that conservation efforts should encompass the entire depth range of reef ecosystems (0-300 m) to achieve ecologically representative marine protection.

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4.7. Figures

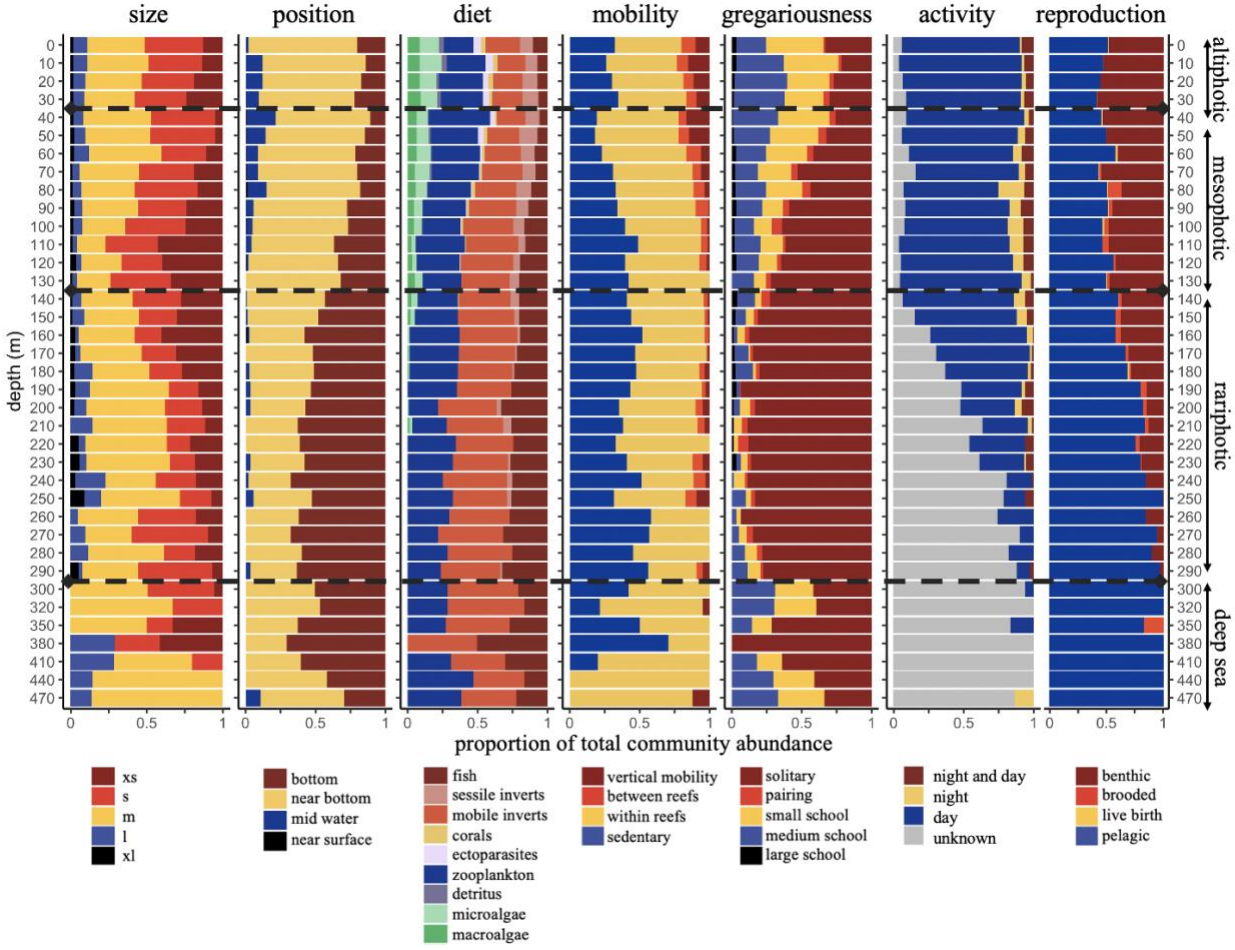

Figure 1: Trait composition across depth. Color fillings represent different trait categories and bar length represents proportion of total abundance. Black segmented lines represent the depth of main taxonomic breaks separating distinct fish communities in the Caribbean.

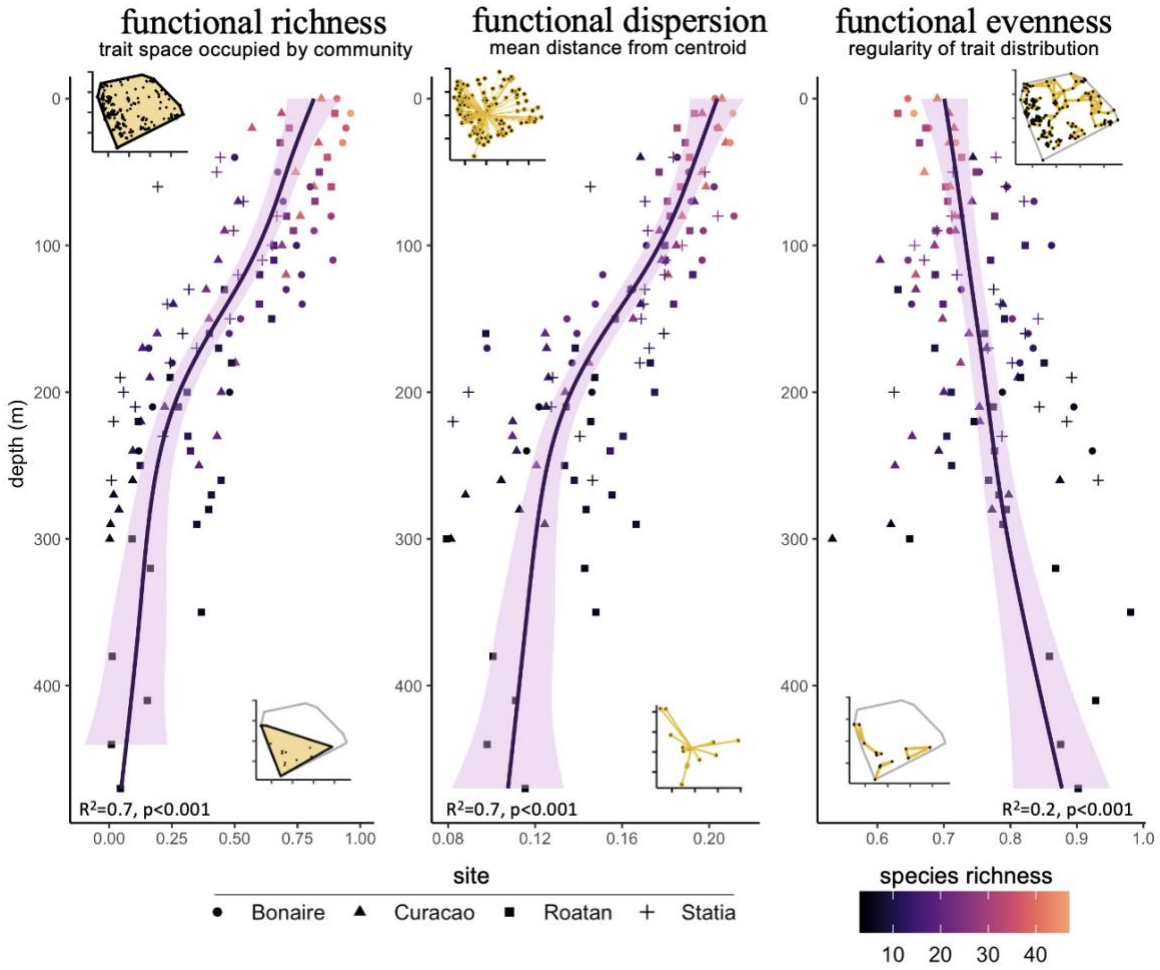

Figure 4.2. Functional richness, evenness, and dispersion of fish communities across depth. Each dot represents a community from a given 10m depth bin at a given study site. Shapes of dots indicate the study site and color of dots indicate the species richness of the community. Dark lines represent the loess-smoothers fitted to the data and purple shading indicates the 95% confidence interval associated with the model. Residual standard errors (RSE) associated with the loess regressions are indicated in each panel.

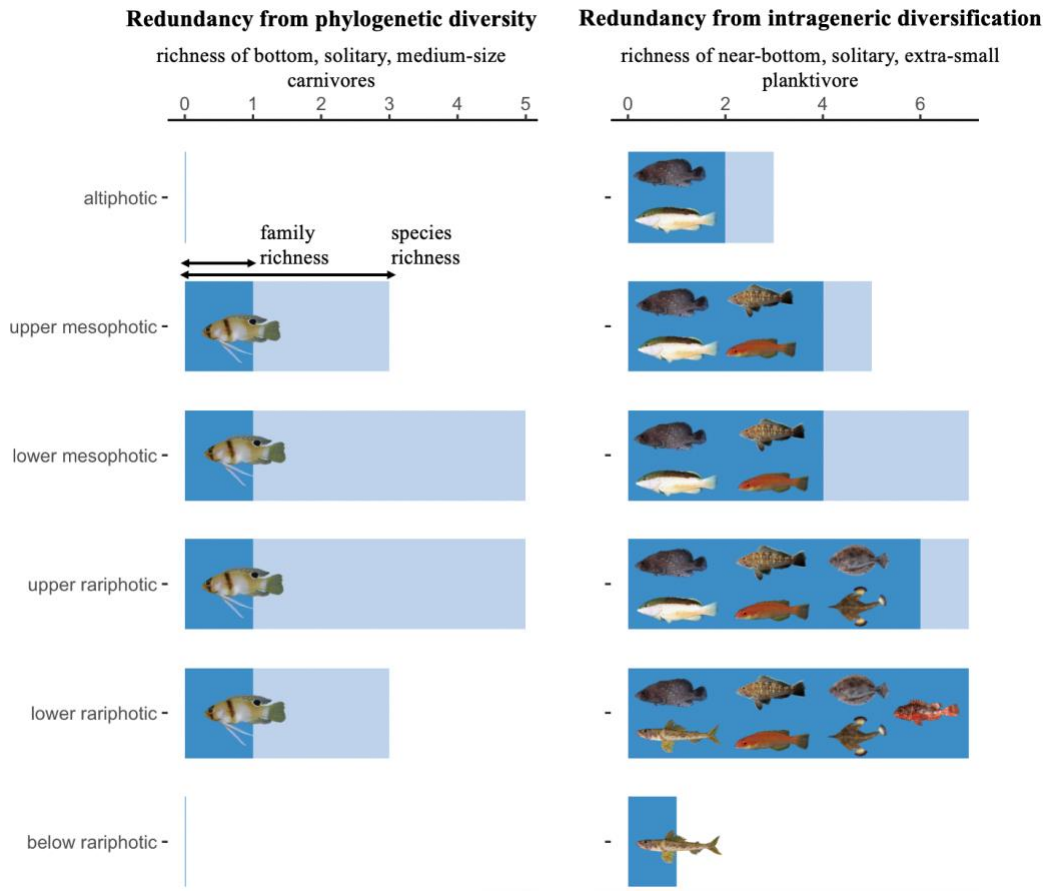

Figure 4.3. Species and family redundancy supporting two ecological roles on reefs across depth. The height of dark blue bars denotes family redundancy and light blue bars species redundancy. Each family is represented in the figure by an image of one of its members.

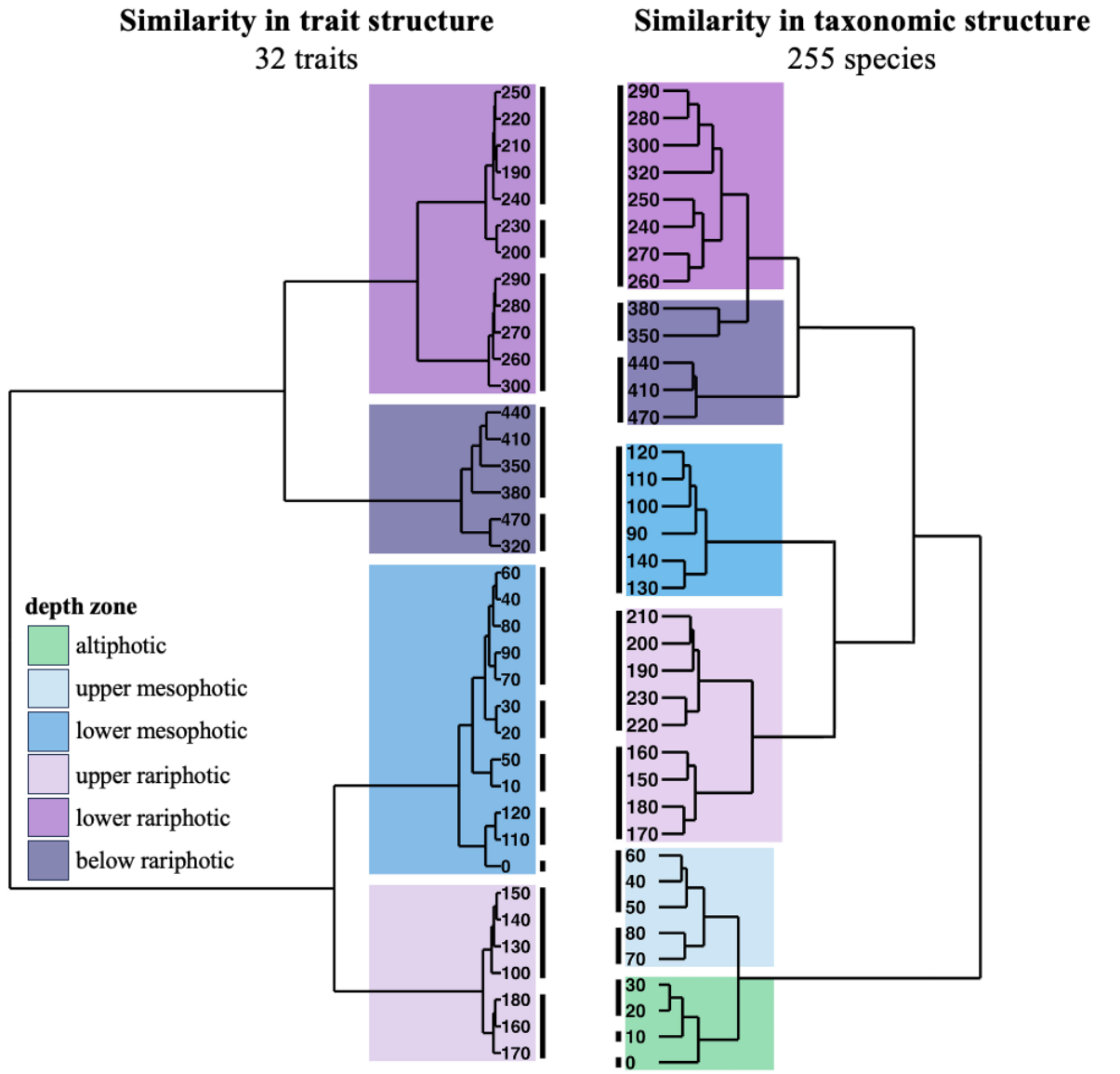

Figure 4.4. Dissimilarity analyses of reef fish communities across depths based on trait structure (left dendrogram) and on taxonomic structure (right dendrogram). Length of branches in the dendrogram is commensurate to the dissimilarity between depth bins based on Bray–Curtis distance. Significant clusters (SIMPROF analyses, Ward linkage) are indicated by thick black vertical lines. Underlying coloring indicates the depth zone of clusters.

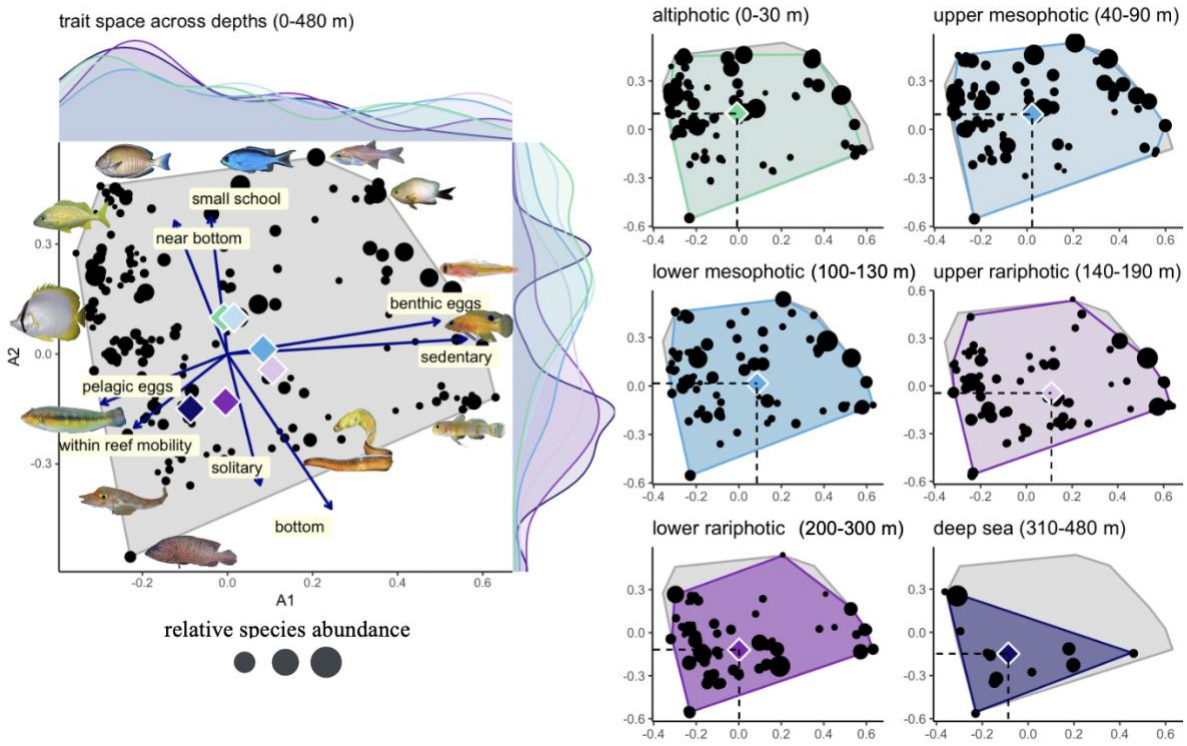

Figure 4.5. Trait space occupied by fish communities across depths (grey polygons) and by communities from individual depth zones (right plots) along the first two Principal Coordinate Analyses (PCoA) axes. Black points represent species' position in the trait space and size of points represents their relative abundance. Colored diamonds indicate the trait centroid for each depth zone. Vectors (left plot) represent the correlation of traits to the PCoA axes. A complete labeling of species occupying the trait space in each depth zone is available in Fig. S6 to S11.

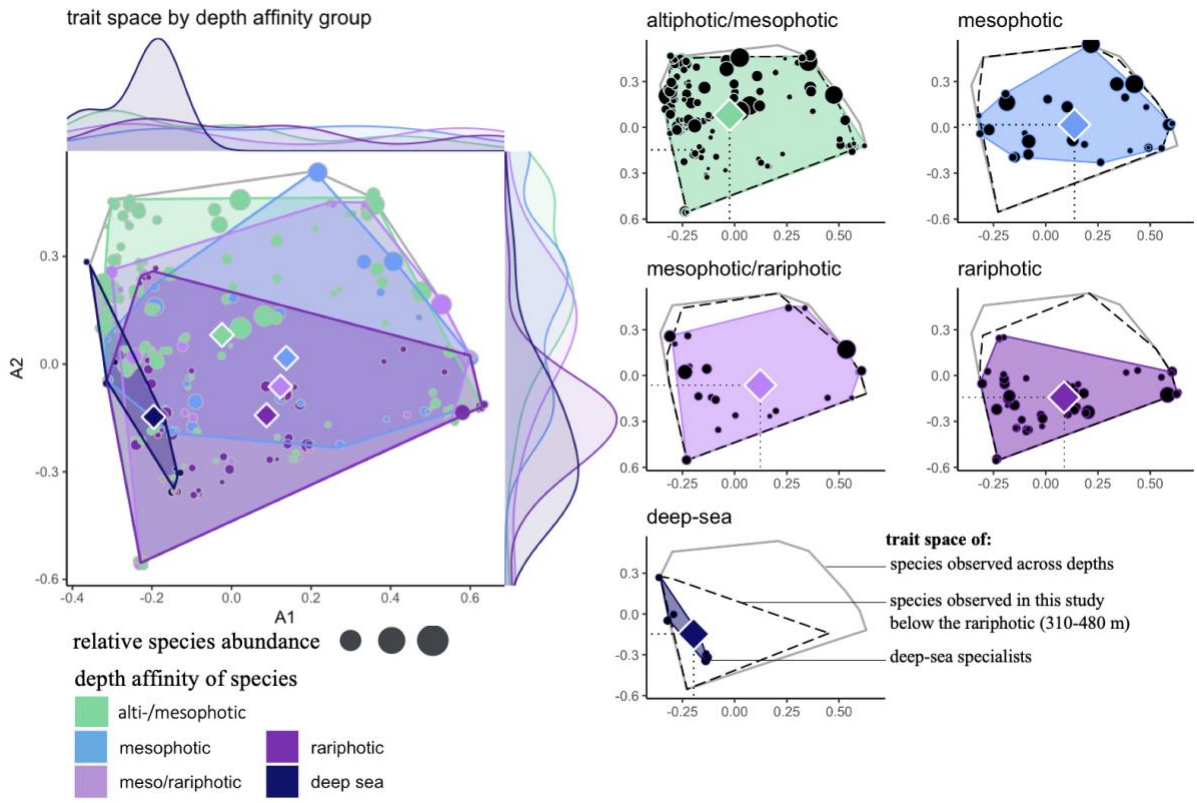

Figure 4.6. Trait space occupied by fish species across depth affinity groups (left panel) and for individual depth affinity groups (right panels) along the first two Principal Coordinate Analyses (PCoA) axes. Points represent species' position in the trait space and size of points represents their relative abundance. Colored diamonds indicate the trait centroid of each depth affinity group. The grey outline delineates the functional space occupied by all species, the dotted outline represents the space occupied by species observed at a given depth zone, and the inner colored polygon represents the space occupied by the corresponding depth affinity groups.

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SYNTHESIS

Marine protected areas can be efficient tools to protect and rebuild marine life. However, designing effective conservation tools requires an understanding of the pathways through which ecological benefits accrue, which itself requires an understanding of ecosystem functioning and of the socio-economic dynamics in which MPAs are embedded (Roberts, 2000). Furthermore, understanding the range of benefits that can be expected from MPAs is paramount to set realistic expectations and to adequately decide when MPAs constitute a relevant tool given a set of management goals (Sullivan-Stack et al., 2024).

Changing climatic conditions have raised fears that MPAs will not be able to provide ecological benefits in the future because range shifts of species will produce spatial mismatches between protected areas and species distributions (Weinert et al., 2021) and because marine life will primarily be impacted by climatic pressures, which cannot be mitigated by local conservation. Other authors have argued that the ecological benefits generated by MPAs will contribute to enhance the climatic resilience of marine life (Roberts et al., 2017) and that 'climate-smart' designs can maintain the effectiveness of MPAs even under changing climatic conditions (Brito-Morales et al., 2022; Wilson et al., 2020; Zentner et al., 2023). However, most publications fueling this debate remained until recently qualitative, and primary literature linking MPAs to ecological resilience were indirect, dispersed, and showing a broad spectrum of results. By conducting a systematic review and meta-analysis of the effect of MPAs on socio-ecological pathways contributing to resilience, we found that marine conservation can significantly enhance carbon sequestration, coastal protection, biodiversity and reproductive capacity of marine organisms, as well as fishers' catch and income. Most of these benefits were only achieved by fully or highly protected areas and increased with MPA age. However, we found very few primary studies directly documenting the effect of MPAs on climate resilience, and those that did focused on corals, which are not organisms that directly benefit from local conservation efforts (Bruno et al., 2019). Since the publication of Chapter 1 in 2022, multiple publications have advanced our mechanistic understanding of the resilience pathways that MPAs can support (White et al., 2025) and have empirically tested whether MPAs support the climate resilience of marine ecosystems (Benedetti-Cecchi et al., 2024; Smith et al., 2023; Srednick & Swearer, 2024). These publications have reported conflicting and ambiguous results, with evidence of strong resilience benefits from conservation (Benedetti-Cecchi et al., 2024), clear absence of benefits (Smith et al., 2023), or weak and metric-dependent benefits (Srednick & Swearer, 2024). These diverse outcomes reflect the complexity of factors at play in determining the climate effectiveness of MPAs and the resilience attributes of ecosystems (Carpenter et al., 2001; Oliver et al., 2015). In this sense, this growing literature confirms one of the main conclusions of Chapter 1: climate benefits of MPAs are highly context-dependent and require high standards of conservation to accrue (i.e., high levels of protection over multiple years). Importantly, MPAs should not be expected to fully offset climatic impacts to marine life. Rather, MPAs should be

understood as one tool in the portfolio of solutions to enhance climate resilience, which primarily acts by abating other human pressures (Sumaila & Tai, 2020).

Another point of controversies in marine conservation revolves around the capacity of MPAs to provide ecological benefits to deep and offshore ecosystems. While technical and legal barriers have until now impeded the implementation of MPAs in the high seas, the BBNJ agreement and the 30x30 targets are creating opportunities and incentives to extend MPAs to deeper areas. However, some argue that the ecological characteristics of offshore and deep species are not compatible with the characteristics of MPAs, given that most pelagic species have ranges that expand beyond typical MPA borders. Before delving into these considerations, it is important to understand the conservation status and pressures experienced across the depth zones of the ocean to determine their conservation needs. In Chapter 2, we conducted a conservation and fishing effort assessment in three dimensions (3D) to determine conservation priorities across space and depth. This approach was very novel as it proposed for the first time a spatial assessment framework that accounts for the third dimension of the ocean, depth. Through this approach, we found that the shallowest depths and the deepest areas within economic exclusive zones are those that benefit from the greatest conservation effort, while important conservation gaps affect mesophotic, rariphotic, and abyssal depths. We also found that MPAs were predominantly located in areas with low fishing effort, which likely reflects the global trend of residual conservation, i.e., the siting of MPAs where they least interfere with human uses (Devillers et al., 2015). Furthermore, Chapter 2 highlighted immense knowledge gaps regarding the depth range of fishing activities and underscored the importance of accounting for depth distributions and vertical zonations in marine spatial planning to achieve targets of ecological representations and appropriately report conservation progress.

In addition to developing frameworks that can support 3D marine spatial planning, knowledge on deep ecosystems is required to extend science-informed management beyond shallow areas. Technical difficulties and low societal interest have led to the deep ocean (below 300 m) being vastly understudied compared to the shallowest coastal habitats, although deep ecosystems represents over 90% of the ocean (Hetherington et al., 2024; Levin, 2021). Even mesophotic and rariphotic ecosystems (60-300 m), which are among the 4% shallowest depths of the ocean, are vastly understudied compared to altiphotic (0-30 m) habitats. Chapter 3 and 4 aimed at advancing the ecological understanding of deep-reef communities occurring at mesophotic and rariphotic depths to inform their sustainable management. Chapter 3 and 4 demonstrated that multiple distinct fish assemblages occur on Caribbean coastal reef systems. While the distinctiveness of mesophotic assemblages has been established for at least a decade, this Dissertation comforted the taxonomic and functional distinctiveness of a deeper ‘rariphotic’ assemblage, the existence of which was first suggested by Baldwin et al., (2018). We further refined the description of the vertical zonation of reef-fish communities by establishing that the lower limit of reef-affiliated fish assemblages occurs around 300 m, and that mesophotic and rariphotic communities are subdivided into taxonomically distinct ‘upper’ and ‘lower’ assemblages. We also showed that the functional structure of reef fishes is relatively

homogenous across altiphotic and mesophotic communities, but that important trait losses create functionally distinct communities in the rariphotic and below, likely due to the environmental constraints experienced at these depths. Given the distinct biodiversity occurring on deep reefs, our results highlight that conservation networks must include the entire depth range of reef slopes to achieve ecological representation. Indeed, protecting only the shallowest sections of reefs, as it is the case for many MPAs that end at the 60-m isobath (Pulido Mantas et al., 2024), does not allow to ensure the protection for a large number of reef species. In addition to ecological representation targets, multiple vertical connectivity processes between shallow and deep reefs have been established, suggesting that holistic approaches to reef conservation should encompass the entire reef slope.

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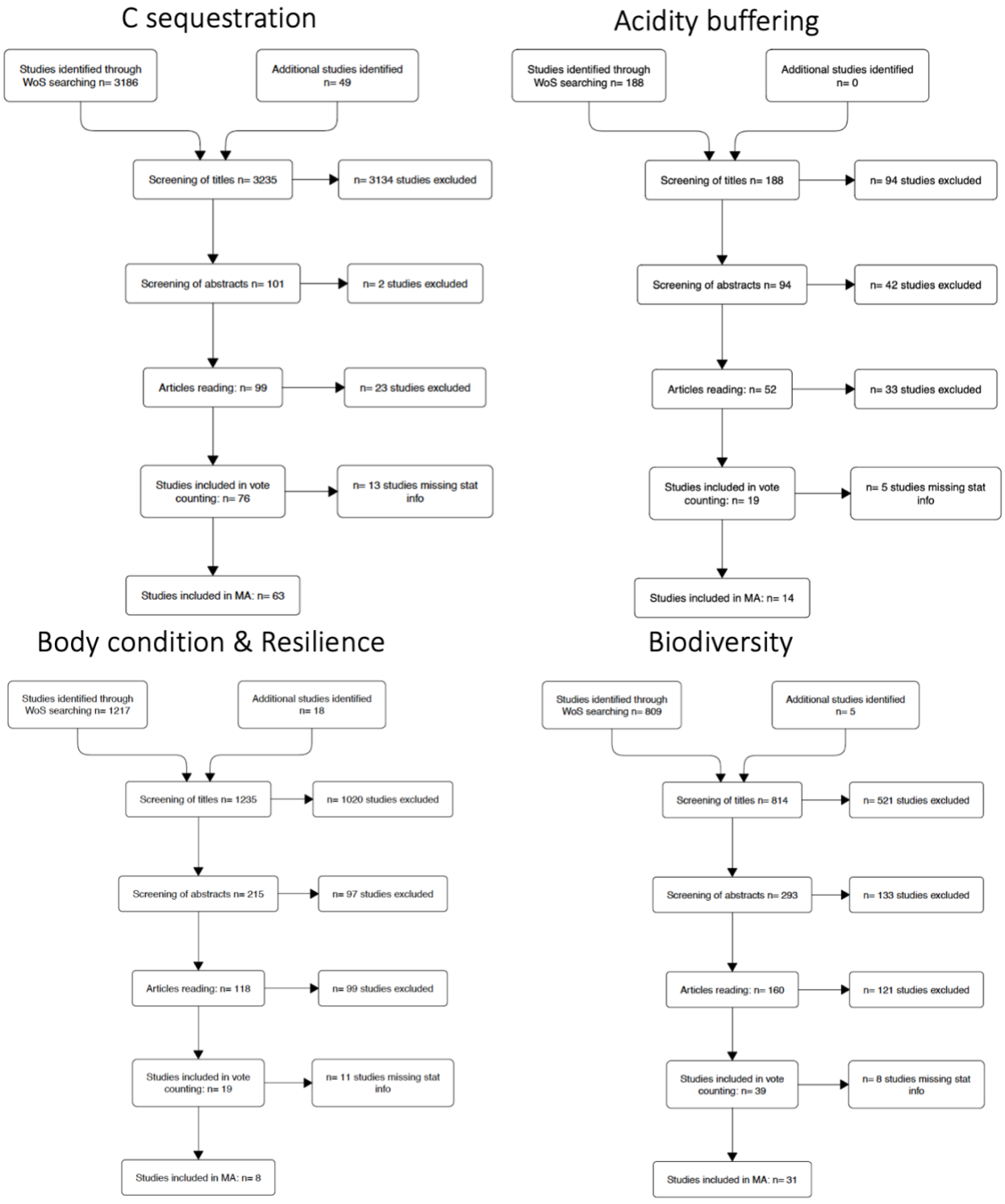
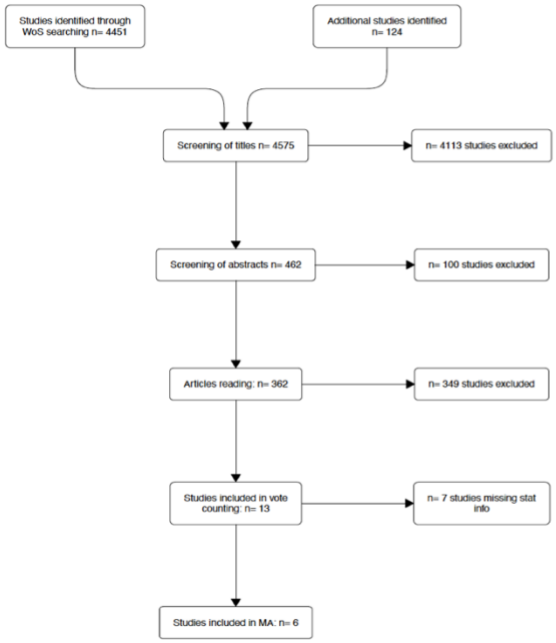
APPENDICES

CHAPTER 1 APPENDIX



Coastal Protection



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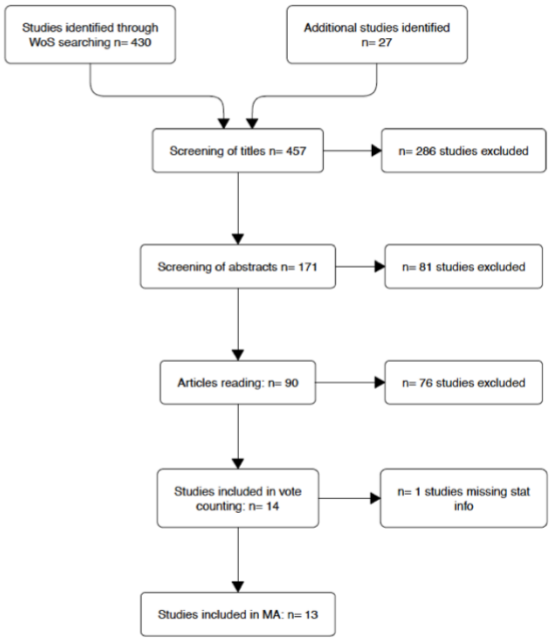
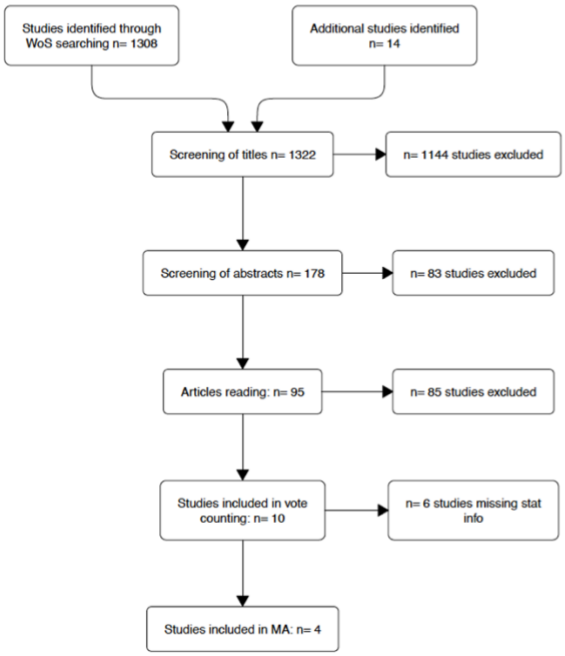
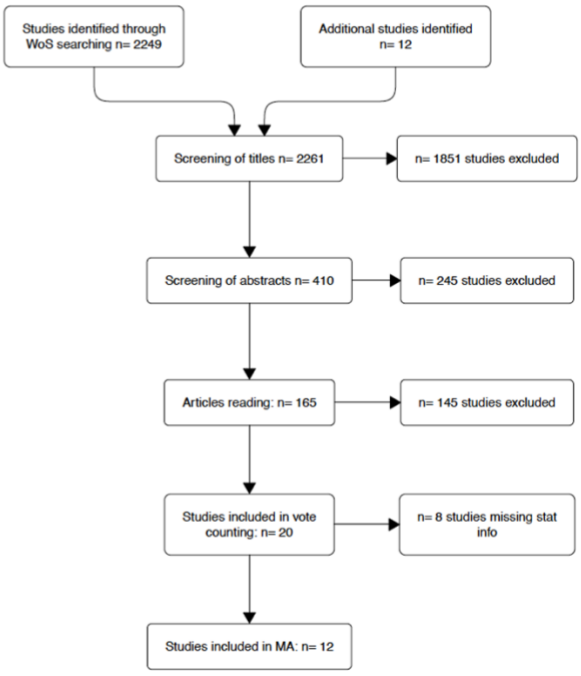


Stability



Reproduction & Connectivity



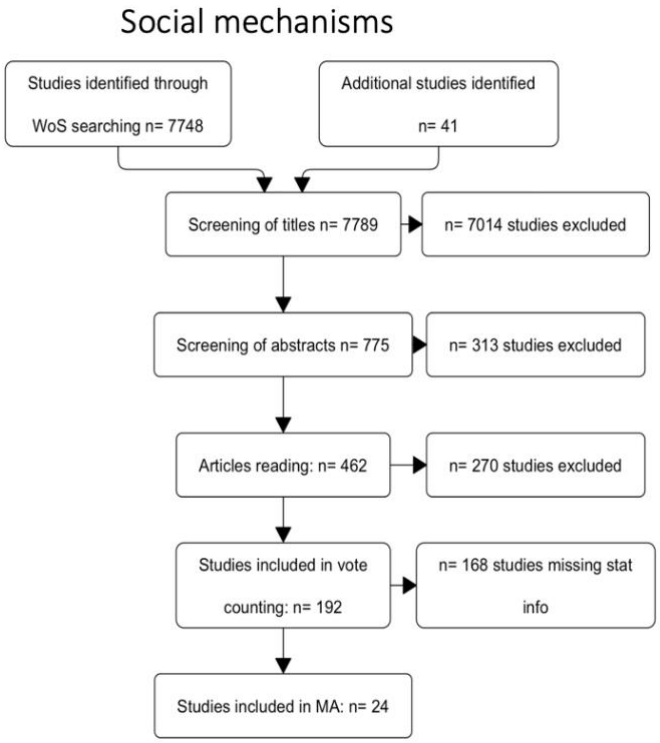


Figure S1. PRISMA plots detailing the selection phases of each systematic review carried out. PRISMA plots were obtained using the plot_PRISMA() function from the {metagear} package in R. Sample size (n=) indicate the number of studies selected or excluded at each phase. Related to figure 1.

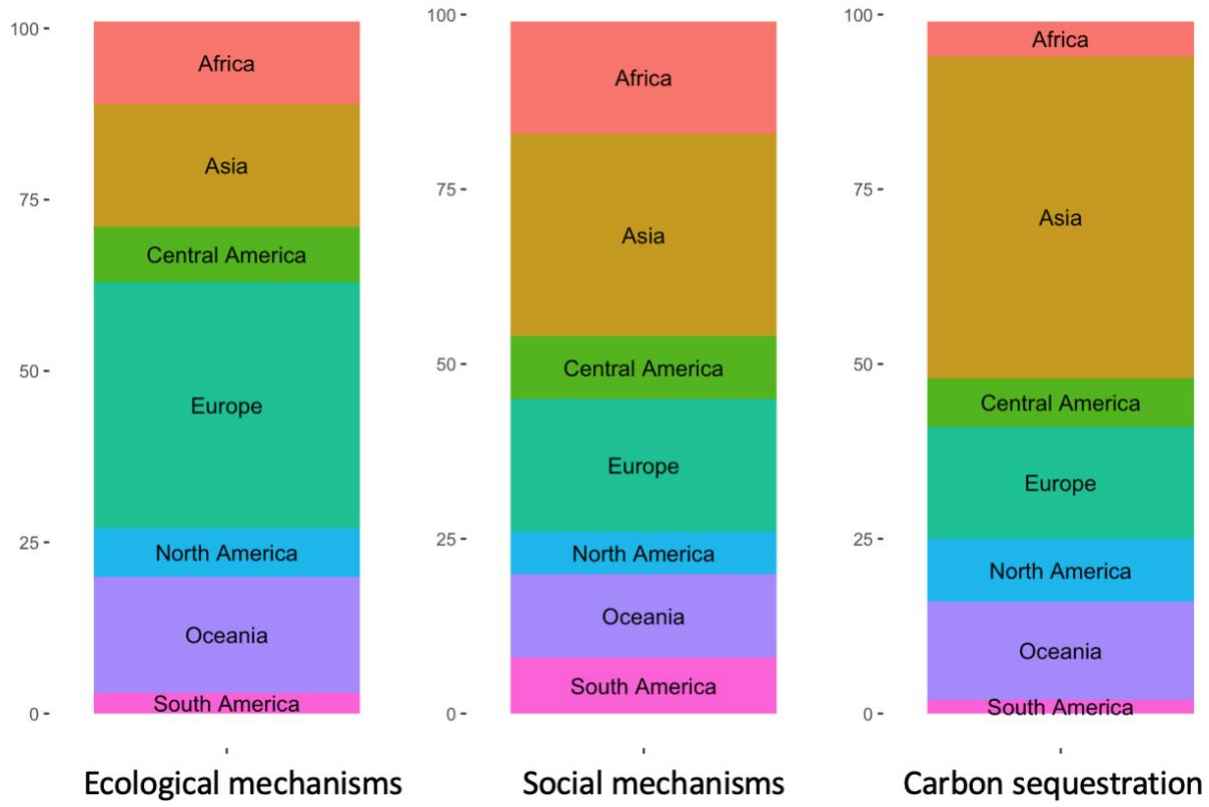


Figure S2. Distribution of studies included in our review among continents. Y-axis represent %. Related to Figure 1.

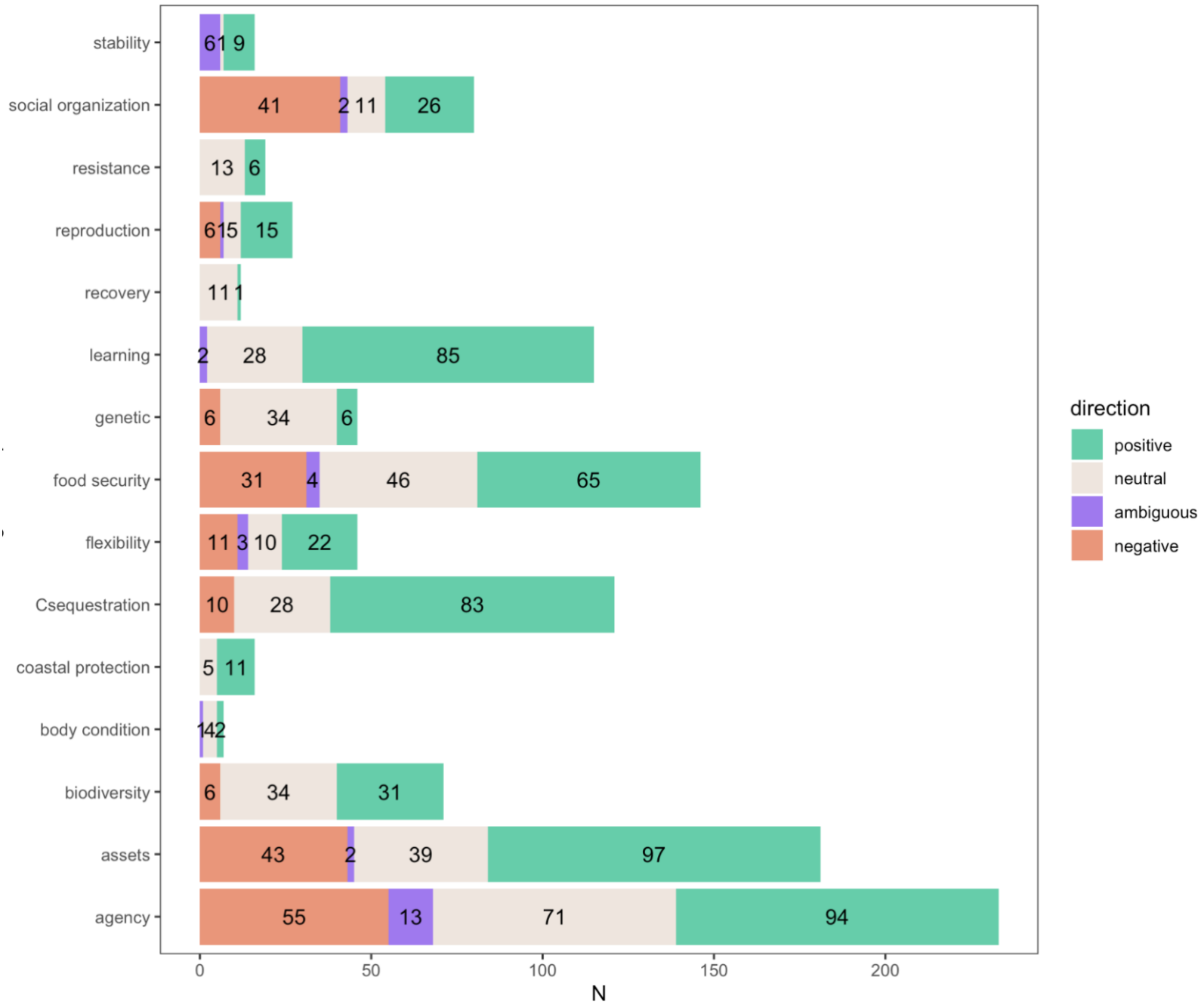


Figure S3. MPA outcomes on all studied mechanisms obtained through vote-counting. X-axis indicates the cumulative number of data points (N) included in the vote counting for each pathway. Numbers in the barplots represent the number of data points of each direction (positive, neutral, ambiguous and negative). Related to Figure 2.

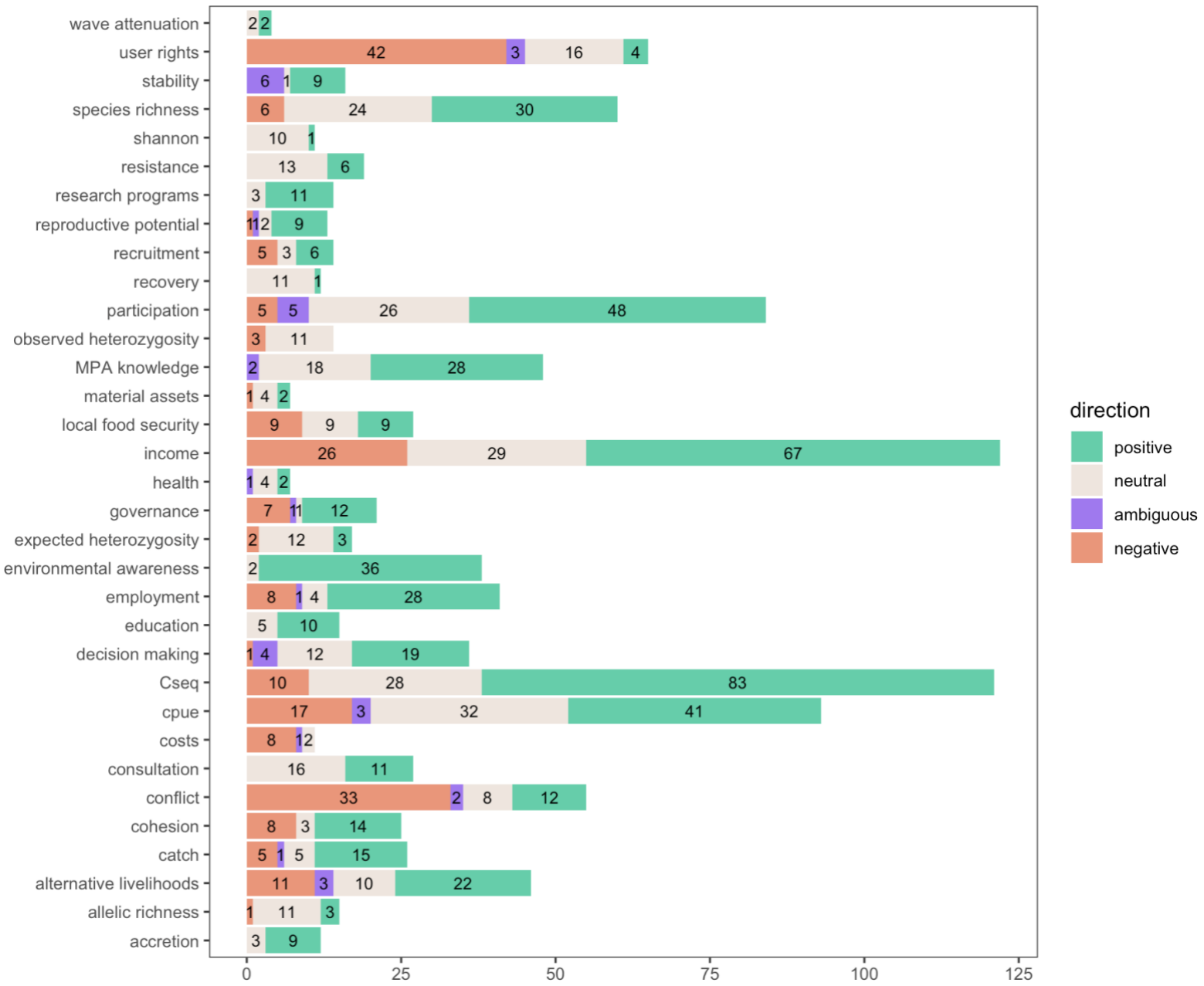
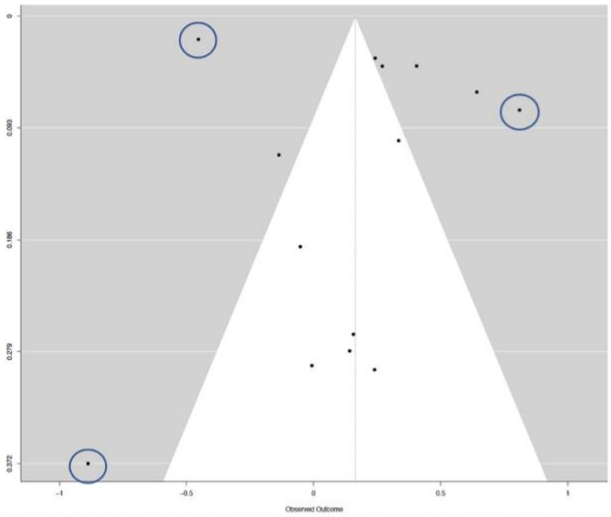
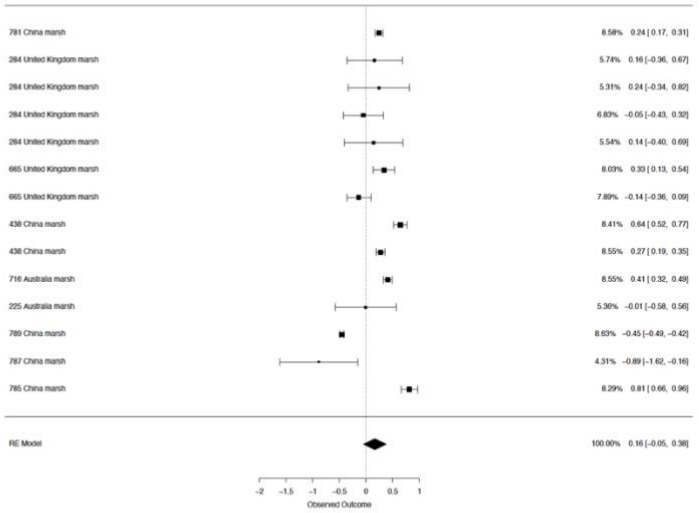


Figure S4. MPA outcomes on all studied indicators, obtained through vote-counting. X-axis indicates the cumulative number of datapoints (N) included in the vote counting for each pathway. Numbers in the barplots represent the number of data points of each direction (positive, neutral, ambiguous and negative). Related to Figure 2.

Tidal marsh

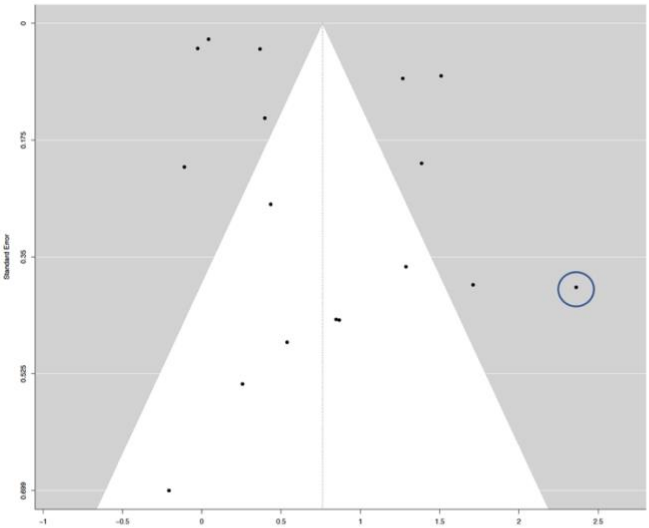


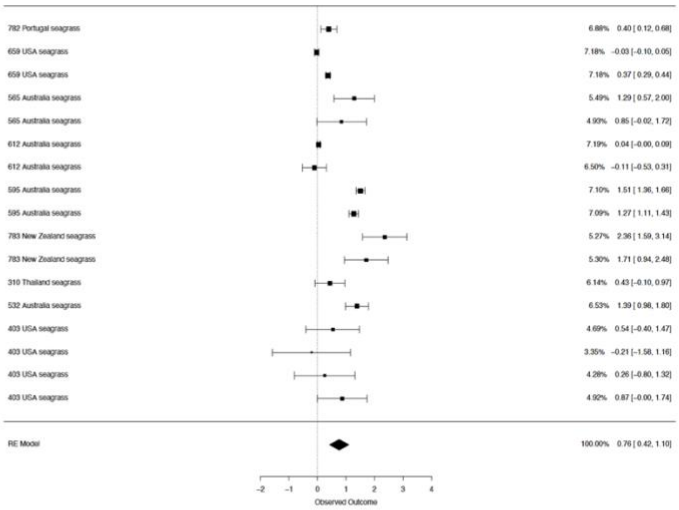



```
tau^2 (estimated amount of total heterogeneity): 0.1374 (SE = 0.0642)
tau (square root of estimated tau^2 value):      0.3706
I^2 (total heterogeneity / total variability):   97.51%
H^2 (total variability / sampling variability):  40.08

Test for Heterogeneity:
Q(df = 13) = 945.3977, p-val < .0001
```

Seagrass

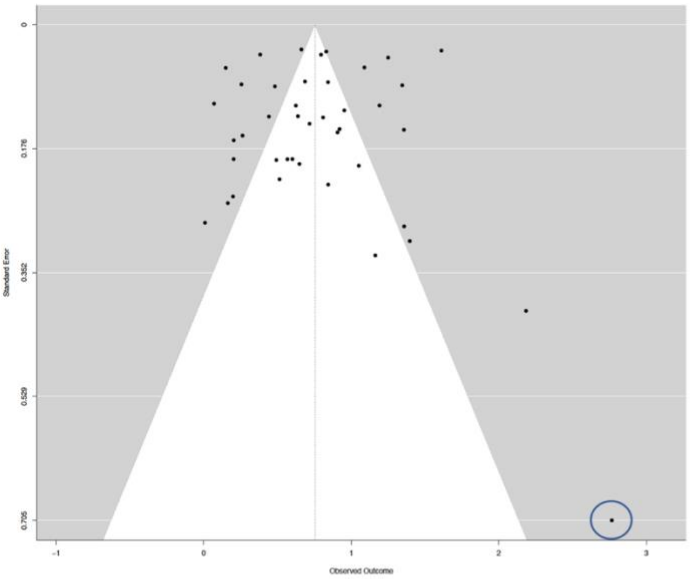


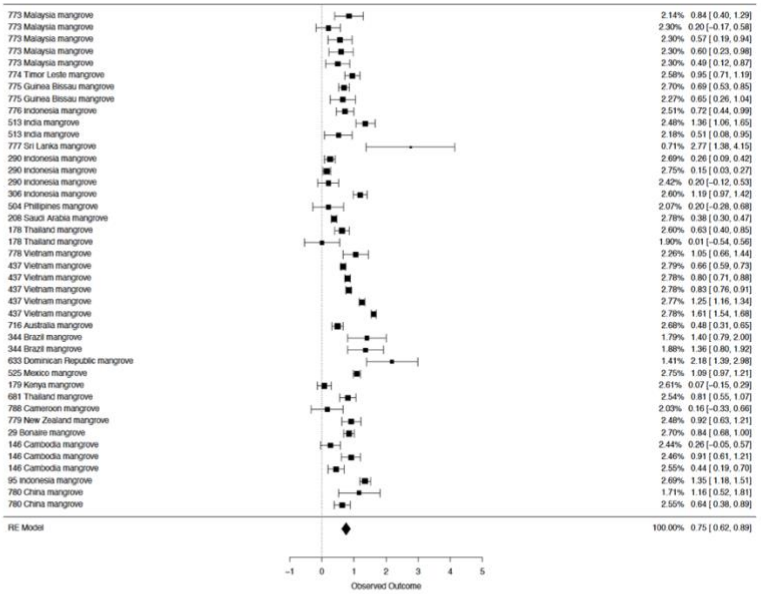



```
tau^2 (estimated amount of total heterogeneity): 0.4259 (SE = 0.1814)
tau (square root of estimated tau^2 value):      0.6526
I^2 (total heterogeneity / total variability):   98.49%
H^2 (total variability / sampling variability):  66.39

Test for Heterogeneity:
Q(df = 16) = 634.0726, p-val < .0001
```

Mangrove

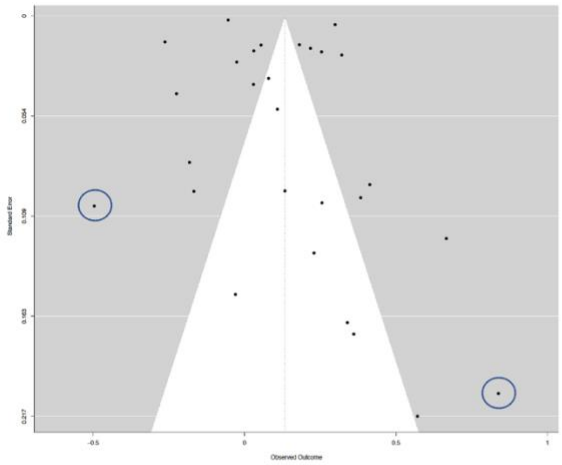


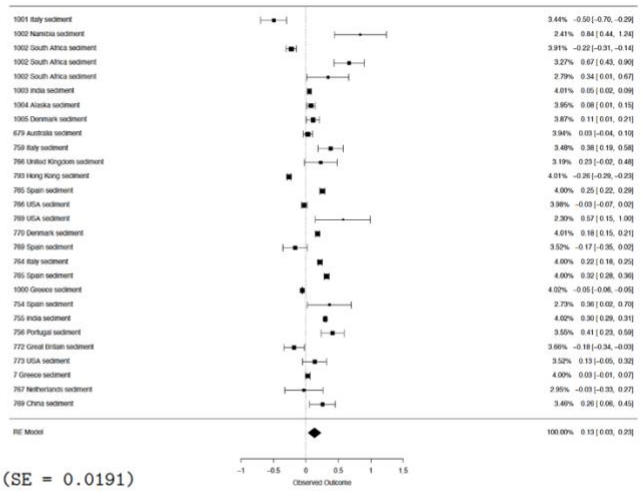



```
tau^2 (estimated amount of total heterogeneity): 0.1668 (SE = 0.0428)
tau (square root of estimated tau^2 value):      0.4084
I^2 (total heterogeneity / total variability):   95.79%
H^2 (total variability / sampling variability):  23.76

Test for Heterogeneity:
Q(df = 41) = 1086.4676, p-val < .0001
```

Sediment






```
tau^2 (estimated amount of total heterogeneity): 0.0629 (SE = 0.0191)
tau (square root of estimated tau^2 value):      0.2508
I^2 (total heterogeneity / total variability):   99.65%
H^2 (total variability / sampling variability):  283.72

Test for Heterogeneity:
Q(df = 27) = 5799.9624, p-val < .0001
```

Figure S5.1: Funnel plots and forest plots of the effect sizes included in the Carbon sequestration meta-analyses (from top to bottom: tidal marshes, seagrass, mangrove and sediments). Effect sizes circled in the funnel plots are identified outliers that were checked. Related to Figure 2.

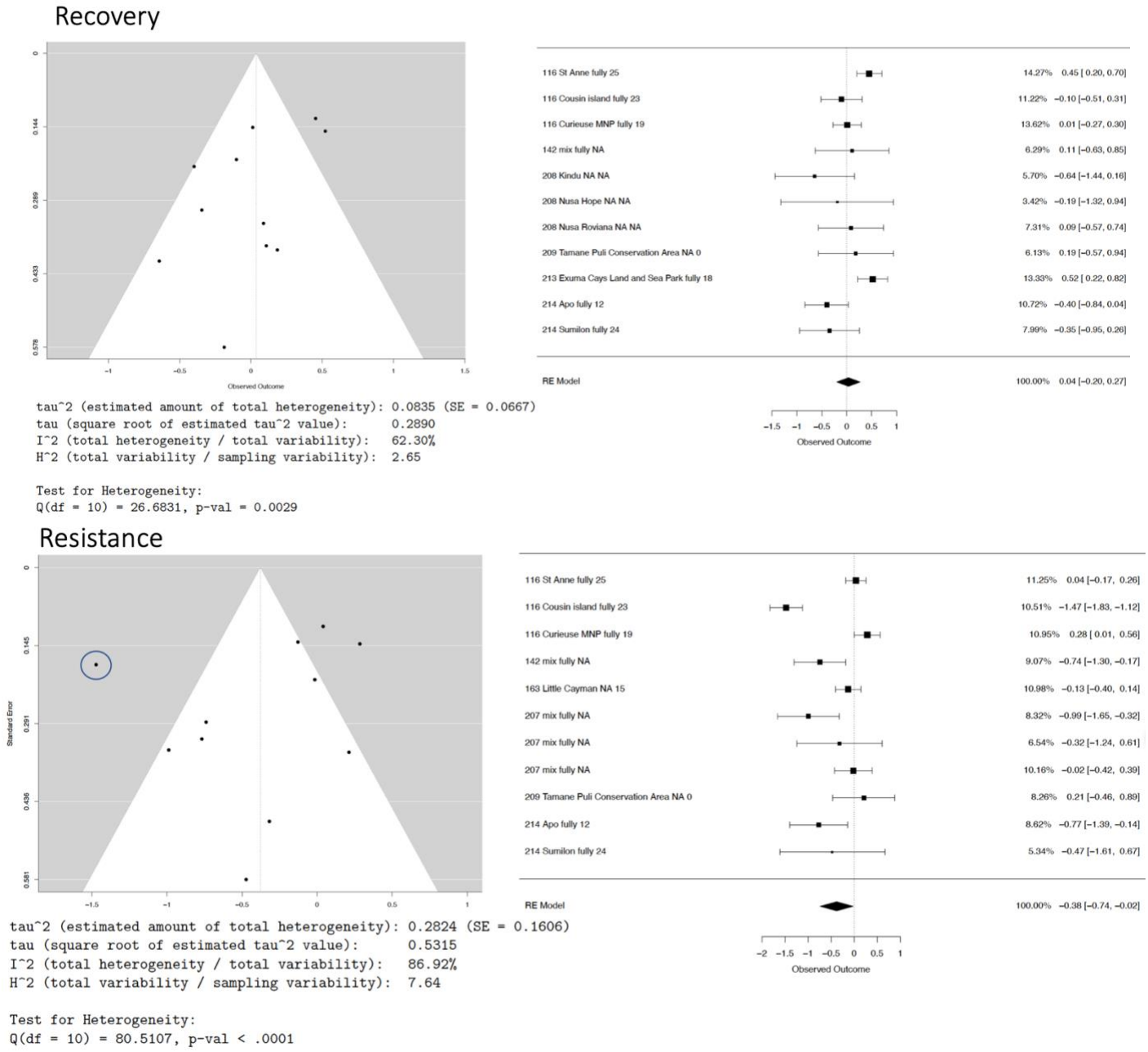


Figure S5.2: Funnel plots and forest plots of the effect sizes included in the resilience meta-analyses (from top to bottom: recovery and resistance indicators). Effect sizes circled in the funnel plots are identified outliers that were checked. Related to Figure 4.

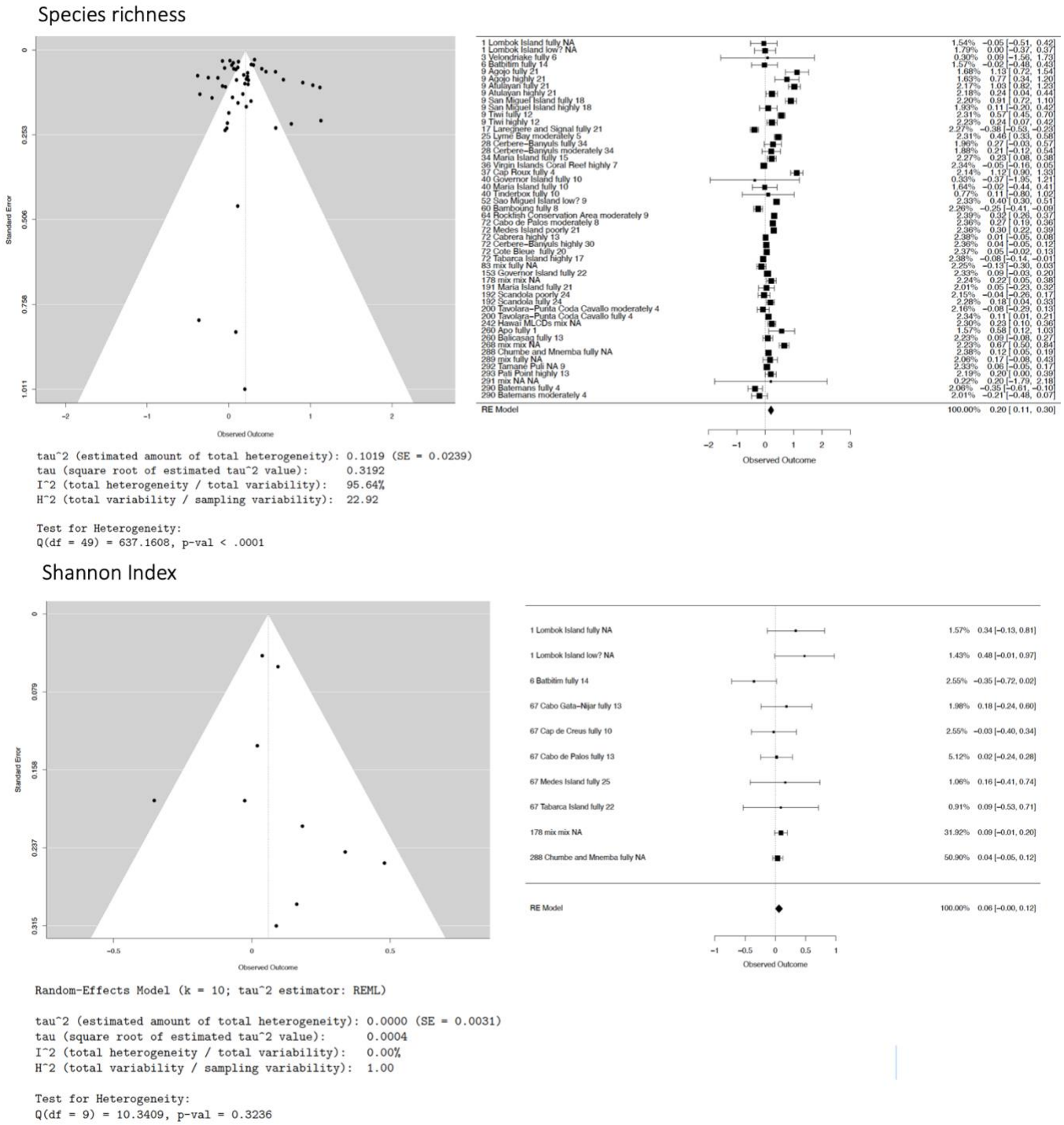
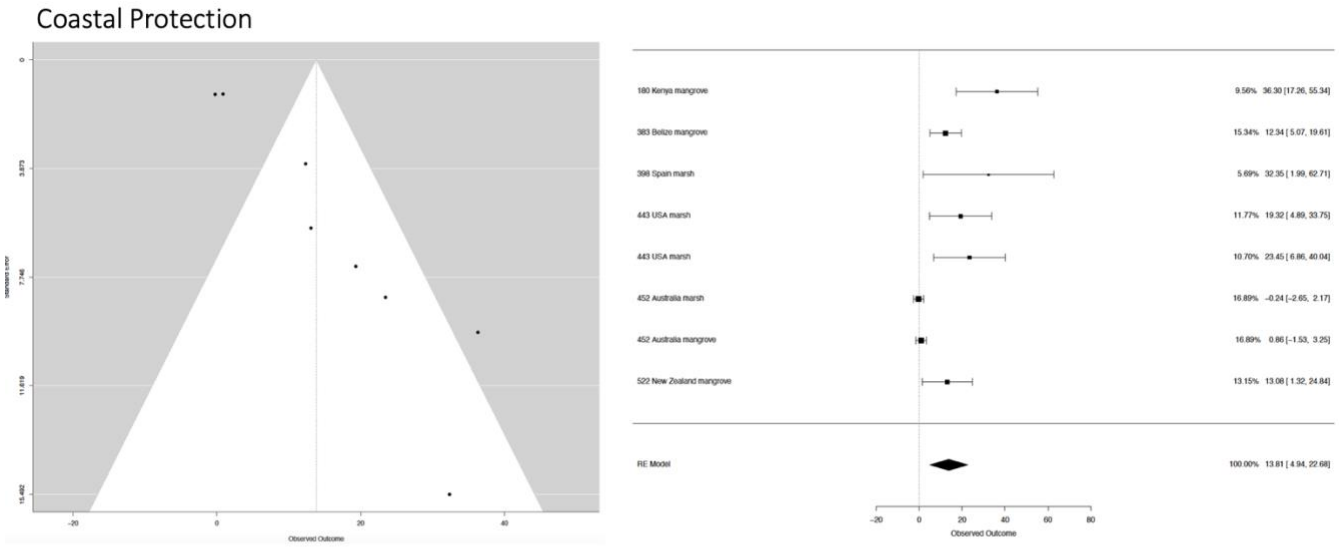


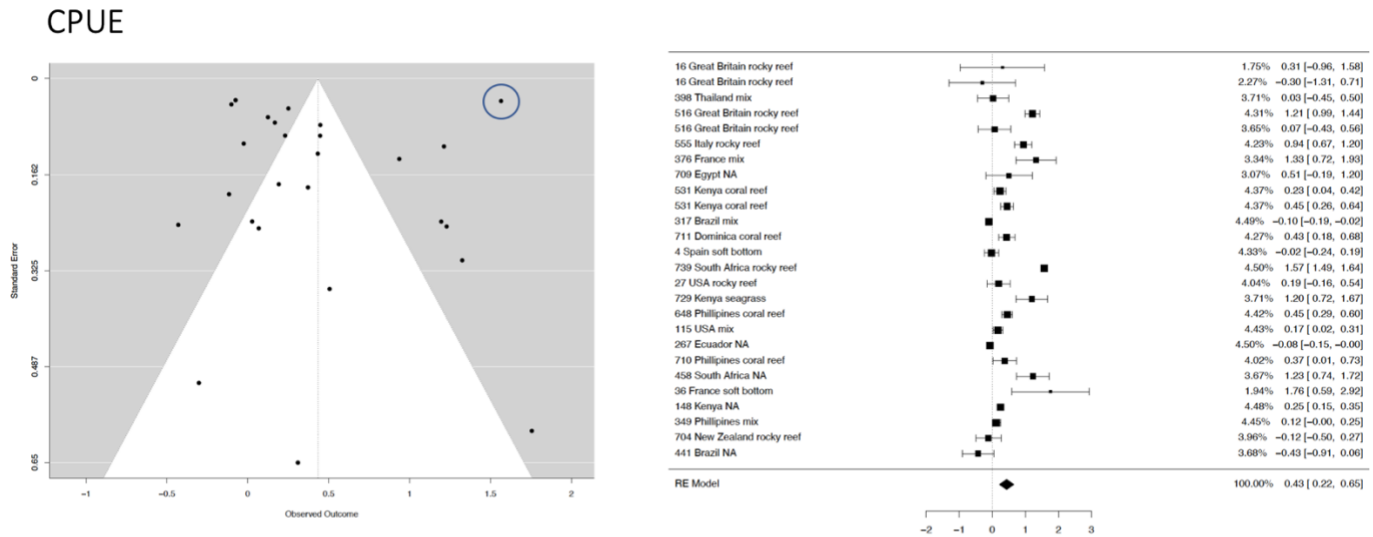
Figure S5.3: Funnel plots and forest plots of the effect sizes included in the biodiversity meta-analyses (from top to bottom: species richness and Shannon index indicators). Related to Figure 2.




```
tau^2 (estimated amount of total heterogeneity): 119.7531 (SE = 85.3773)
tau (square root of estimated tau^2 value):      10.9432
I^2 (total heterogeneity / total variability):   93.74%
H^2 (total variability / sampling variability):  15.97

Q(df = 7) = 43.6237, p-val < .0001
```

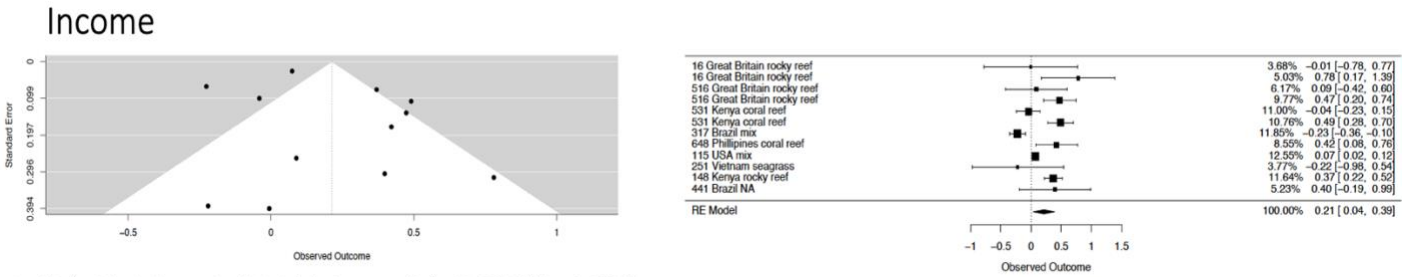
Figure S5.4: Funnel plots and forest plots of the effect sizes included in the coastal protection meta-analyses. Related to Figure 2.




```
tau^2 (estimated amount of total heterogeneity): 0.2676 (SE = 0.0875)
tau (square root of estimated tau^2 value):      0.5173
I^2 (total heterogeneity / total variability):   97.13%
H^2 (total variability / sampling variability):  34.85

Test for Heterogeneity:
Q(df = 25) = 1418.4759, p-val < .0001
```

Figure S5.5: Funnel plots and forest plots of the effect sizes included in the CPUE meta-analysis Effect sizes circled in the funnel plots are identified outliers that were checked. Related to Figure 2.




```
tau^2 (estimated amount of total heterogeneity): 0.0635 (SE = 0.0391)
tau (square root of estimated tau^2 value):      0.2520
I^2 (total heterogeneity / total variability):   87.15%
H^2 (total variability / sampling variability):  7.78

Test for Heterogeneity:
Q(df = 11) = 70.6295, p-val < .0001
```

Figure S5.6: Funnel plots and forest plots of the effect sizes included in the income meta-analysis Effect sizes circled in the funnel plots are identified outliers that were checked. Related to Figure 2.

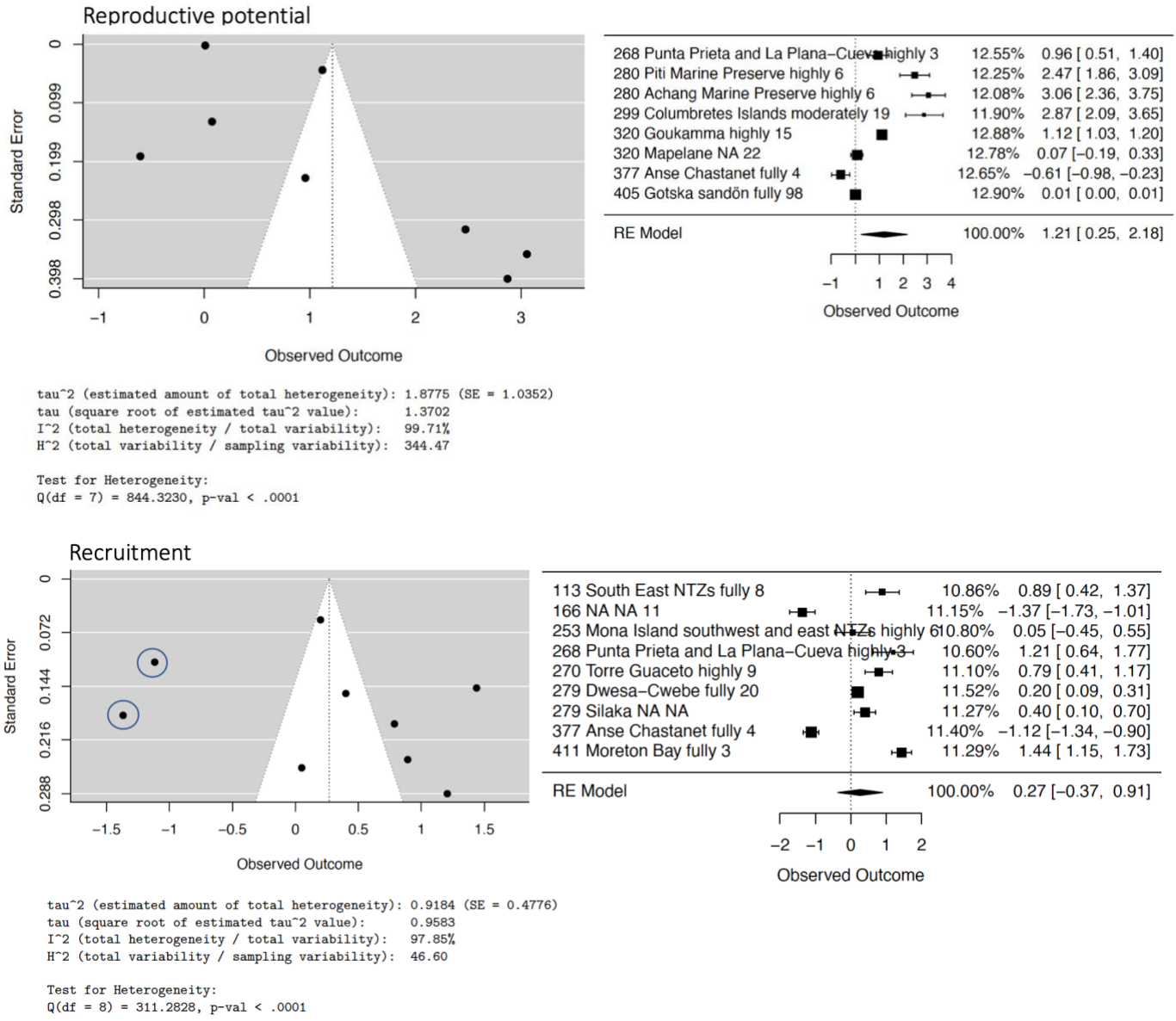


Figure S5.7: Funnel plots and forest plots of the effect sizes included in the reproduction meta-analyses (from top to bottom: reproductive potential and recruitment indicators). Effect sizes circled in the funnel plots are identified outliers that were checked. Related to Figure 2.

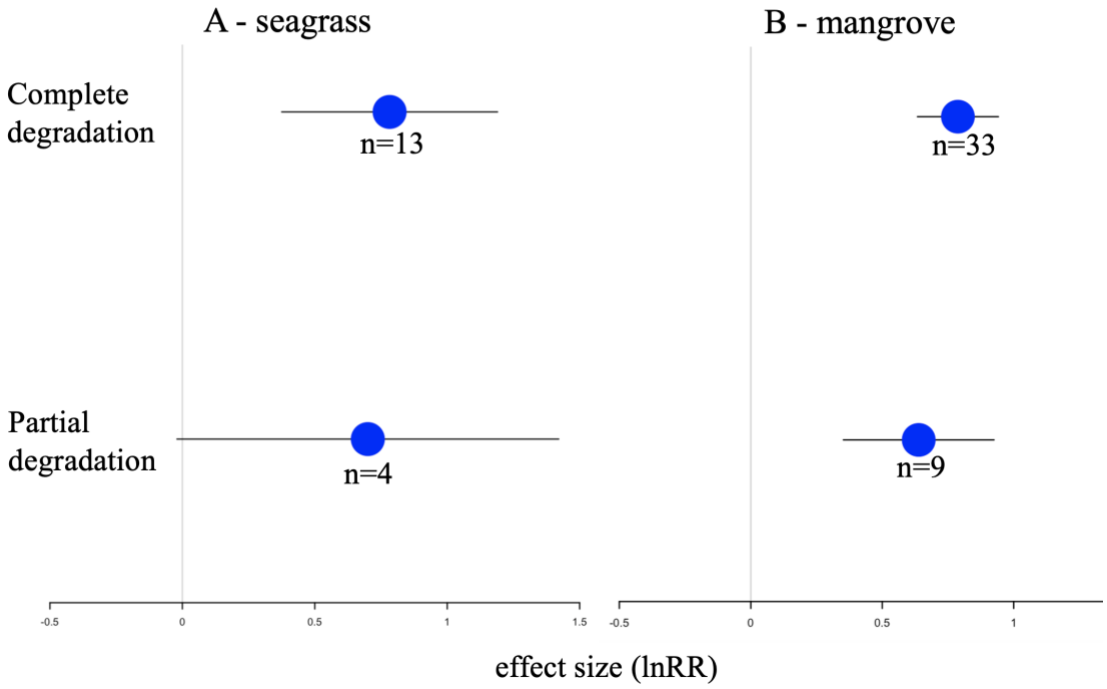


Figure S6. Effect of the level of degradation of habitats on the Carbon sequestration benefits achieved from protection of seagrass (A) and mangrove (B). Error bars are 95% confidence interval. Sample size (n=) indicate the number of data point from which the effect size was calculated. Related to Figure 2.

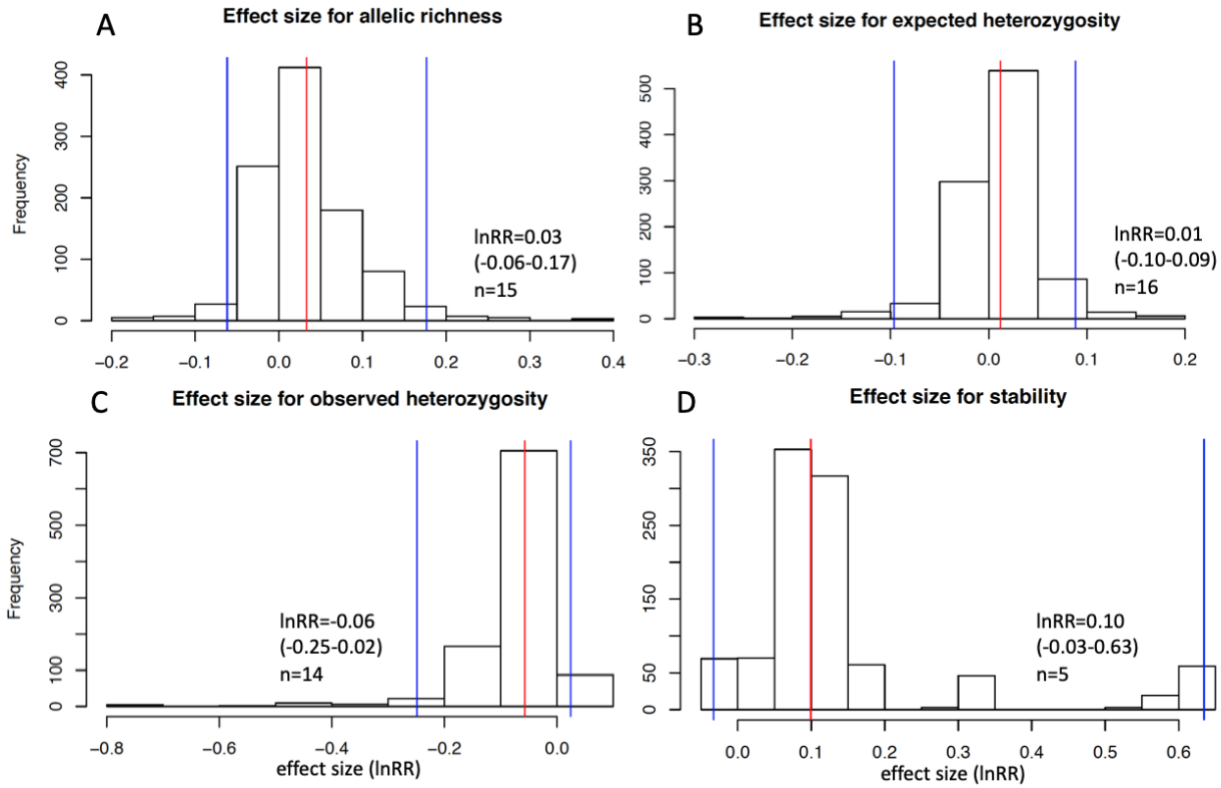


Figure S7. Effect size obtained by boot-strapping. Genetic diversity indicators (A-C) and stability indicator (D). Barplots represent the number of times each value of effect size was obtained out of 1000 iterations. The red vertical line represents the mean effect size value obtained, and the blue lines the 95% confidence interval associated. Sample size (n=) indicate the number of data points from which the effect size was calculated. Related to Figure 2.

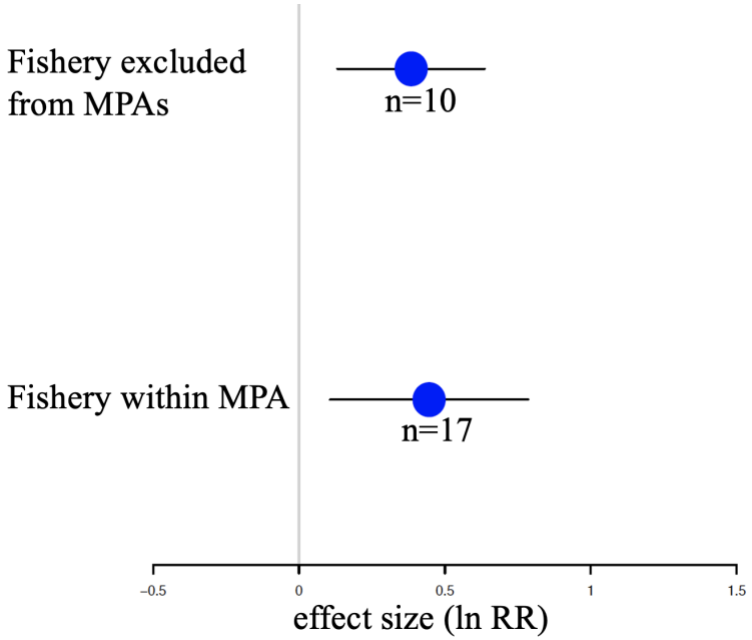


Figure S8. Changes in CPUE measured in fisheries excluded from MPAs and measured in fisheries allowed in MPAs. Effect size represent log ratios. Error bars are 95% confidence interval. Sample size (n=) indicate the number of data point from which the effect size was calculated. Related to Figure 2.

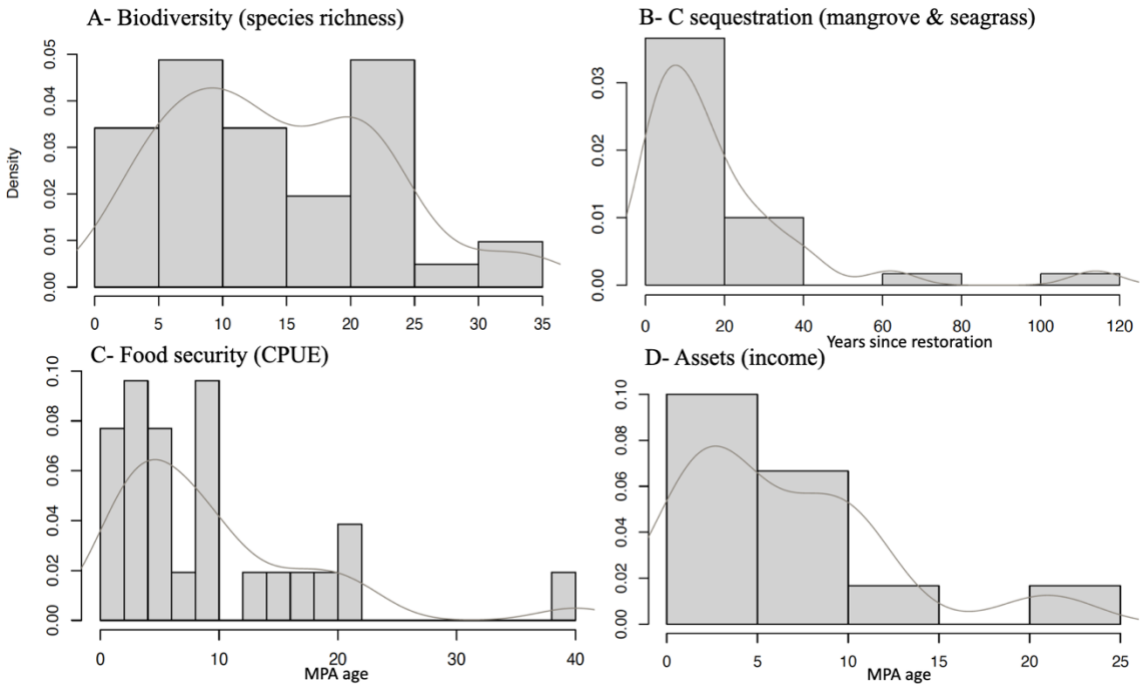


Figure S9.1. Distribution of the age of MPAs (log transformed) included in the meta-analyses on Biodiversity, C sequestration, Food Security and Assets.

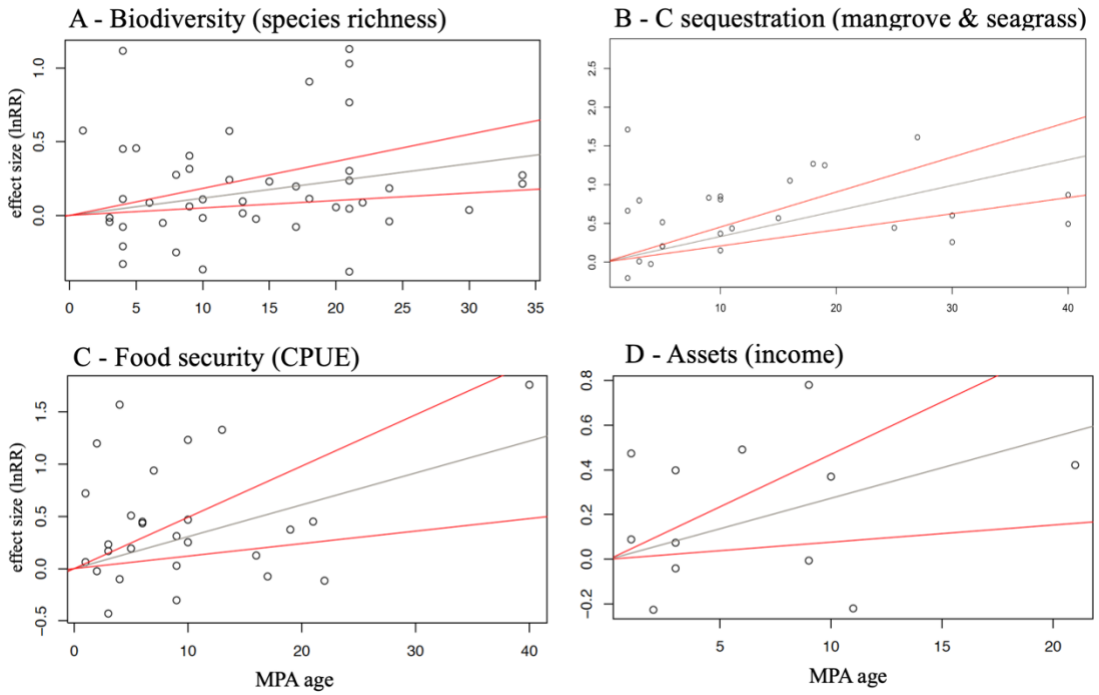


Fig. S9.2. Effect of MPA age on Biodiversity, Carbon (C) Sequestration, Food Security and Assets. For C sequestration, only mangrove and seagrass C pools were included in the analysis. Grey line indicates the regression coefficient of the model, and the red lines the 95% confidence interval associated with the regression coefficient of the model. Dots indicate data points obtained from individual studies.

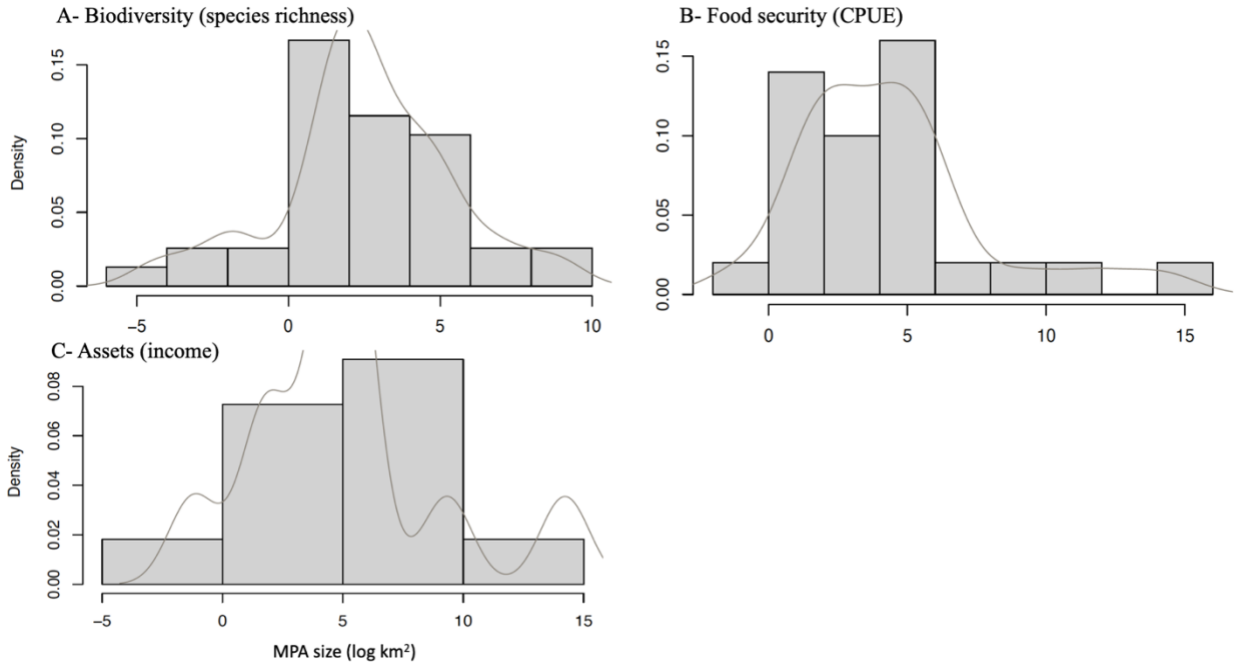


Figure S10.1. Distribution of the size of MPAs (log transformed) included in the meta-analyses on Biodiversity, Food Security and Assets.

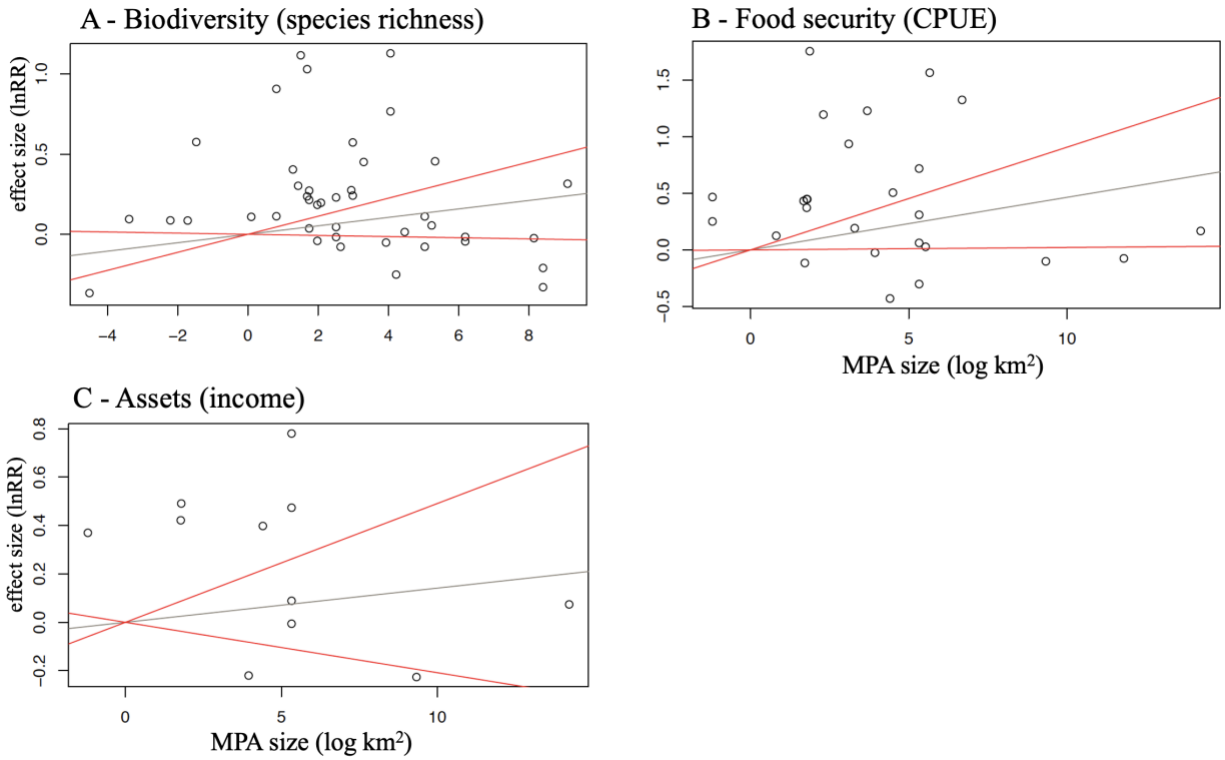


Figure S10.2. Effect of MPA size (log transformed) on Biodiversity, Food Security and Assets. grey line indicates the regression coefficient of the model, and the red lines the 95% confidence. interval associated with the regression coefficient of the model. Dots indicate data points obtained from individual studies.

Table S1. Identification of mitigation and adaptation pathways from elements listed in five reviews. Related to Figure 1.

Source	Elements of climate adaptation and mitigation identified	Mitigation and adaptation pathways
Roberts et al. (2017). Marine reserves can mitigate and promote adaptation to climate change. (Figure 1)	promotes genetic diversity	genetic diversity
	maintains carbon sequestration and storage processes	carbon sequestration
	prevents biodiversity loss	biodiversity
	provides stepping stones for dispersal	connectivity
	enhances CO2 absorption and buffers acidification	acidification buffering
	greater reproductive output	reproductive potential
	confers increased stability to coastal habitats	stability
	prevents the release of carbon from sediments	carbon sequestration
Bates et al. (2019). Climate resilience in marine protected areas and the "Protection Paradox". (Figure 1)	increase biogenic habitat	not a direct adaptation pathway, but contributes to C sequestration, coastal protection and acidity buffering
	intact food webs	stability
	increase community diversity	biodiversity
	increase population diversity	genetic diversity + body condition
Cinner et al. (2018). Building adaptive capacity to climate change in tropical coastal communities. (Figure 1)	assets	assets
	flexibility	flexibility
	organization	organization
	learning	learning
	agency	agency
Ban et al. (2019). Well-being outcomes of marine protected areas. (Figure 2)	social	organization
	health	food security
	culture	learning
	economic	assets + flexibility
	governance	agency
	environment	coastal protection
Berhardt et al. (2013). Resilience to climate change in coastal marine ecosystems. (Table 1)	functional redundancy	biodiversity
	response diversity	genetic diversity
	high connectance	connectivity

	population connectivity	connectivity
	ecosystem connectivity	connectivity
	biological legacies	connectivity
	modularity	stability
	plasticity	phenotypic plasticity
	dispersal ability	connectivity
	population size	genetic diversity, stability, connectivity
	genetic variation	genetic diversity

Table S2. Definition and indicators used to measure the variables tested in vote counting and meta-analysis. Related to Figure 1.

		Pathway	definition	indicator	unit
mitigation	ecological	C sequestration	ability to sequester carbon (> 100 years)	sequestered C	kg C area^{-1} (continuous)
		acidity buffering	ability to provide a local increase in pH	mean local pH	pH unit (continuous)
adaptation	ecological	phenotypic plasticity	ability to acclimate to changing conditions	range of metabolical, physiological or morphological features	range (continuous)
		connectivity	exchanges of genes, organisms, nutrients between spatially distinct habitats	genetic connectivity	fixation index (FST) (continuous)
		stability	ability of an ecosystem to remain stable over time	temporal dissimilarity	mean distance to centroid (nMDS metric), coefficient of variation (SD/mean) (continuous)
		biodiversity	diversity of species within an ecosystem	species richness	number of species observed (continuous)
				Shannon index	Shannon index (continuous)
		genetic diversity	diversity of genes within a species	allelic richness	number of alleles at a loci (continuous)
				observed heterozygosity	0 to 1 (continuous)
				expected heterozygosity	0 to 1 (continuous)
		body condition	health condition of individuals	health	frequency of disease and bleaching (continuous)
		reproduction	ability of a population to produce offsprings and to retain recruits	reproductive output	larval or egg abundance, female fecundity (continuous)
				recruitment	recruits surface^{-1} (continuous)
		coastal protection	ability to protect the coastline and coastal inhabitants from waves and sea level rise	accretion	cm year^{-1} (continuous)
				wave attenuation	wave energy or wave height (continuous)
	social	assets	ability to access financial and material goods	material assets	infrastructure or material goods (binary)
				fishing cost	\$ fisher^{-1} trip^{-1} (continuous)
				employment	number of employment opportunities (integer)
				income	\$ fisher^{-1} month^{-1} (continuous)
		flexibility	ability to switch between adaptation strategies	occupational diversity	occupational diversity available to local communities (integer)
		social organization	ability of coastal communities to cooperate	cohesion	sense of community belonging and solidarity (binary)
				conflict	tensions between local actors (binary)
		learning	ability to generate, absorb and process new information	education	attendance to school, highest degree (integer)
				research program	presence of research programs promoted by the MPA (binary)
				MPA knowledge	awareness of local actors or visitors of MPA existence and regulations (binary)
				environmental awareness	environmental sensitivity and knowledge (binary)
		agency		user rights	increase or decrease of rights (binary)

			ability to have free choice in responding to environmental change	decision-making	ability of local actors' to influence decision-making (binary)
				consultation	consultation of local actors' opinions (binary)
				participation	involvement of local actors in management activities (binary)
		food security	ability to access nutritious food	local nutrition	quality, diversity and quantity of food intake by local inhabitants (continuous)
				catch	kg year-1 (continuous)
				catch per unit effort	kg hour-1 fisher-1 (continuous)
resilience	ecological	resistance	capacity to maintain attributes during a disturbance	resistance	% coral cover loss, % mortality after a disturbance (continuous)
		recovery	capacity to restore attributes after a disturbance	recovery	% coral cover gain after a disturbance (continuous)

Table S3. Results of the meta-analyses performed. (A) Meta-analysis performed for the climate pathways; (B) Meta-analysis performed for observed resistance, recovery and expected resilience; (C) Meta-analysis performed for baseline capacity of habitats to provide pH buffering and C sequestration. Statistical values associated with each meta-analysis are detailed in Table S4. Mean values are given as log ratios in S3.A and S3.B and in pH unit or in Mg C km^{-2} in S3.C. Lower and upper CI are the lower and upper boundaries of the 95% confidence interval associated with the mean value. n is the number of values from which the mean was calculated, Qt is the between-study heterogeneity, df is the degree of freedom and p the p-value. Related to Figure 2-4.

A	**indicator**	**mean value**	**lower CI**	**upper CI**	**p-value**	**n**	**Qt**	**df**	**p (Qt test)**
C sequestration	blue carbon	0.63	0.51	0.76	**0.0001**	73	5342	72	**0.0001**
	sediments	0.13	0.03	0.23	**0.0080**	28	5799	27	**0.0080**
	fish biomass	1.10	0.52	1.68	**0.0002**	3	3.3	2	0.1913
biodiversity	species richness	0.20	0.11	0.30	**0.0001**	50	642.9	49	**0.0001**
	Shannon index	0.06	0.00	0.12	0.0518	10	10.3	9	0.32
food security	cpue	0.43	0.22	0.65	**0.0001**	26	1418.5	25	**0.0001**
assets	income	0.21	0.04	0.39	**0.0175**	12	70.6	11	**0.0001**
reproduction	recruitment	0.27	-0.37	0.91	0.4104	9	311.3	8	**0.0001**
	reproductive potential	1.21	0.25	2.18	**0.0138**	8	844.3	7	**0.0001**
coastal protection	accretion*	13.81	4.94	22.68	**0.0023**	8	43.6	7	**0.0001**
genetic diversity	allelic richness	0.03	-0.07	0.18		15	boot strapping		
stability	stability	0.10	-0.03	0.63		5	boot strapping		

* the effect size for accretion was calculated as a Euclidian difference and not a log ratio.

B **indicator**	**mean value**	**lower CI**	**upper CI**	**p-value**	**n**	**Qt**	**df**	**p (Qt test)**
observed resistance	-0.38	-0.74	-0.02	**0.0377**	10	80.5	10	**0.0001**
observed recovery	0.04	-0.20	0.27	0.7656	11	26.6	10	**0.0029**
expected resilience	0.31	0.03	0.87		6	boot strapping		

C	**indicator**	**mean value**	**lower CI**	**upper CI**	**n**	**Qt**	**df**	**p**
pH buffering (change in mean pH)	mangrove	-0.13	-0.26	-0.01	5	1.23	4	0.8721
	seagrass	0.03	-0.03	0.09	12	4.56	11	0.9505
	macroalgae	-0.04	-0.12	0.05	4	0.37	3	0.9457
C sequestration (Mg C km^{-2})	macroalgae	340	78	601	7	71.77	6	**0.0001**

Table S4. Model heterogeneity, residual heterogeneity and regression results associated with the features tested. Related to Figure 2.

		Model heterogeneity			Residual heterogeneity			Regression results		
pathway	**feature**	**Qm**	**df**	**p**	**Qe**	**df**	**p**	**estimate**	**p**	**CI**
C sequestration	habitat	12.9	2	**0.0016**	3192.2	70	**0.0001**			
	partial or complete degradation	0.002	1	0.9602	4899.8	71	**0.0001**			
	conservation or restoration	0.825	1	0.3636	3931.1	71	**0.0001**			
	age				1716	29	**0.0001**	0.0109	**0.0125**	0.007
biodiversity	level of protection	0.4	2	0.8052	468.8	42	**0.0001**			
	presence of FPA	0.11	1	0.7379	502.4	35	**0.0001**			
	age				697.4	43	**0.0001**	0.0117	**0.0006**	0.006
	size				729.4	41	**0.0001**	0.0264	0.08	0.03
assets (income)	level of protection	2.59	2	0.2731	34.2	10	**0.0002**			
	presence of FPA	0.057	1	0.8109	62.72	11	**0.0001**			
	age				47.9	11	**0.0001**	0.0273	**0.0064**	0.0196
	size				85.99	10	**0.0001**	0.0141	0.4280	0.0350
food security (cpue)	level of protection	1.1	2	0.578	894.6	22	**0.0001**			
	presence of FPA	0.379	1	0.5377	1320.3	23	**0.0001**			
	age				1911	25	**0.0001**	0.0306	**0.0034**	0.0204
	size				1854	24	**0.0001**	0.0525	**0.0269**	0.0465
	fishery inside or outside MPA	0.019	1	0.88	1411.8	24	**0.0001**			

Table S5: Values used for the global extent and the baseline capacity of habitats to provide C sequestration, wave attenuation and accretion services. Values are followed by the reference of the studies from which they were extracted. Related to Figure 3.

Habitat	global extent (km^2)	C sequestration (Mg C km^{-2})	wave attenuation (%)	accretion (mm $year^{-1}$)
mangrove	83495 (Hamilton and Casey, 2016)	73890 (Alongi, 2020)	27 (Narayan et al., 2016)	1.87 (Duarte et al., 2013)
seagrass	266562 (McKenzie et al., 2020)	14220 (Fourqurean et al., 2012)	31 (Narayan et al., 2016)	-0.08 (Duarte et al., 2013)
marsh	128000 (Murray et al., 2019)	41840 (Lovelock et al., 2017)	54 (Narayan et al., 2016)	3.76 (Duarte et al., 2013)
sediments	348000000 (Atwood et al., 2020)	8983 (Atwood et al., 2020)	NA	NA
macroalgae	3540000 (Krause-Jensen and Duarte, 2016)	340 (present study)	NA	NA
coral reef	527072 (Mora et al., 2006)	NA	53 (Narayan et al., 2016)	NA

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CHAPTER 2 APPENDIX

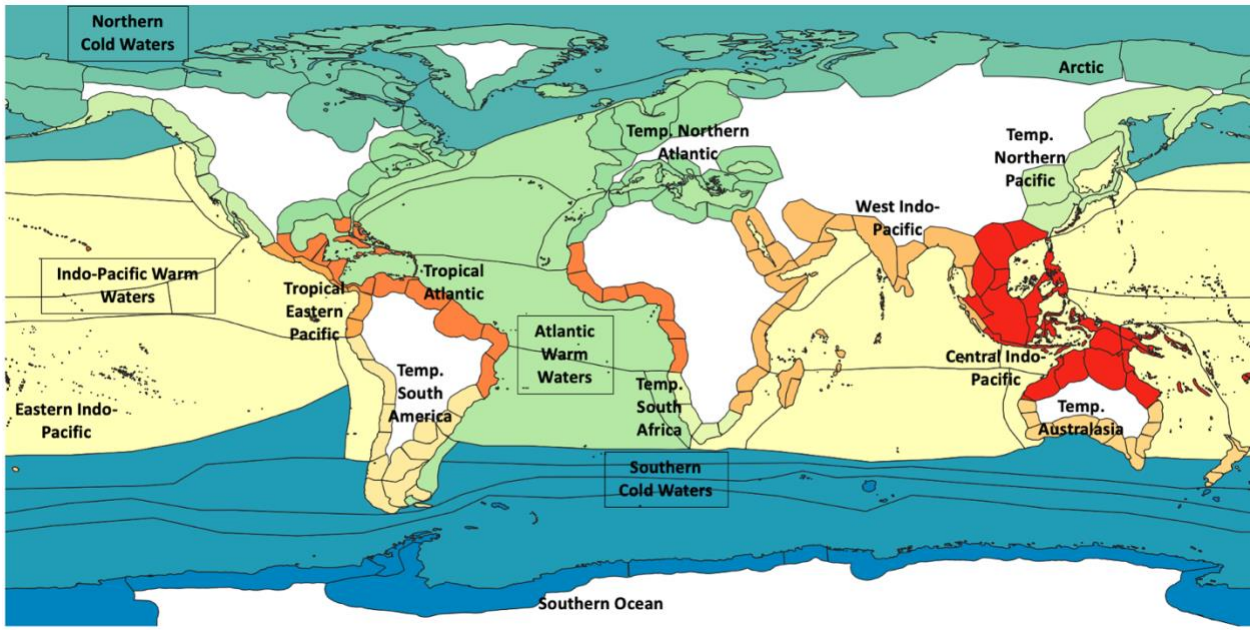

Fig. S1. Location of 2D marine ecoregions. Off-shore ecoregions are indicated by square outlines. Each ecoregion is depicted in a different color. Black lines represent the limits of pelagic provinces, a subdivision of off-shore realms defined in Spalding et al., (2012) but not considered in our analysis.

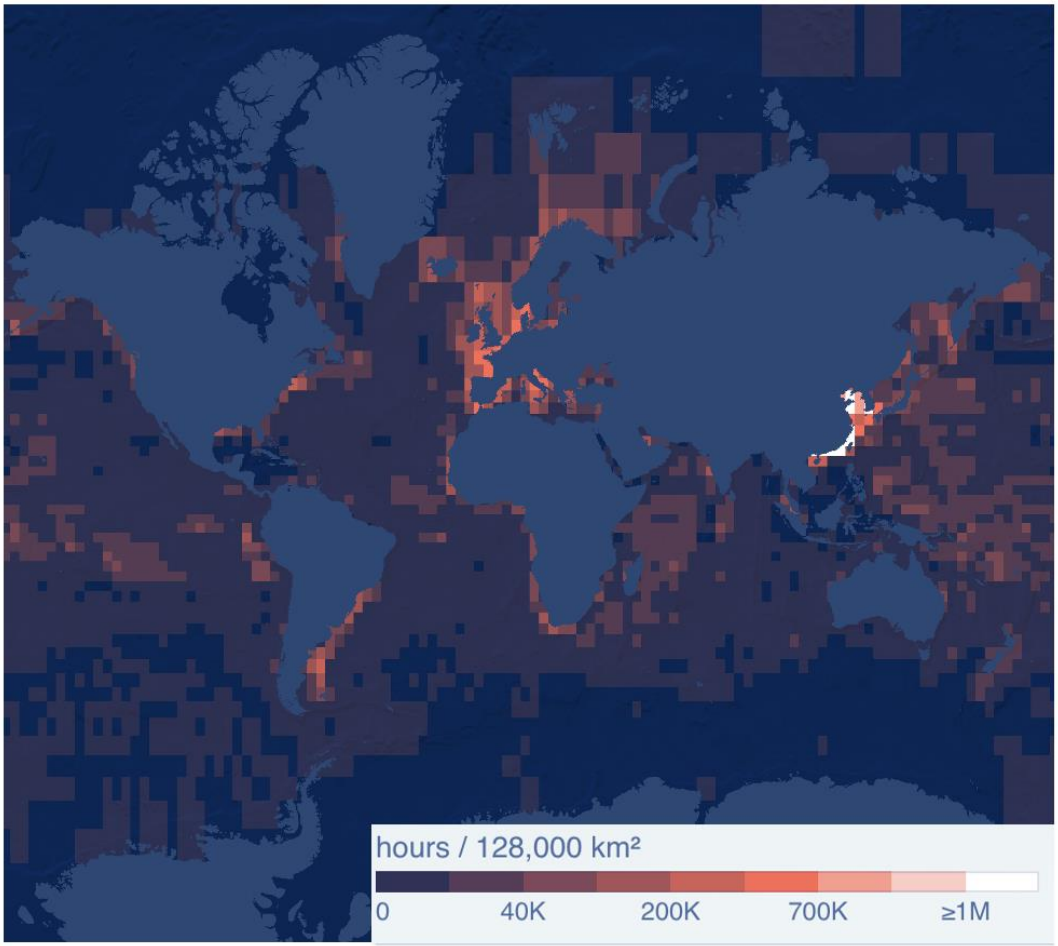

Fig. S2. Total fishing hours per unit area in 2019. Data and map display from the Global Fishing Watch online interface.

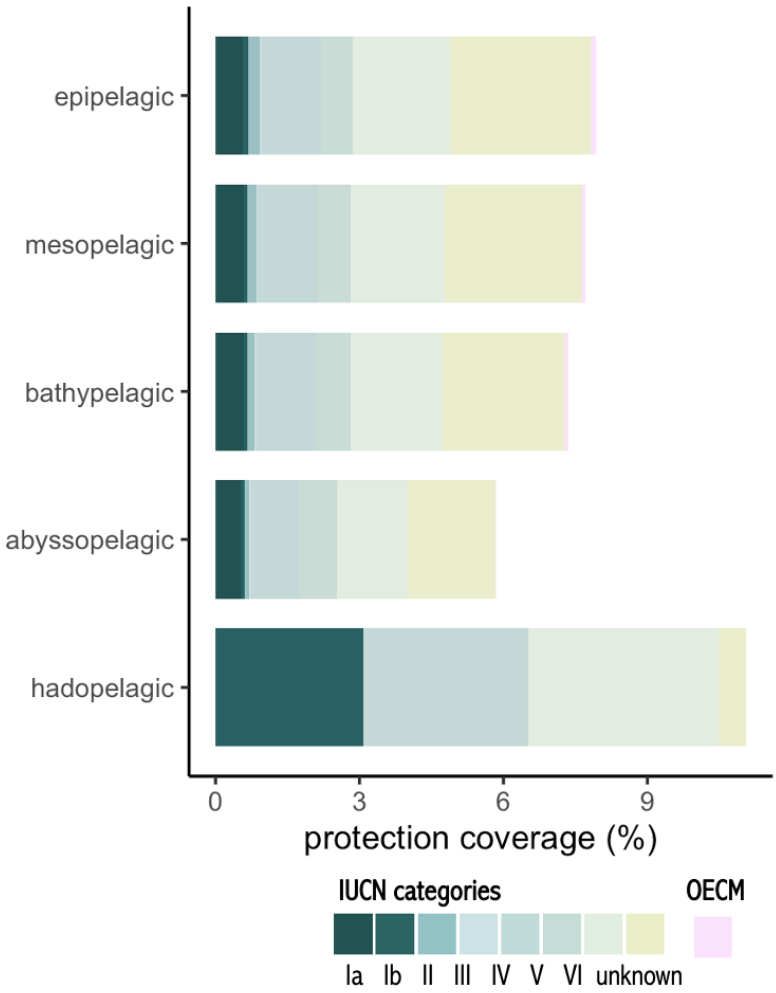

Fig. S3. Distribution of protection coverage across pelagic depth realms.

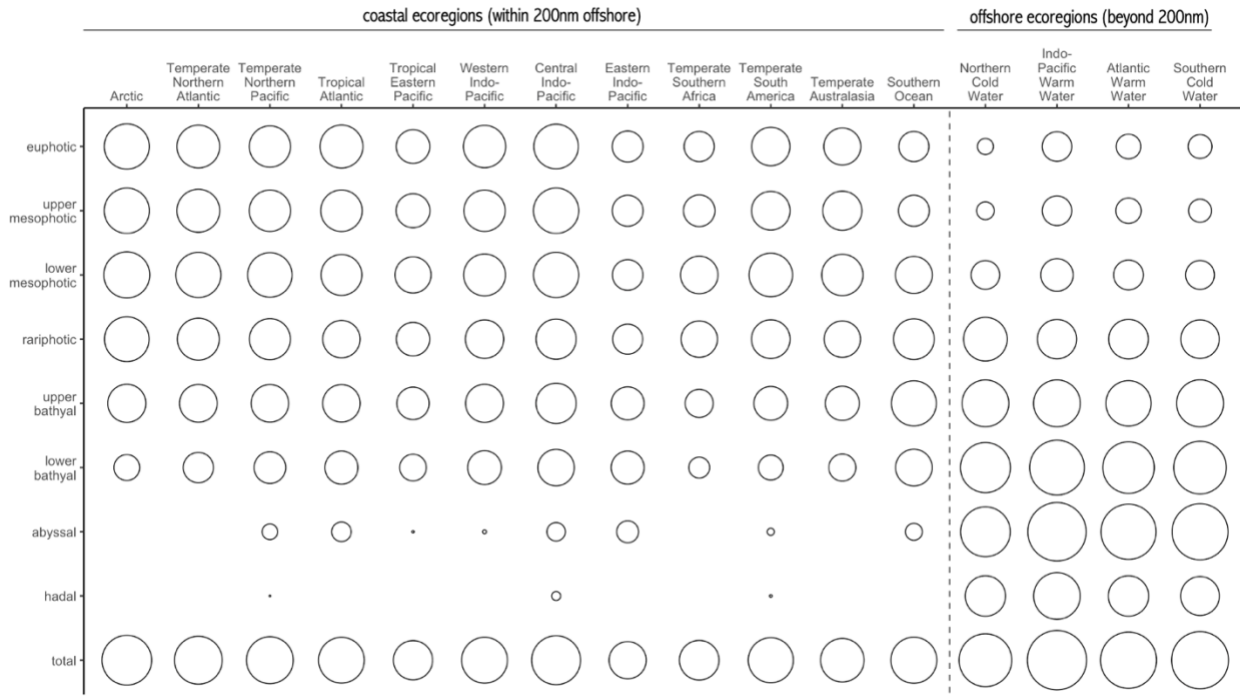

Fig. S4. Relative extent of each 3D realm. The size of circles is proportional to the spatial extent (log km^2) of each 3D realm.

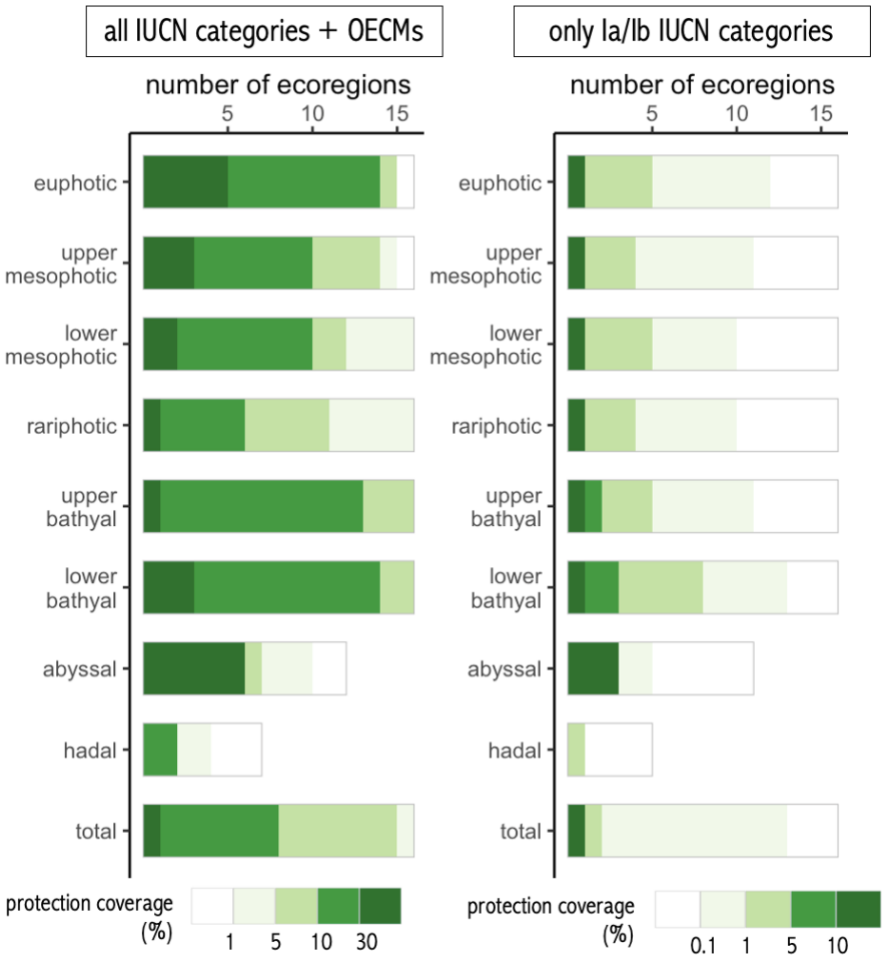

Fig. S5. Number of ecoregions having reached protection coverage targets for each depth realms. Left panel indicates protection coverage across all IUCN categories and OECMs, the right panel indicated protection coverage for Ia and Ib IUCN categories only.

Table S1. Description of IUCN categories as given by the World Database of Protected Areas.

IUCN category	Description
Ia – Strict Nature Reserve	Human visitation, use and impact are strictly controlled and limited to ensure protection of conservation values
Ib – Wilderness Area	Area with minimal human influence protected and managed to preserve their natural condition.
II- National Park	Large natural area managed to protect large-scale ecological processes while allowing for cultural, scientific and visiting activities.
III – Natural Monument or Feature	Area managed to protect a specific natural monument.
IV- Habitat/Species Management Area	Area managed to protect particular species or habitats, often involving active restoration.
V- Protected Landscape/seascape	Area managed to sustainably preserve culturally important human uses and interactions with the landscape.
VI – Protected area with sustainable use of natural resource	Area managed to conserve ecosystems together with associated cultural values and traditional resource management systems.

Table S2. Description of fishing gear categories as given by the Global Fishing Watch.

Gear category	GFW description
fishing	a combination of vessels of unknown fishing gear
fixed gear	a category that includes potential set longlines, set gillnets and pots and traps
pots and traps	vessel that deploys pots (small, portable traps) or traps to catch fish
set longlines	vessel that fishes by setting longlines anchored to the seafloor. These lines have shorter hooked, typically baited, lines hanging from them
set gillnets	vessel that fishes by setting gillnets anchored to the seafloor
trawlers	trawlers, all types
dredge fishing	vessel that tows a dredge and scrapes up edible bottom dwellers such as scallops or oysters
drifting longlines	drifting longlines
driftnets	
pole and line	vessel from which people fish with pole and line
squid jigger	squid jiggers, mostly large industrial pelagic operating vessels
trollers	vessel that tows multiple fishing lines
tuna purse seines	large purse seines primarily fishing for tuna
purse seines	purse seines, both pelagic and demersal
other purse seines	purse seiners fishing for mackerel, anchovies, etc, often smaller and operating nearer the coast than tuna purse seines.
seiners	vessels using seine nets, including potential purse seine vessels targeting tuna and other species, as well as danish and other seines
other seines	danish seines and other seiners not using purse seines.

Table S3. Depth range of fishing gear types registered in the Global Fishing Watch. Table A presents depth range for benthic fishing gear and Table B for pelagic fishing gear.

A	traps	dredge fishing	demersal seines	set gillnets	pots	set longlines	bottom trawlers
euphotic (0-30m)	x	x	x	x	x	x	x
up mesophotic (30-60m)	x	x	x	x	x	x	x
low mesophotic (60-150m)		x	x	x	x	x	x
rariphotic (150-300)			x	x	x	x	x
up bathyal (300-1000m)					x	x	x
low bathyal (1000-3500m)							x
abyssal (3500-6000m)							
hadal (< 6000m)							
min depth	5	6	0	15	10	80	20
max depth	50	200	300	150	1000	270	3000

B	trollers	driftnets	pole and line	seines	squid jigger	mid-water trawlers	drifting longlines
epipelagic (0-200)	x	x	x	x	x	x	x
mesopelagic (200-1500)						x	x
bathypelagic (1500-3500)							
abyssopelagic (3500-6000)							
hadopelagic (< 600 m)							
min depth	0	10	0	0	60	10	25
max depth	50	45	30	300	120	1000	350

Table S4. Total area (km^2) and protection coverage (%) across benthic depth realms.

benthic depth realm	lower bathymetric limit (m)	total area (km^2)	protection coverage (all IUCN categories, %)	protection coverage (Ia/Ib categories only, %)	Total fishing effort (10^6 hours $year^{-1}$)
euphotic	-30	6.4E+06	15.1	1.2	15.3 ± 0.9
upper mesophotic	-60	6.6E+06	10.6	0.9	8.9 ± 0.5
lower mesophotic	-150	1.0E+07	8.4	0.6	10.1 ± 0.4
rariphotic	-300	5.9E+06	8.4	1.0	4.2 ± 0.05
upper bathyal	-1000	1.4E+07	16.3	0.6	5.2 ± 0.3
lower bathyal	-3500	8.0E+07	11.9	0.8	3.5 ± 0.04
abyssal	-6000	2.4E+08	5.8	0.6	8.4 ± 0.2
hadal	-11000	3.7E+06	11.1	3.1	0.2 ± 0.03

CHAPTER 3 APPENDIX

Supplementary information on study sites

Curaçao and Bonaire are two neighboring oceanic islands in the westernmost part of the Lesser Antilles, situated 60 km north of Venezuela. Islands are separated from the South American mainland and from each other by a deep-water trench (4000 - 5000 m) from which they experience strong influence of deep oceanic waters (Frade et al., 2019). Both islands experience a semi-arid climate, with average annual precipitation below 500 mm and sea surface temperature varying between 26 and 29 °C . Both islands are surrounded by steep fringing reefs on their leeward sides and intermittent patches of mangrove, and display some of the best coral cover of the Caribbean (Jackson et al., 2014). Bonaire and Curaçao harbor among the best studied mesophotic ecosystems of the world, thanks to ongoing research conducted since the 1970s, a result of easily accessible deep reefs and favorable geopolitical context (Frade et al., 2019). Curaçao is the largest island of the Dutch West Indies at 61 km long and 14 km wide, for a total surface of 444 km^2. The island is surrounded by a fringing reef 20–250 m from the coast, covering a total surface of 7.85 km^2 (Pinheiro et al., 2016). The estimated mean coral cover in Curacao averages 20-30 % on shallow southern reefs where the submersible dives were conducted (Jackson et al., 2014). Bonaire is located immediately East of Curaçao. It is 40 km long and 12 km wide, for a total surface of 288 km^2, and displays coral cover of 38%.

Sint Eustatius (Statia) is a 21 km^2 island situated in the northeastern Caribbean Sea. Statia is surrounded by a narrow 200 m shelf, which is most extensive on the leeward, western side. Statia displays low habitat diversity and poorly developed, low-relief coral reefs, in part due to the lack of deep embayment on the sheltered western side, required for the development of fringing and back-reefs (Robertson et al., 2020). At the sampling site a shallow reef flat extends to ~40-50 m depth before transitioning into the outer reef slope. All waters from the coast to the 30 m isobath are part of the St. Eustatius Marine Park, but only two reserves within the park are designated as no-take and no-anchoring. Shallow reef fish from Statia have been extensively sampled and are described in Robertson et al. (2020).

Roatán is an elongated island of ~ 85 km^2 offshore Honduras, which is part of the Mesoamerican Barrier Reef system. Roatan displays high habitat diversity, notably a combination of fringing- and barrier reefs separated from the island by lagoons, and extensive mangroves. The entire island is surrounded by a narrow ~1 km wide shelf. At the sampling site off Half-moon Bay, West End, a shallow lagoonal reef from 0 to ~20 m gives way to a steep (sometimes vertical) outer slope that extends down to >700 m within 2 km from shore.

These four sites fall within the same biogeographical province of the Greater Caribbean, commonly referred to as the Central Province, although Bonaire and Curaçao are at the very edge of this province and are sometimes associated with the Southern upwelling-affected Province of the Caribbean (Robertson & Cramer, 2014; Spalding et al., 2007). These sites represent three distinct ecoregions within the Great Caribbean province (Robertson and Cramer, 2014; Spalding et al., 2007): the Southern Caribbean (Curaçao and Bonaire), the Eastern Caribbean (Statia), and the Western Caribbean (Roatán).

Frade, P. R., Bongaerts, P., Baldwin, C. C., Trembanis, A. C., Bak, R. P. M., & Vermeij, M. J. A. (2019). Bonaire and Curaçao. In Y. Loya, K. A. Puglise, & T. C. L. Bridge (Eds.), *Mesophotic Coral Ecosystems* (Vol. 12, pp. 149–162). Springer International Publishing. https://doi.org/10.1007/978-3-319-92735-0_9

Jackson, E. J., Donovan, M., Cramer, K., & Lam, V. (2014). *Status and trends of Caribbean Coral Reefs: 1970-2012*. Global Coral Reef Monitoring Network, IUCN.

Pinheiro, H. T., Goodbody-Gringley, G., Jessup, M. E., Shepherd, B., Chequer, A. D., & Rocha, L. A. (2016). Upper and lower mesophotic coral reef fish communities evaluated by underwater visual censuses in two Caribbean locations. *Coral Reefs*, *35*(1), 139–151. https://doi.org/10.1007/s00338-015-1381-0

Robertson, D. R., & Cramer, K. L. (2014). Defining and Dividing the Greater Caribbean: Insights from the Biogeography of Shorefishes. *PLoS ONE*, *9*(7), e102918. https://doi.org/10.1371/journal.pone.0102918

Robertson, D. R., Estapé, C. J., Estapé, A. M., Peña, E., Tornabene, L., & Baldwin, C. C. (2020). The marine fishes of St Eustatius Island, northeastern Caribbean: An annotated, photographic catalog. *ZooKeys*, *1007*, 145–180. https://doi.org/10.3897/zookeys.1007.58515

Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M., Halpern, B. S., Jorge, M. A., Lombana, A., Lourie, S. A., Martin, K. D., McManus, E., Molnar, J., Recchia, C. A., & Robertson, J. (2007). Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas. *BioScience*, *57*(7), 573–583. https://doi.org/10.1641/B570707

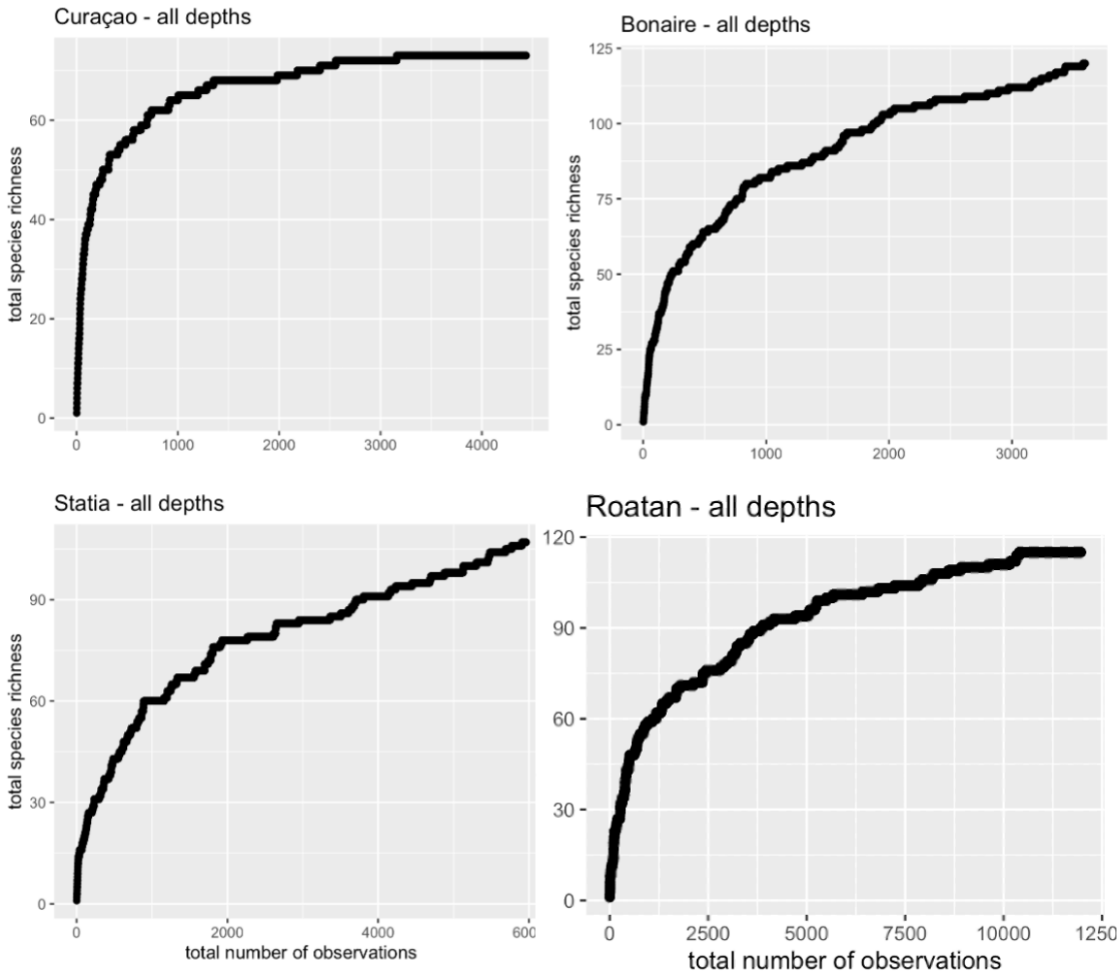

Figure S1: Rarefaction curves associated with the sampling effort of deep-reef fish diversity at the four studied sites, between 40 and 300 m.

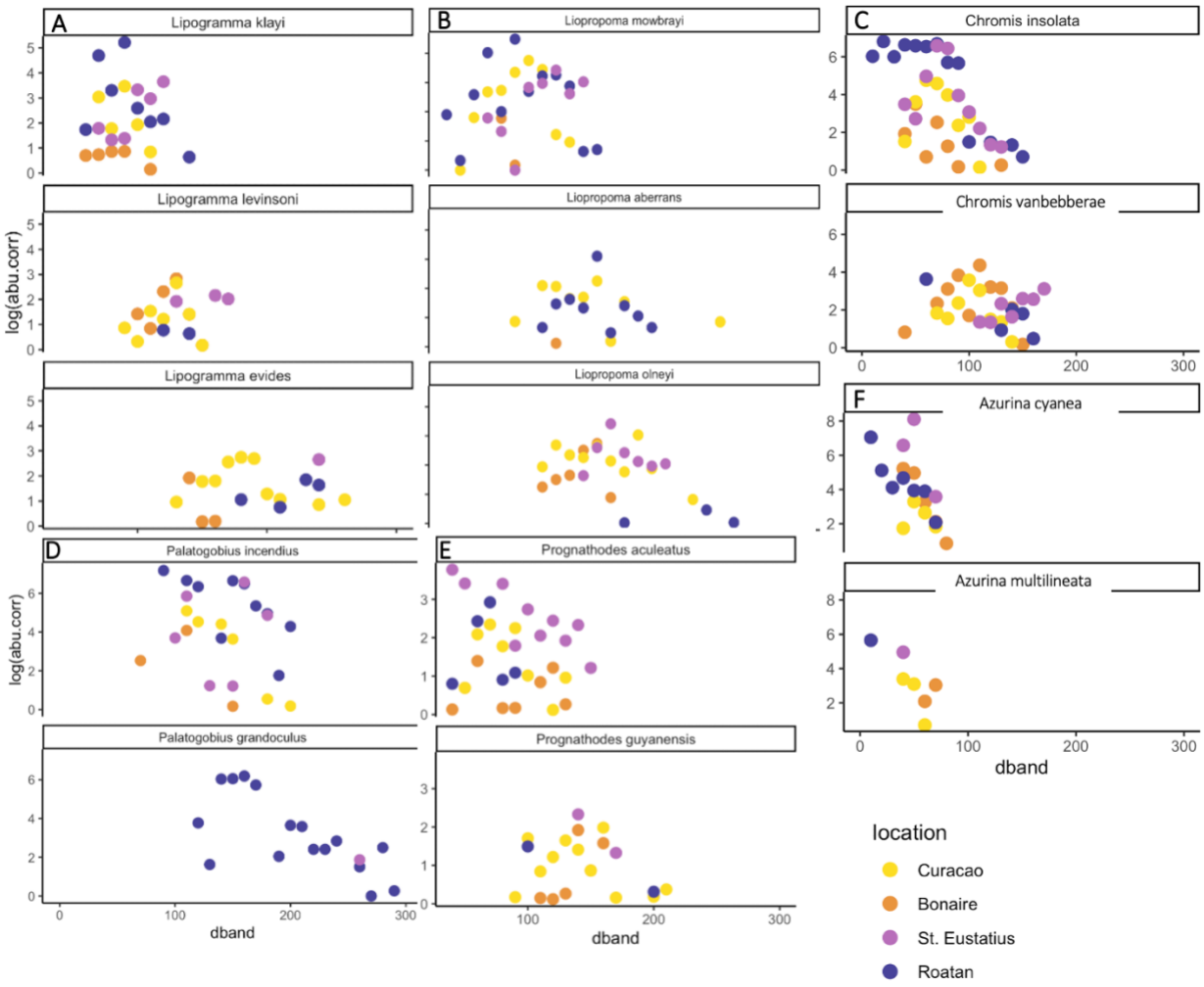

Fig S2. Depth distribution of congeners at the four study sites. Each dot represents abundance (log-transformed) at a given 10 m depth bin and location. Color of dots indicate location. The genera investigated from left to right and top to bottom are *Lipogramma* (A), *Liopropoma* (B), *Chromis* (C), *Palatogobius* (D), *Prognathodes* (E), *Azurina* (F).

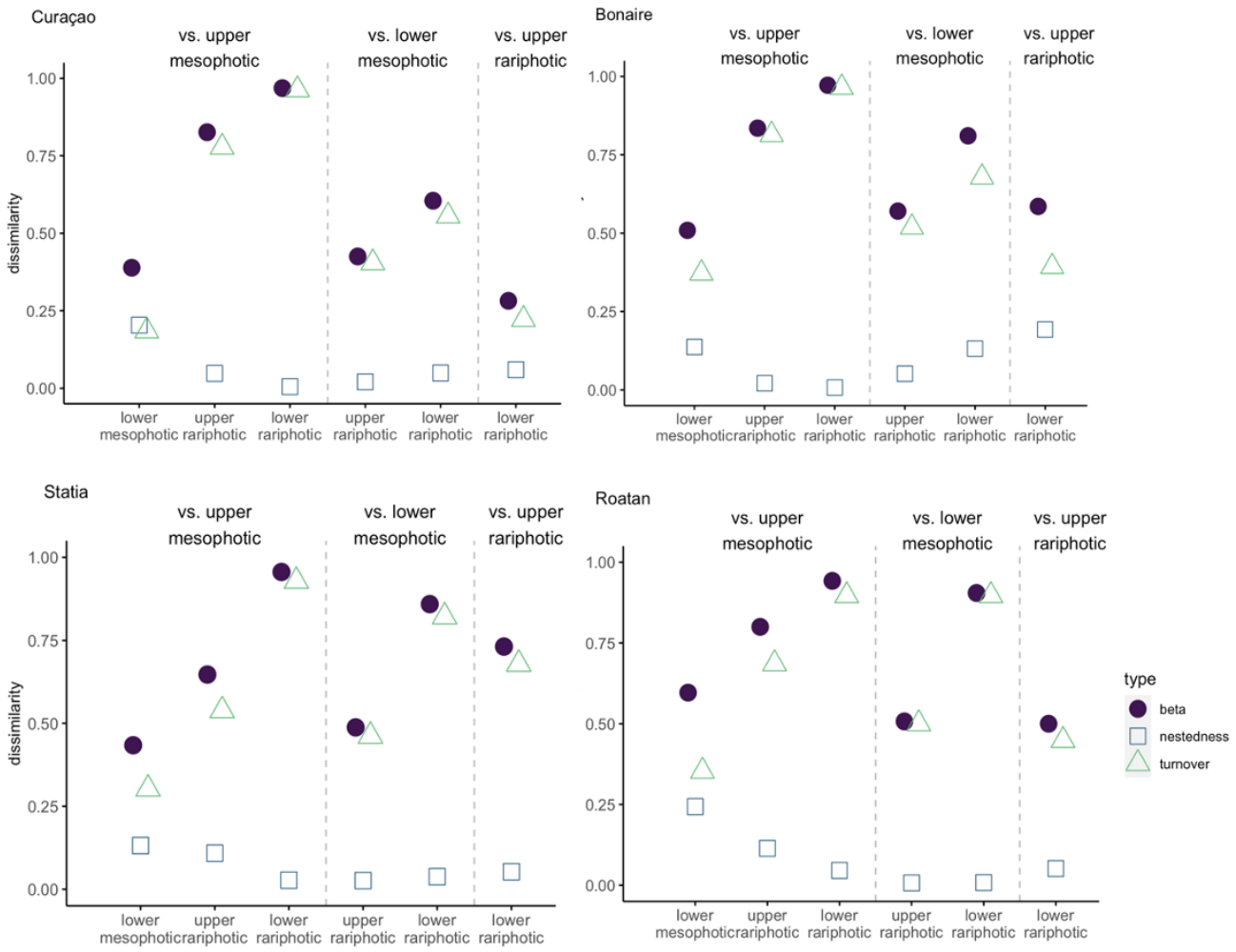

Figure S3: Beta-diversity and its components, nestedness and turnover, between reef-fish communities of different depth zones at each study site. Shape and color of points indicate values of overall beta-diversity (purple circles), nestedness (blue square), and turnover (green triangle).

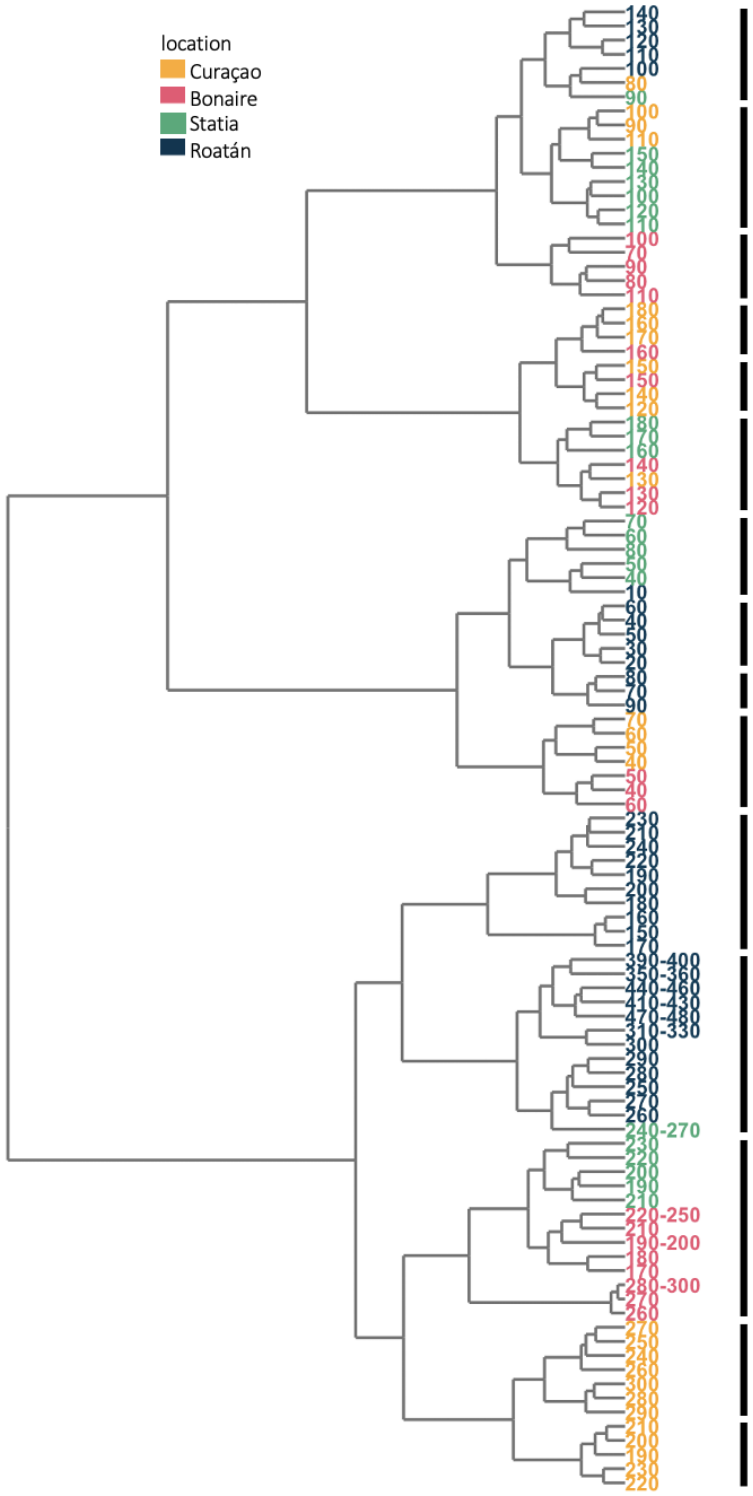

Figure S4: Trans-site hierarchical clustering analysis of deep-reef fish communities from 10 to 480 m. Length of branches in the dendrogram is commensurate to the dissimilarity between depth bins based on Bray-Curtis distance. Font color indicates sites. Significant clusters (SIMPROF analyses, Ward linkage) are indicated by thick black vertical lines.

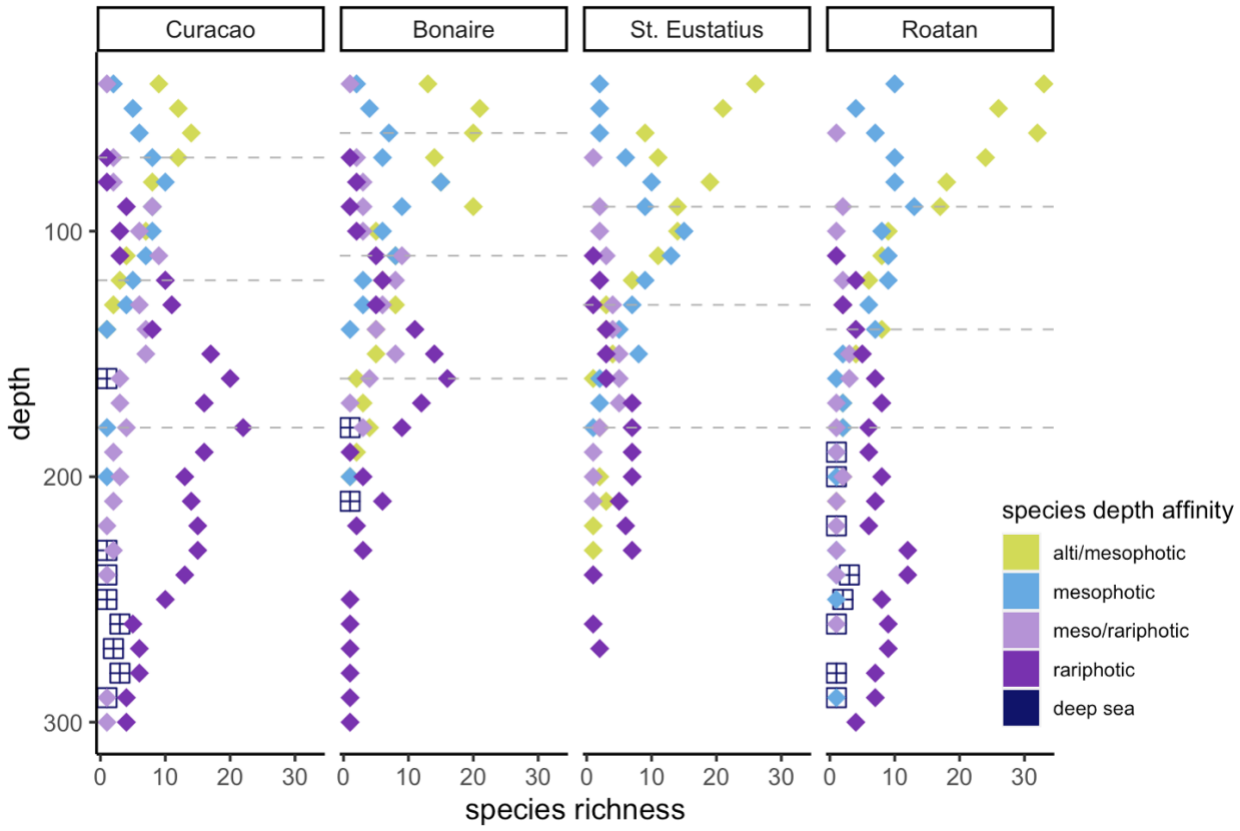

Figure S5: Contribution of depth affinity groups to fish richness across depth at the four study locations. Colors and symbols indicate depth affinities. Dashed lines represent the depth of site-specific community breaks.

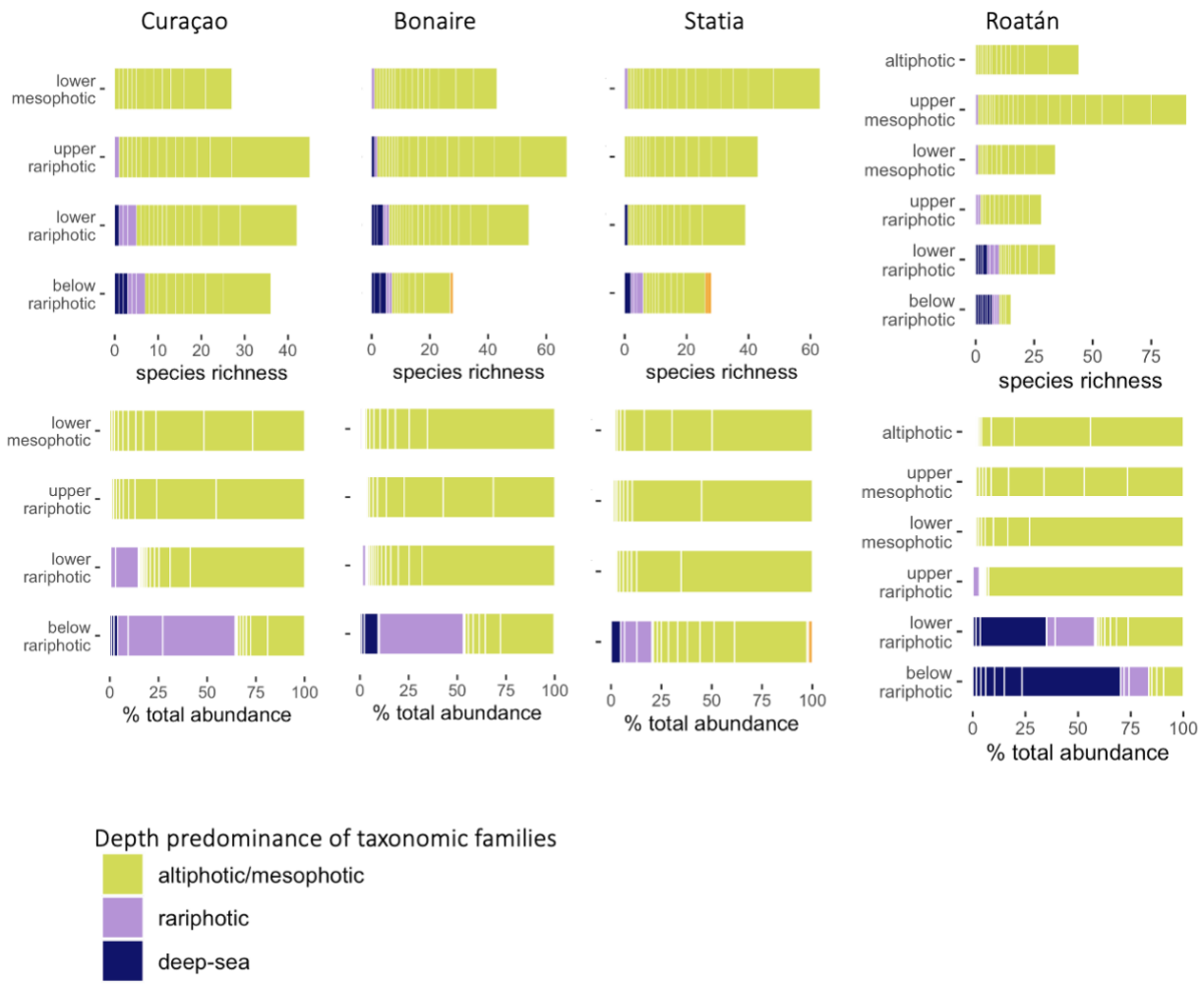

Figure S6: Depth-zone predominance of fish families in each depth zone and at each site and their contribution to species richness (top panels) and abundance (bottom panels). White lines in barplots distinguish species from different families. Filling colors indicate the depth-zone predominance of taxonomic families.

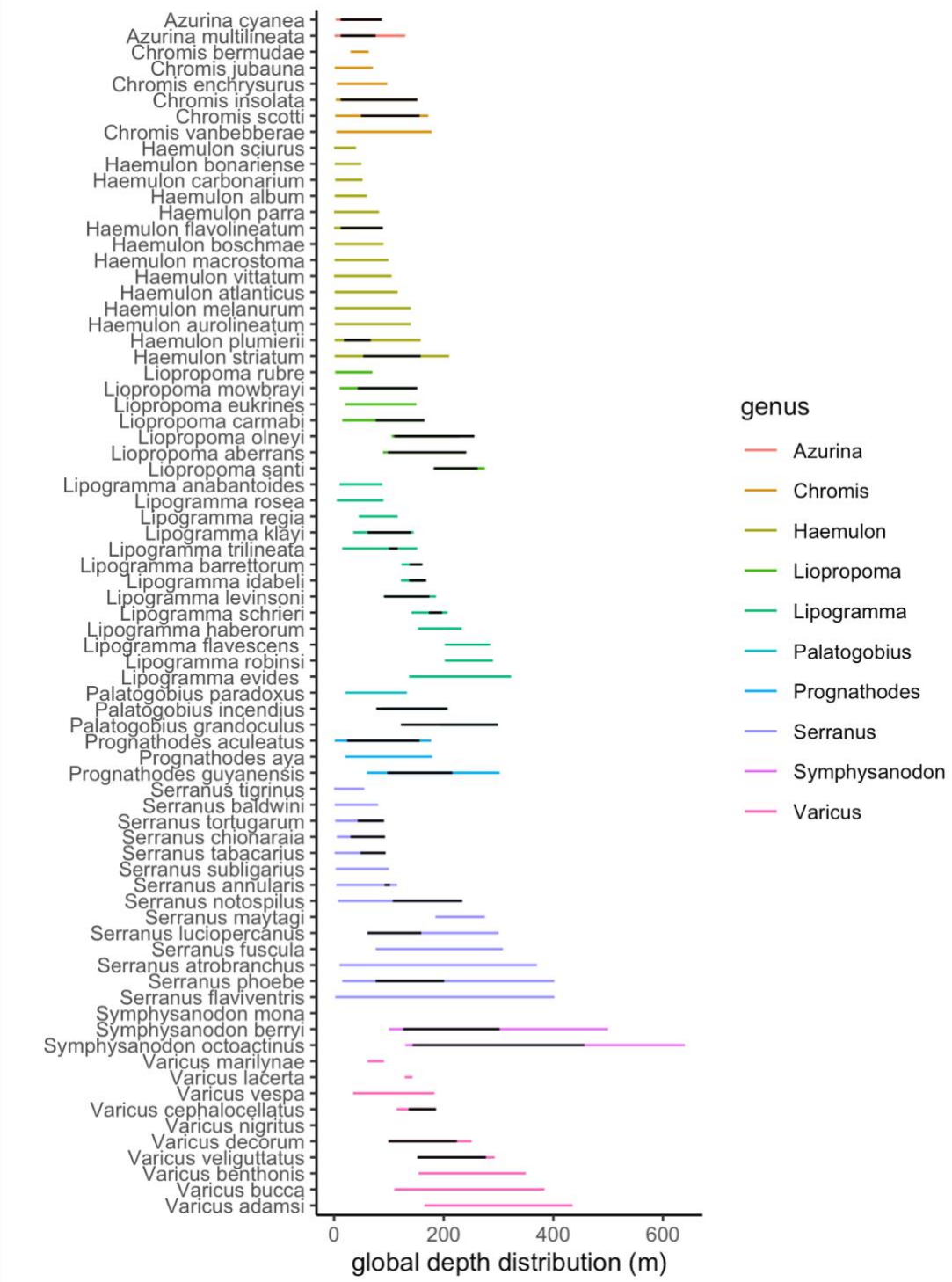

Figure S7: Depth range of the ten genera displayed in Figure 7. Colored lines represent global depth ranges (global minima and maxima), and black lines represent depth ranges observed at the sampling sites of this study. Colors denote distinct genera.

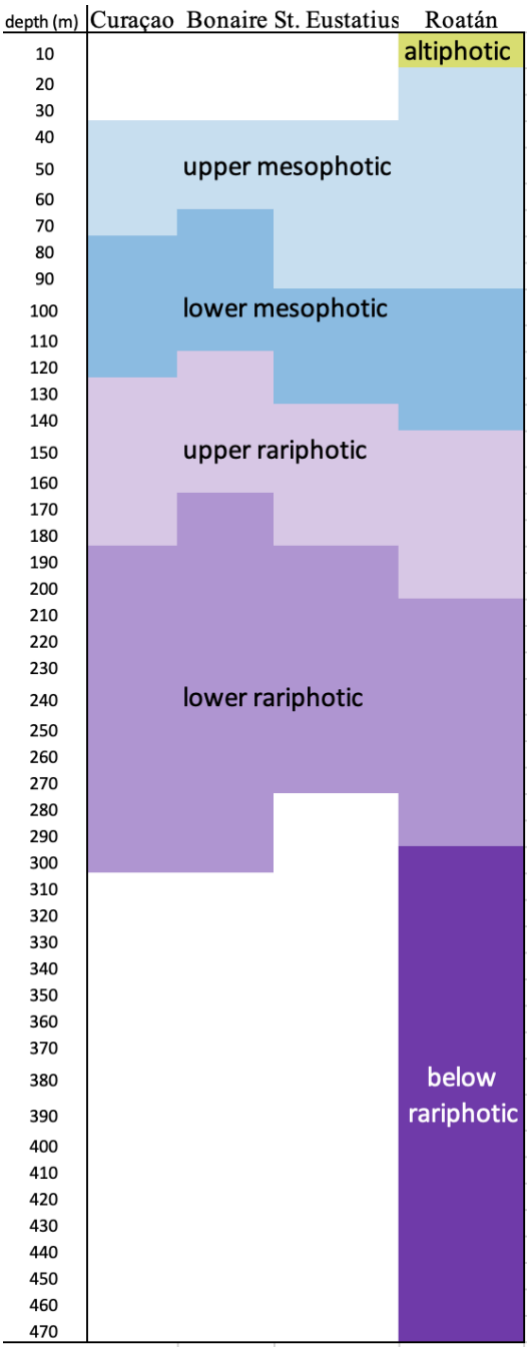

Figure S8: Site-specific limits of depth zones, as informed from fish-community dissimilarity analyses.

Table S1: List of species observed organized by taxonomic family. The predominant depth of families, the predominant depth of species, the presence (1) / absence (0) of the species at the four sites studied, and the overall minimal and maximal depths at which these species have been observed in the Greater Caribbean (Robertson and Van Tassell, 2023). The predominant depth of species are coded as follows: altiphotic/mesophotic (AM), mesophotic (M), mesophotic/rariphotic (MR), rariphotic (R), deep sea (DS). Species new to science at the time of their observation are indicated in bold font.

species	family predominant depth	species predominant depth	Curaçao	Bonaire	Statia	Roatán	overall min depth	overall max depth
ACANTHURIDAE								
Acanthurus chirurgus	altiphotic/mesophotic	AM	0	0	1	1	0	107
Acanthurus coeruleus	altiphotic/mesophotic	AM	0	1	1	1	0	76
Acanthurus tractus	altiphotic/mesophotic	AM	0	1	1	1	0	117
ACROPOMATIDAE								
Synagrops bellus	deep-sea	DS	0	1	0	1	60	1174
Synagrops egretta	deep-sea	DS	0	1	0	0	NA	NA
Verilus sordidus	deep-sea	MR	0	0	0	1	100	600
ANTIGONIIDAE								
Antigonia capros	rariphotic	R	1	0	1	0	27	900
APOGONIDAE								
Apogon gouldi	altiphotic/mesophotic	MR	1	1	0	1	55	262
Apogon lachneri	altiphotic/mesophotic	AM	0	0	0	1	5	106
Apogon maculatus	altiphotic/mesophotic	AM	0	1	0	0	1	128
Apogon pillionatus	altiphotic/mesophotic	AM	0	0	1	0	7	122
Apogon pseudomaculatus	altiphotic/mesophotic	AM	0	1	0	0	1	134
Paroncheilus affinis	altiphotic/mesophotic	M	1	1	1	0	15	300

AULOPIDAE								
Aulopus filamentosus	rariphotic	MR	0	0	0	1	50	1000
AULOSTOMIDAE								
Aulostomus maculatus	altiphotic/mesophotic	AM	0	0	0	1	2	300
BALISTIDAE								
Canthidermis sufflamen	altiphotic/mesophotic	AM	0	0	1	1	0.5	300
Melichthys niger	altiphotic/mesophotic	AM	0	0	0	1	0	406
Xanthichthys ringens	altiphotic/mesophotic	M	1	1	1	0	0	190
BEMBROPIDAE								
Bembrops sp.	rariphotic	R	0	0	0	1	NA	NA
Chrionema squamentum	rariphotic	R	1	1	1	1	115	306
CALLIONYMIDAE								
Foetorepus agassizii	altiphotic/mesophotic	R	1	0	0	0	NA	NA
CARANGIDAE								
Caranx bartholomaei	altiphotic/mesophotic	AM	0	1	0	0	0	104
Caranx ruber	altiphotic/mesophotic	AM	0	1	1	1	0	155
Caranx latus	altiphotic/mesophotic	AM	0	1	0	1	0	151
Caranx lugubris	altiphotic/mesophotic	M	0	0	1	1	3	380
Decapterus sp.	altiphotic/mesophotic	AM	0	0	0	1	NA	NA
Seriola dumerili	altiphotic/mesophotic	R	0	0	0	1	3	385
Seriola rivoliana	altiphotic/mesophotic	MR	0	0	1	0	3	340
Trachinotus goodei	altiphotic/mesophotic	M	0	0	0	1	0	40
CHAETODONTIDAE								
Chaetodon capistratus	altiphotic/mesophotic	AM	1	0	1	1	0	130

Chaetodon ocellatus	altiphotic/mesophotic	AM	0	0	0	1	0	110
Chaetodon sedentarius	altiphotic/mesophotic	AM	0	1	1	1	0	172
Chaetodon striatus	altiphotic/mesophotic	AM	0	1	1	1	0	151
Prognathodes aculeatus	altiphotic/mesophotic	M	1	1	1	1	1	177
Prognathodes guyanensis	altiphotic/mesophotic	MR	1	1	1	1	60	302
CHAUNACIDAE								
Chaunax pictus	deep-sea	DS	1	0	0	1	200	1183
CYCLOPSETTIDAE								
Syacium gunteri	generalist	R	0	1	0	0	10	174
EPIGONIDAE								
Epigonidae sp.	deep-sea	MR	0	0	0	1	NA	NA
Sphyraenops bairdianus	deep-sea	DS	1	0	0	0	200	1750
FISTULARIIDAE								
Fistularia sp.	altiphotic/mesophotic	AM	0	1	1	0	NA	NA
GEMPYLIDAE								
Neoepinnula americana	deep-sea	DS	0	0	0	1	166	1027
GOBIESOCIDAE								
Derilissus lombardii	altiphotic/mesophotic	M	0	0	1	0	30	132
GOBIIDAE								
Antilligobius nikkiae	altiphotic/mesophotic	M	1	1	1	1	73	205
Bollmannia boqueronensis	altiphotic/mesophotic	M	0	1	0	0	14	112
Bollmannia eigenmanni	altiphotic/mesophotic	M	0	1	0	0	37	200
Coryphopterus curasub	altiphotic/mesophotic	M	1	1	0	0	70	97
Coryphopterus personatus	altiphotic/mesophotic	AM	0	0	0	1	2	73

Elacatinus chancei	altiphotic/mesophotic	AM	0	0	1	1	4	119
Elacatinus lobeli	altiphotic/mesophotic	AM	0	0	0	1	2	27
Gnatholepis thompsoni	altiphotic/mesophotic	AM	0	1	1	1	0	85
Oxyurichthys stigmalophius	altiphotic/mesophotic	M	0	1	0	0	2	101
Palatogobius grandoculus	altiphotic/mesophotic	R	0	0	1	1	194	299
Palatogobius incendius	altiphotic/mesophotic	MR	1	1	1	1	88	205
Palatogobius paradoxus	altiphotic/mesophotic	R	0	0	0	1	20	133
Pinnichthys aimoriensis	altiphotic/mesophotic	MR	0	1	1	0	70	163
Priolepis hipoliti	altiphotic/mesophotic	AM	0	1	0	0	2	117
Psilotris laurae	altiphotic/mesophotic	R	0	1	0	0	114	250
Ptereleotris helenae	altiphotic/mesophotic	AM	1	1	1	1	3	180
Varicus adamsi	altiphotic/mesophotic	R	0	0	0	1	165	435
Varicus cephalocellatus	altiphotic/mesophotic	R	0	1	1	0	114	186
Varicus decorum	altiphotic/mesophotic	R	1	1	0	0	99	251
Varicus veliguttatus	altiphotic/mesophotic	R	1	0	1	1	152	293
Vomerogobius flavus	altiphotic/mesophotic	M	0	0	0	1	14	42
GRAMMATIDAE								
Gramma linki	altiphotic/mesophotic	M	0	0	1	1	20	180
Gramma loreto	altiphotic/mesophotic	AM	1	1	0	1	2	130
Gramma melacara	altiphotic/mesophotic	M	0	0	0	1	15	180
Lipogramma barrettorum	altiphotic/mesophotic	R	1	0	0	0	NA	NA
Lipogramma evides	altiphotic/mesophotic	R	1	1	1	1	NA	NA
Lipogramma flavescens	altiphotic/mesophotic	MR	0	0	0	1	NA	NA
Lipogramma haberi	altiphotic/mesophotic	R	1	0	0	0	NA	NA

Lipogramma idabeli	altiphotic/mesophotic	MR	0	0	0	1	122	165
Lipogramma klayi	altiphotic/mesophotic	M	1	1	1	1	NA	NA
Lipogramma levinsoni	altiphotic/mesophotic	MR	1	1	1	1	NA	NA
Lipogramma regium	altiphotic/mesophotic	M	0	0	1	0	NA	NA
Lipogramma schrieri	altiphotic/mesophotic	R	1	0	0	0	NA	NA
Lipogramma trilineata	altiphotic/mesophotic	M	0	0	1	0	NA	NA
HAEMULIDAE								
Anisotremus surinamensis	altiphotic/mesophotic	AM	0	1	0	0	0	109
Anisotremus virginicus	altiphotic/mesophotic	AM	0	0	0	1	1	112
Haemulon bonariense	altiphotic/mesophotic	AM	0	0	0	1	1	50
Haemulon chrysargyreum	altiphotic/mesophotic	AM	0	1	0	0	0	42
Haemulon flavolineatum	altiphotic/mesophotic	AM	1	1	0	1	0	89
Haemulon plumierii	altiphotic/mesophotic	AM	0	0	0	1	1	158
Haemulon sciurus	altiphotic/mesophotic	AM	0	0	0	1	0	40
Haemulon striatum	altiphotic/mesophotic	AM	1	1	1	1	1	210
Haemulon vittata	altiphotic/mesophotic	AM	1	0	0	0	0	105
HOLOCENTRIDAE								
Corniger spinosus	altiphotic/mesophotic	R	1	1	1	1	42	275
Flammeo marianus	altiphotic/mesophotic	M	1	1	1	1	15	151
Holocentrus adscensionis	altiphotic/mesophotic	AM	0	1	1	0	1	274
Holocentrus rufus	altiphotic/mesophotic	AM	0	0	1	1	1	330
Myripristis jacobus	altiphotic/mesophotic	AM	1	1	1	0	1	210
Neoniphon coruscum	altiphotic/mesophotic	AM	0	1	0	0	2	140
Ostichthys trachypoma	altiphotic/mesophotic	R	1	1	1	1	37	550

Sargocentron bullisi	altiphotic/mesophotic	MR	0	1	0	0	0	128
Sargocentron poco	altiphotic/mesophotic	AM	0	0	0	1	2	152
LABRIDAE								
Bodianus pulchellus	altiphotic/mesophotic	AM	0	0	0	1	10	120
Bodianus rufus	altiphotic/mesophotic	AM	0	1	1	1	1	130
Clepticus parrae	altiphotic/mesophotic	AM	1	1	1	1	0	145
Decodon puellaris	altiphotic/mesophotic	R	1	0	1	0	18	275
Decodon shallow	altiphotic/mesophotic	MR	1	1	1	0	NA	NA
Halichoeres bathyphilus	altiphotic/mesophotic	M	0	1	1	0	18	275
Halichoeres garnoti	altiphotic/mesophotic	AM	0	1	1	1	2	130
Halichoeres maculipinna	altiphotic/mesophotic	AM	0	0	0	1	2	50
Halichoeres pictus	altiphotic/mesophotic	AM	0	0	0	1	5	55
Lachnolaimus maximus	altiphotic/mesophotic	AM	0	0	0	1	0	91
Polylepion sp.	altiphotic/mesophotic	MR	1	0	0	1	NA	NA
Scarus iseri	altiphotic/mesophotic	AM	0	0	0	1	0	68
Scarus taeniopterus	altiphotic/mesophotic	AM	0	1	1	1	1	107
Scarus vetula	altiphotic/mesophotic	AM	0	1	0	1	1	71
Sparisoma atomarium	altiphotic/mesophotic	AM	0	0	0	1	0	106
Sparisoma aurofrenatum	altiphotic/mesophotic	AM	0	0	1	1	1	117
Sparisoma chrysopterum	altiphotic/mesophotic	AM	0	0	0	1	1	61
Sparisoma rubripinne	altiphotic/mesophotic	AM	0	0	0	1	0	60
Sparisoma viride	altiphotic/mesophotic	AM	0	1	1	1	0	107
Thalassoma bifasciatum	altiphotic/mesophotic	AM	0	0	1	1	0	130
LABRISOMIDAE								

Haptoclinus dropi	altiphotic/mesophotic	MR	1	0	0	1	157	274
LATILIDAE								
Caulolatilus dooleyi	deep-sea	AM	0	1	0	0	208	256
LUTJANIDAE								
Apsilus dentatus	altiphotic/mesophotic	M	0	0	0	1	12	300
Etelis oculatus	altiphotic/mesophotic	R	0	0	0	1	100	533
Ocyurus chrysurus	altiphotic/mesophotic	AM	0	1	0	1	0	180
Pristipomoides aquilonaris	altiphotic/mesophotic	R	0	1	0	0	24	650
Pristipomoides freemani	altiphotic/mesophotic	R	0	1	0	0	61	220
Pristipomoides macrophthalmus	altiphotic/mesophotic	R	1	0	1	0	100	611
MALACANTHIDAE								
Malacanthus plumieri	rariphotic	AM	0	1	1	1	10	184
MONACANTHIDAE								
Cantherhines sp.	altiphotic/mesophotic	AM	0	0	0	1	NA	NA
MORIDAE								
Physiculus fulvus	deep-sea	R	0	1	0	0	69	800
MULLIDAE								
Mulloidichthys martinicus	altiphotic/mesophotic	AM	0	1	1	1	1	135
Pseudupeneus maculatus	altiphotic/mesophotic	AM	0	0	0	1	1	110
MURAENIDAE								
Gymnothorax funebris	altiphotic/mesophotic	AM	0	1	0	0	0	286
Gymnothorax moringa	altiphotic/mesophotic	AM	0	1	0	0	0	304
Gymnothorax ocellatus	altiphotic/mesophotic	AM	0	1	1	0	1	445
Muraena retifera	altiphotic/mesophotic	AM	0	1	0	0	20	169

BATHYCLUPEIDAE								
Bathyclupea sp.	deep-sea	DS	0	0	0	1	NA	NA
OGCOCEPHALIDAE								
Ogcocephalus corniger	deep-sea	R	0	0	1	0	29	253
Ogcocephalus parvus	deep-sea	R	0	1	0	0	29	360
Zalieutes mcgintyi	deep-sea	R	0	0	1	0	90	660
OPHIDIIDAE								
Brotula barbata	generalist	R	0	0	1	0	1	650
OPISTOGNATHIDAE								
Opistognathus aurifrons	altiphotic/mesophotic	AM	0	0	0	1	2	65
Opistognathus schrieri	altiphotic/mesophotic	R	1	0	0	1	152	152
OSTRACIIDAE								
Acanthostracion polygonius	altiphotic/mesophotic	AM	0	0	1	0	2	121
Acanthostracion quadricornis	altiphotic/mesophotic	AM	0	0	1	1	2	108
Lactophrys trigonus	altiphotic/mesophotic	AM	0	0	0	1	1	110
Lactophrys triqueter	altiphotic/mesophotic	AM	0	1	0	1	2	79
PARALICHTHYIDAE								
Gastropsetta frontalis	generalist	AM	0	0	1	0	35	212
POMACANTHIDAE								
Centropyge argi	altiphotic/mesophotic	AM	1	1	1	1	3	170
Holacanthus ciliaris	altiphotic/mesophotic	AM	0	1	1	1	1	128
Holacanthus tricolor	altiphotic/mesophotic	AM	0	0	1	1	1	143
Pomacanthus arcuatus	altiphotic/mesophotic	AM	0	1	0	1	1	101
Pomacanthus paru	altiphotic/mesophotic	AM	0	1	1	1	1	157

Abudefduf saxatilis	altiphotic/mesophotic	AM	0	0	0	1	0	41
Azurina cyanea	rariphotic	AM	1	1	1	1	3	87
Chromis vanbebberae	altiphotic/mesophotic	MR	1	1	1	1	4	178
Chromis insolata	altiphotic/mesophotic	AM	1	1	1	1	3	152
Azurina trieata	altiphotic/mesophotic	AM	1	1	1	1	1	130
Chromis scotti	altiphotic/mesophotic	M	1	1	1	1	2	172
Microspathodon chrysurus	altiphotic/mesophotic	AM	0	0	0	1	0	62
Stegastes diencaeus	altiphotic/mesophotic	AM	0	0	0	1	0	45
Stegastes partitus	altiphotic/mesophotic	AM	1	1	1	1	0	130
Stegastes planifrons	altiphotic/mesophotic	AM	0	0	0	1	0	43
Stegastes variabilis	altiphotic/mesophotic	AM	0	0	0	1	NA	NA
Stegastes xanthurus	altiphotic/mesophotic	MR	0	0	0	1	0	100
PRIACANTHIDAE								
Heteropriacanthus cruentatus	altiphotic/mesophotic	R	0	0	0	1	5	432
Priacanthus arenatus	altiphotic/mesophotic	R	0	0	1	1	10	587
Pristigenys alta	altiphotic/mesophotic	R	1	1	1	1	5	300
SCIAENIDAE								
Equetus lanceolatus	altiphotic/mesophotic	AM	0	1	1	0	2	230
SCORPAENIDAE								
Phenacoscorpius nebris	altiphotic/mesophotic	MR	0	0	0	1	64	606
Pontinus castor	altiphotic/mesophotic	R	1	1	1	1	32	549
Pontinus nematophthalmus	altiphotic/mesophotic	R	1	0	0	0	82	698
Pterois volitans	altiphotic/mesophotic	AM	0	0	0	1	2	304
Scorpaena brasiliensis	altiphotic/mesophotic	R	0	1	0	0	1	204

Scorpaenodes barrybrowni	altiphotic/mesophotic	R	0	1	0	0	95	235
Scorpaenodes caribbaeus	altiphotic/mesophotic	R	0	0	1	0	0	70
SERRANIDAE								
Anthias asperilinguis	altiphotic/mesophotic	MR	1	0	0	1	69	393
Baldwinella vivanus	altiphotic/mesophotic	R	1	1	1	0	20	610
Bathyanthias sp.	altiphotic/mesophotic	R	0	1	1	0	NA	NA
Bullisichthys caribbaeus	altiphotic/mesophotic	M	1	1	1	1	81	548
Centropristis fuscula	altiphotic/mesophotic	MR	1	0	1	0	NA	NA
Cephalopholis cruentata	altiphotic/mesophotic	AM	1	1	1	1	1	170
Cephalopholis fulva	altiphotic/mesophotic	AM	0	0	1	1	1	350
Choranthias tenuis	altiphotic/mesophotic	MR	1	1	0	0	55	915
Epinephelus striatus	altiphotic/mesophotic	AM	0	0	0	1	5	255
Epinephelus adscensionis	altiphotic/mesophotic	AM	0	0	1	0	2	189
Epinephelus guttatus	altiphotic/mesophotic	AM	0	0	1	0	2	181
Gonioplectrus hispanus	altiphotic/mesophotic	R	1	1	1	1	35	460
Hemanthias leptus	altiphotic/mesophotic	MR	1	1	0	0	35	640
Hypoplectrus chlorurus	altiphotic/mesophotic	AM	0	1	0	0	3	74
Hypoplectrus indigo	altiphotic/mesophotic	AM	0	0	1	1	3	54
Hypoplectrus nigricans	altiphotic/mesophotic	AM	0	0	0	1	1	67
Hypoplectrus puella	altiphotic/mesophotic	AM	0	0	1	1	3	90
Hyporthodus niveatus	altiphotic/mesophotic	R	0	1	0	0	10	1066
Jeboehlkia gladifer	altiphotic/mesophotic	R	1	1	0	1	100	395
Liopropoma aberrans	altiphotic/mesophotic	R	1	1	0	1	89	241
Liopropoma carmabi	altiphotic/mesophotic	M	0	1	1	0	15	165

Liopropoma mowbrayi	altiphotic/mesophotic	M	1	1	1	1	10	148
Liopropoma olneyi	altiphotic/mesophotic	R	1	1	1	1	105	229
Liopropoma santi	altiphotic/mesophotic	R	1	0	0	1	182	275
Mycteroperca bonaci	altiphotic/mesophotic	M	0	1	0	1	1	250
Mycteroperca interstitialis	altiphotic/mesophotic	M	0	1	0	1	2	150
Mycteroperca tigris	altiphotic/mesophotic	AM	0	0	0	1	3	135
Paranthias furcifer	altiphotic/mesophotic	AM	1	1	1	0	0	128
Plectranthias garrupellus	altiphotic/mesophotic	R	0	0	1	1	13	375
Plectranthias sp.	altiphotic/mesophotic	MR	1	1	1	0	NA	NA
Pronotogrammus martinicensis	altiphotic/mesophotic	MR	1	1	1	1	35	900
Rypticus maculatus	altiphotic/mesophotic	AM	0	1	0	0	3	100
Rypticus saponaceus	altiphotic/mesophotic	AM	0	1	1	1	0	213
Serranus annularis	altiphotic/mesophotic	AM	0	0	1	0	4	115
Serranus atrobranchus	altiphotic/mesophotic	R	0	1	0	0	10	370
Serranus chionaraia	altiphotic/mesophotic	AM	0	1	0	1	5	93
Serranus luciopercanus	altiphotic/mesophotic	M	1	1	1	1	60	300
Serranus notospilus	altiphotic/mesophotic	R	1	1	1	0	7	234
Serranus phoebe	altiphotic/mesophotic	R	1	1	1	0	15	402
Serranus tabacarius	altiphotic/mesophotic	AM	0	1	1	1	1	94
Serranus tigrinus	altiphotic/mesophotic	M	0	1	0	0	0	55
Serranus tortugarum	altiphotic/mesophotic	M	0	1	1	1	2	91
SPARIDAE								
Calamus calamus	altiphotic/mesophotic	AM	0	0	0	1	1	84
SPHYRAENIDAE								

Sphyraena barracuda	altiphotic/mesophotic	AM	0	1	1	1	0	450
SYMPHYSANODONTIDAE								
Symphysanodon berryi	rariphotic	R	1	0	1	1	100	500
Symphysanodon octoactinus	rariphotic	R	1	1	1	1	130	640
TETRAODONTIDAE								
Canthigaster jamestyleri	altiphotic/mesophotic	AM	1	1	0	1	14	218
Canthigaster rostrata	altiphotic/mesophotic	AM	0	1	1	1	1	155
Sphoeroides dorsalis	altiphotic/mesophotic	AM	0	0	1	0	8	324
TRACHICHTHYIDAE								
Gephyroberyx darwinii	deep-sea	DS	1	0	0	1	10	1250
TRIACANTHODIDAE								
Hollardia hollardi	deep-sea	DS	0	0	0	1	230	915
TRIGLIDAE								
Bellator brachychir	altiphotic/mesophotic	R	1	1	0	0	27	366
Bellator egretta	altiphotic/mesophotic	R	1	1	1	0	40	232
Peristedion brevirostre	altiphotic/mesophotic	R	0	1	0	0	55	550

Table S3. Species significantly contributing to the differences between depth zones at each site (SIMPER analyses). Only species that contributed to >5% of dissimilarity, with p-value<0.05 are shown.

		upper vs. lower mesophotic		lower mesophotic vs. upper rariphotic		upper vs. lower rariphotic	
	species	contribution	p-value	contribution	p-value	contribution	p-value
Bonaire	*Serranus phoebe*					0.052	0.002
	Pronotogrammus martinicensis					0.137	0.001
Curaçao	*Pronotogrammus martinicensis*					0.076	0.001
	Clepticus parrae	0.060	0.009				
	Symphysanodon octoactinus					0.052	0.001
	Palatogobius grandoculus					0.131	0.001
	Palatogobius incendius					0.200	0.001
Roatan	*Canthigaster rostrata*			0.063	0.028		
	Clepticus parrae	0.054	0.004				
	Chromis insolata	0.092	0.003				
	Pronotogrammus martinicensis					0.053	0.003
	Palatogobius incendius					0.097	0.002
	Antilligobius nikkiae					0.131	0.004
Statia	*Bullisichthys caribbaeus*			0.096	0.018		

Table S4: Kruskal-Wallis and Wilcoxon rank sum test assessing differences in the depth distribution of species within the same genera (depth~species).

	Kruskal-Wallis and Wilcoxon rank sum test		
	chi-squared	df	p-value
Lipogramma	241.5	2	<0.001
klayi - evides			<0.001
levinsoni - evides			<0.001
levinsoni - klayi			<0.001
Liopropoma	285.3	2	<0.001
aberrans-olneyi			0.04
mowbrayi-olneyi			<0.001
mowbrayi-aberrans			<0.001
Serranus	436.2	3	<0.001
phoebe-notospilus			<0.001
luciopercanus-notospilus			<0.001
tortugarum-notospilus			<0.001
luciopercanus-phoebe			<0.001
tortugarum-phoebe			<0.001
tortugarum-luciopercanus			<0.001

Table S5: Shapiro test of normality and Wilcoxon rank sum test (depth~species) for genera with two species evaluated.

	Shapiro test		Wilcoxon rank sum test	
	W	p-value	W	p-value
Azurina	0.83	<0.001	200158.00	<0.001
Chromis	0.95	<0.001	1096354.00	<0.001
Prognathodes	0.99	0.15	4873.00	<0.001
Palatogobius	0.92	<0.001	2688437.00	<0.001
Symphysonadon	0.94	<0.001	40802.00	<0.001
Haemulon	0.9	<0.001	11895.00	<0.001
Varicus	0.94	0.11	177.00	<0.001
Liopropoma	0.98	<0.001		
Lipogramma	0.87	<0.001		
Serranus	0.96	<0.001		

Table S6: Species observed below the rariphotic (300 - 480 m) in Roatán and their abundance before (raw) and after (normalized) correcting for sampling effort.

species	abundance normalized	raw abundance
Epigonidae sp.	162.059641	25
Hollardia hollardi	29.141401	7
Gephyroberyx darwinii	14.462922	4
Chrionema squamentum	32.363636	4
Jeboehlkia gladifer	24.272727	3
Neoepinnula americana	7.242157	2
Phenacoscorpius nebris	11.269481	2
Chaunax pictus	16.181818	2
Polylepion sp.	5.235294	1
Neoscopelus macrolepidotus	5.933333	1
Symphysanodon octoactinus	5.933333	1
Anthias asperilinguis	8.090909	1
Aulopus filamentosus	8.090909	1
Haptoclinus dropi	8.090909	1
Verilus sordidus	8.090909	1

Table S7: Summary statistics of the PERMANOVA testing for the effect of depth zone, site location, and the interaction between these two factors, on fish community structure.

	Df	Sum of squares	R2	F	Pr(>F)
depth zone	1	6.45	0.16	23.31	0.001
location	3	5.20	0.13	6.26	0.001
depth zone : location	3	3.57	0.08	4.30	0.001
Residual	95	26.27	0.63		
Total	102	41.49	1		

CHAPTER 4 APPENDIX

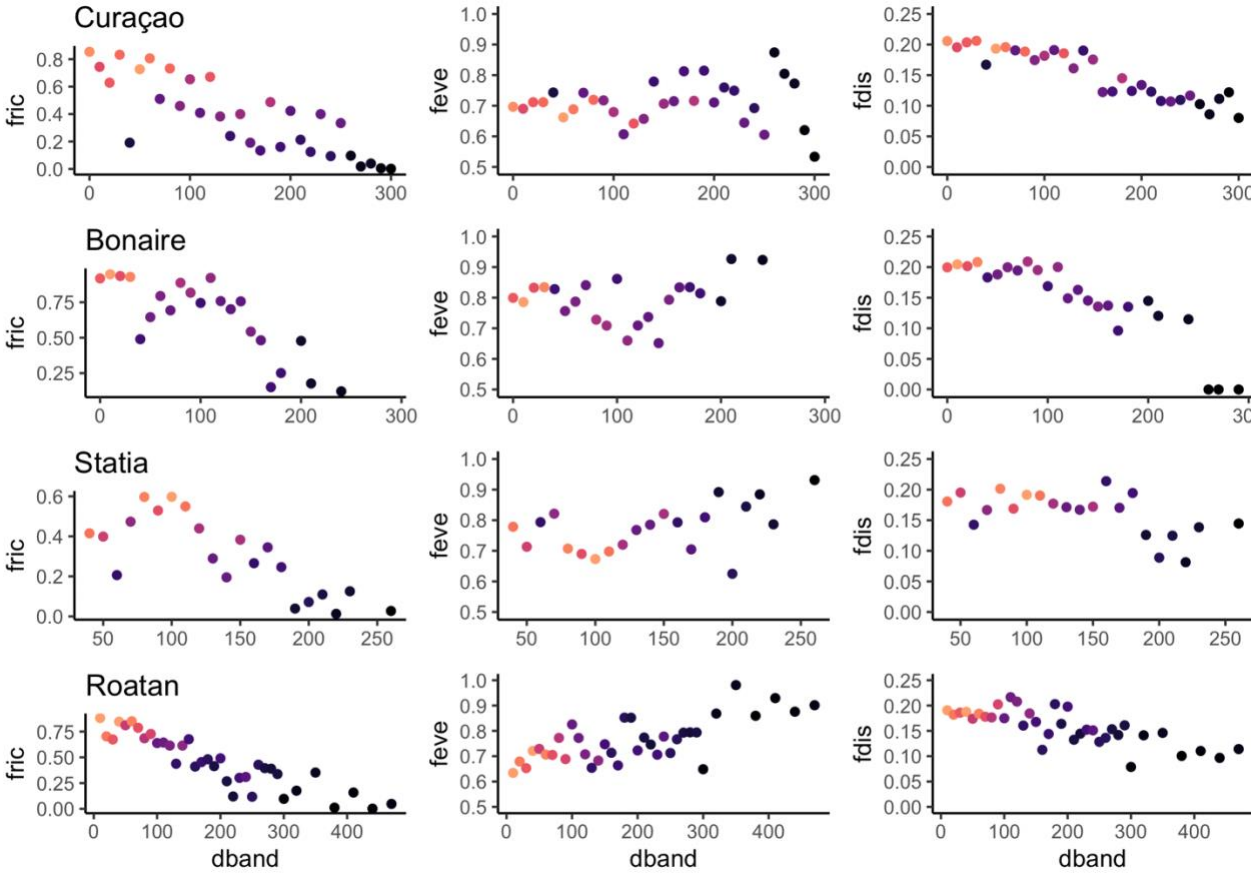

Fig. SA: Functional richness, evenness, and dispersion of reef-fish communities across depth at each of the four study sites. Colors denote species richness of communities.

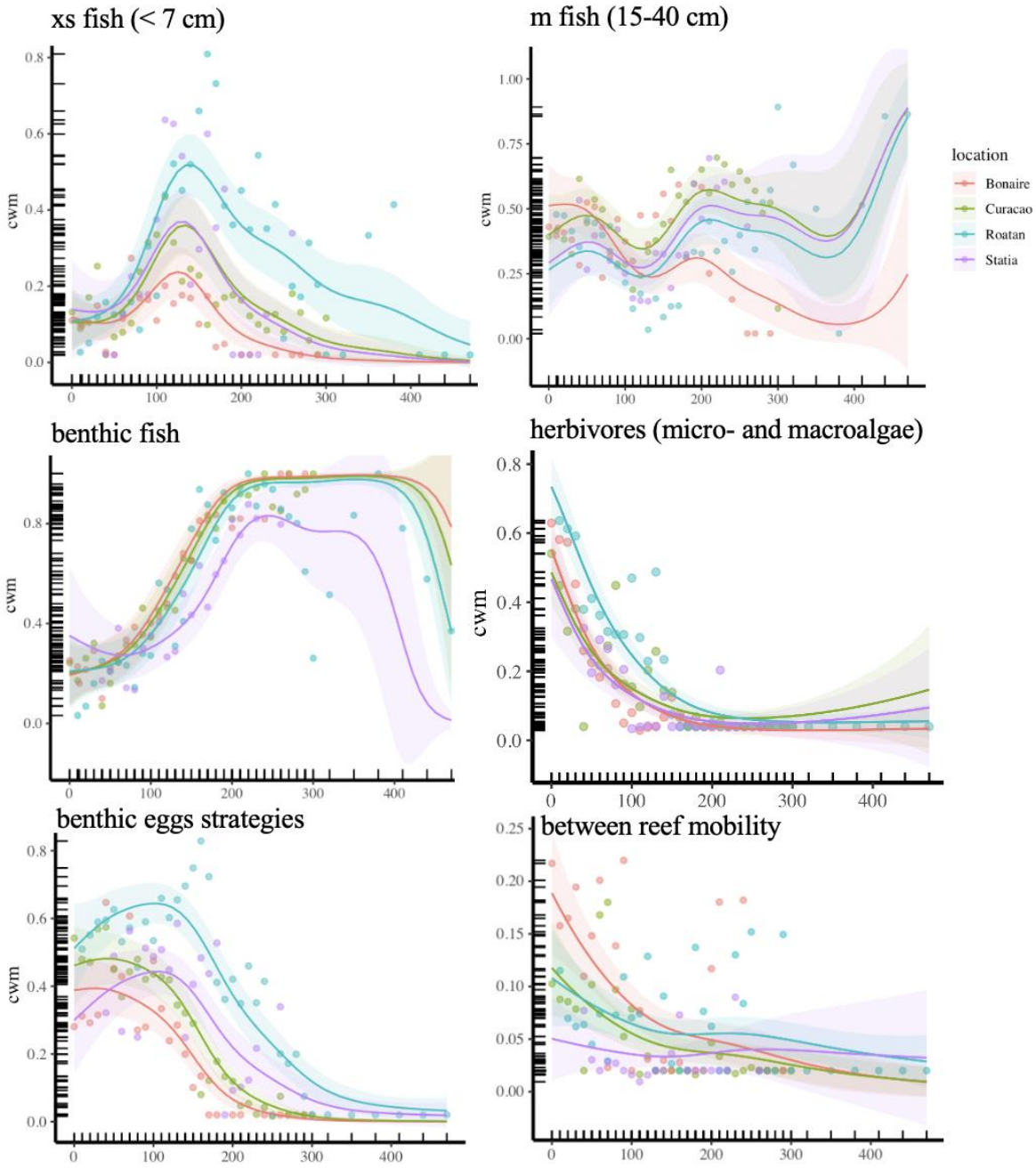

Fig. SB: Community weighted means of functional traits across depth at the four study locations. Data were fitted using General Additive Models with an interaction effect between depth and location. Shaded area depicts 95% confidence interval. Points represents observed values and colors indicate sites.

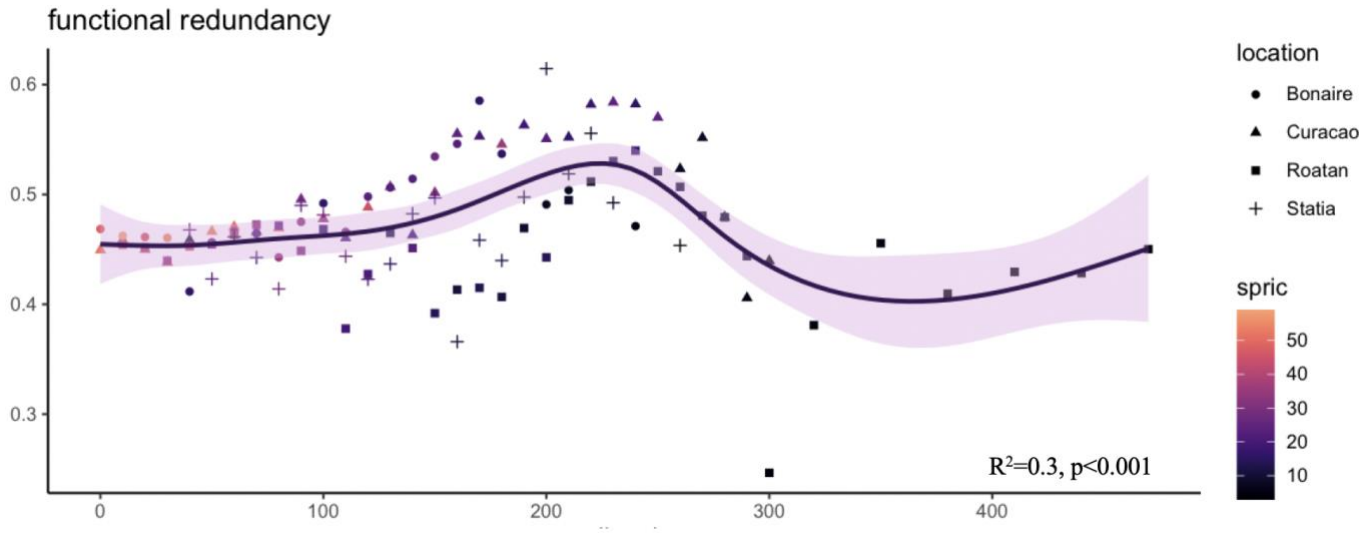

Fig. SC: Functional redundancy of fish communities across depth. Each dot represents a community from a given 10m depth bin at a given study site. Shapes of dots indicate the study site and color of dots indicate the species richness of the community. Dark lines represent the loess regressions fitted to the data and purple shading indicates the 95% confidence interval associated with the model. Residual standard errors (RSE) associated with the loess regressions are indicated in each panel.

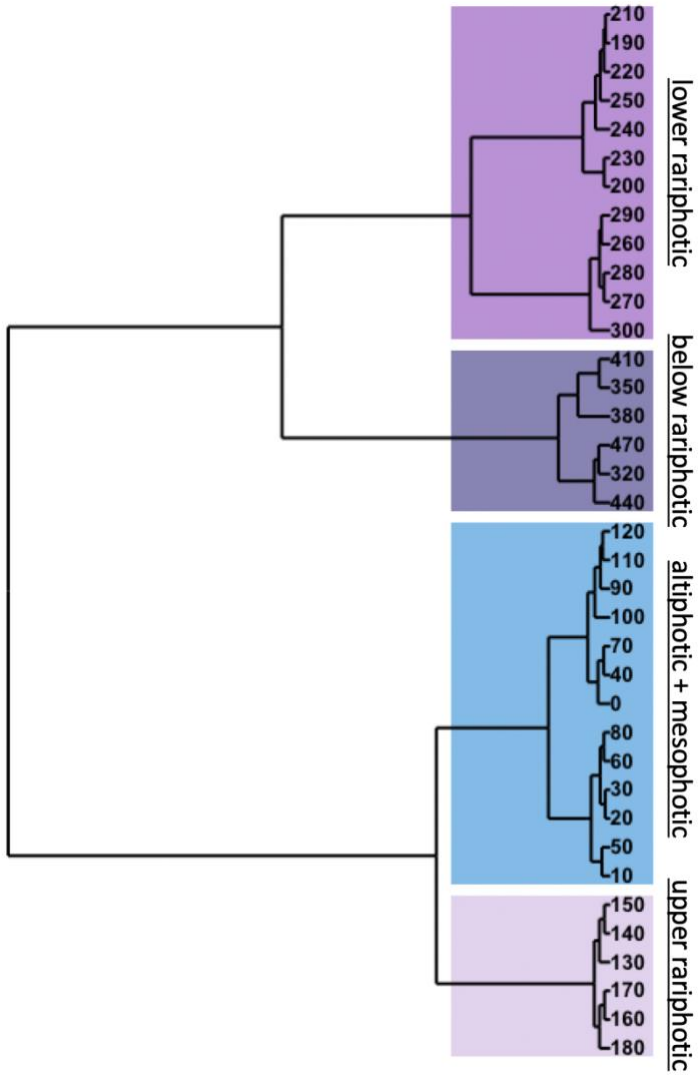

Figure SD: Hierarchical clustering dendrograms based on trait composition of fish communities across depths. The four main clusters are distinguished by differing colorations. Depth bins are labeled with the minimum depth of each 10 m depth interval (e.g., “100 m” = 100–109 m).

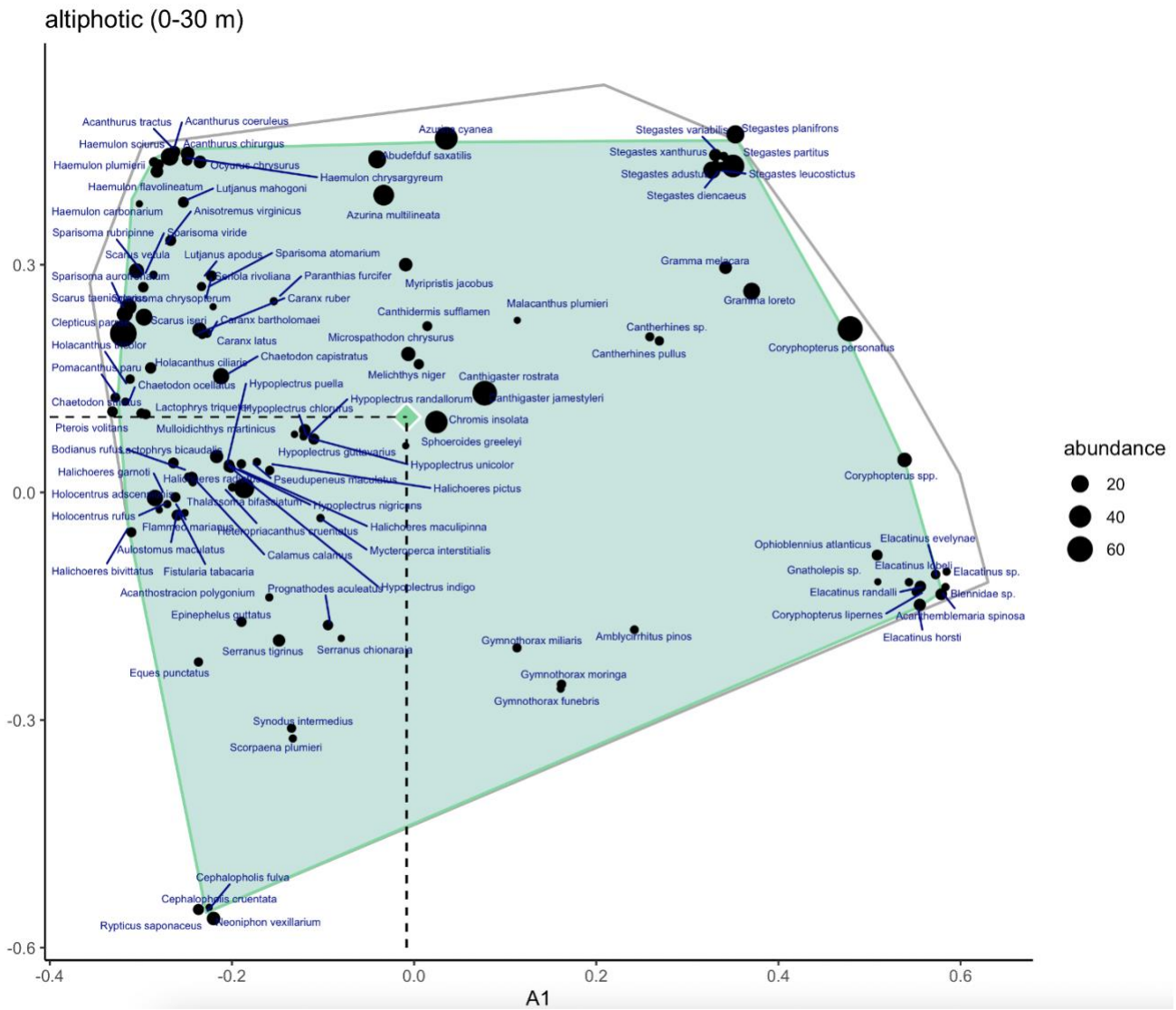

Figure SE: Species composing the trait space of altiphotic communities

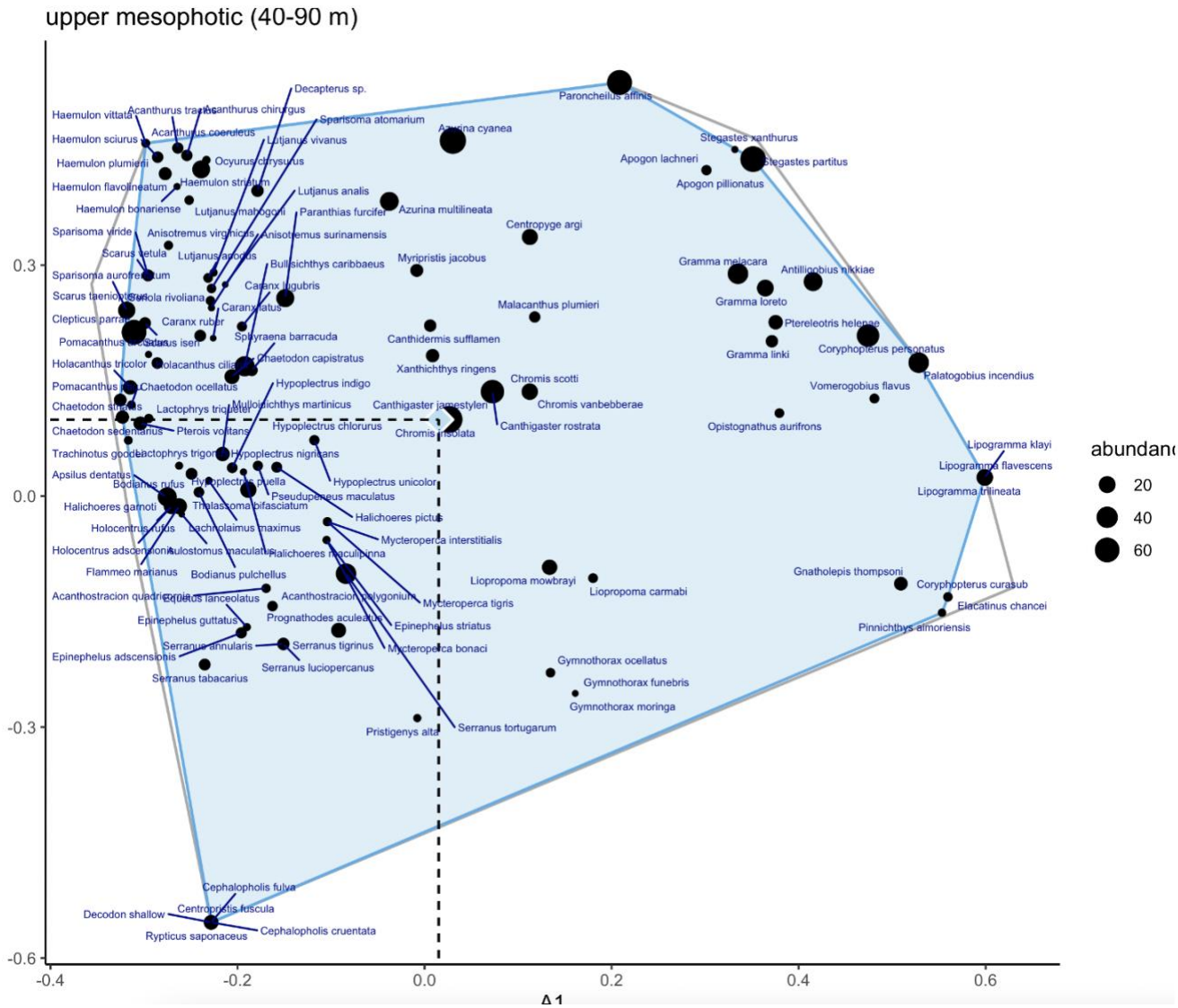

Figure SF: Species composing the trait space of upper mesophotic communities

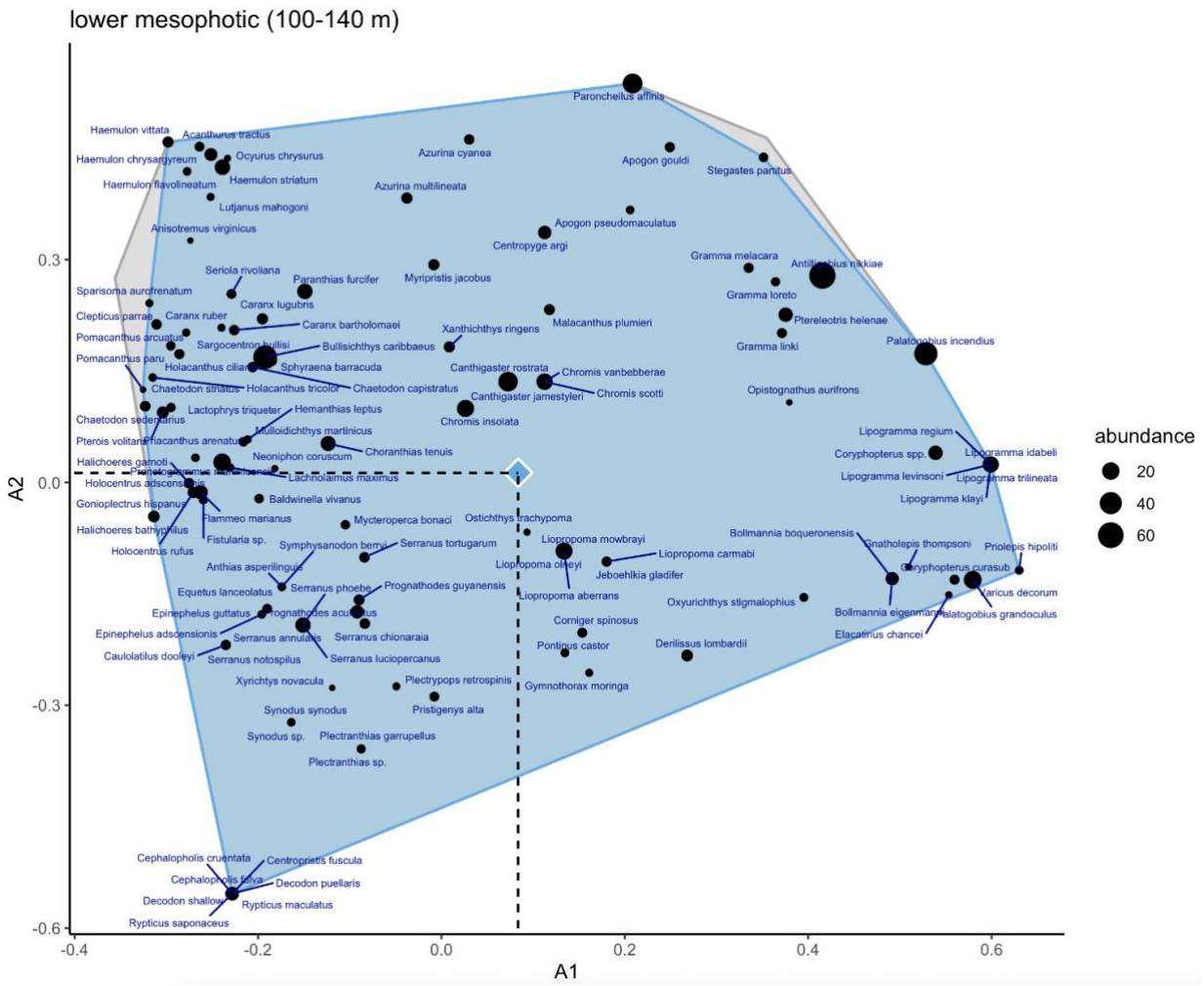

Figure SG: Species composing the trait space of lower mesophotic communities

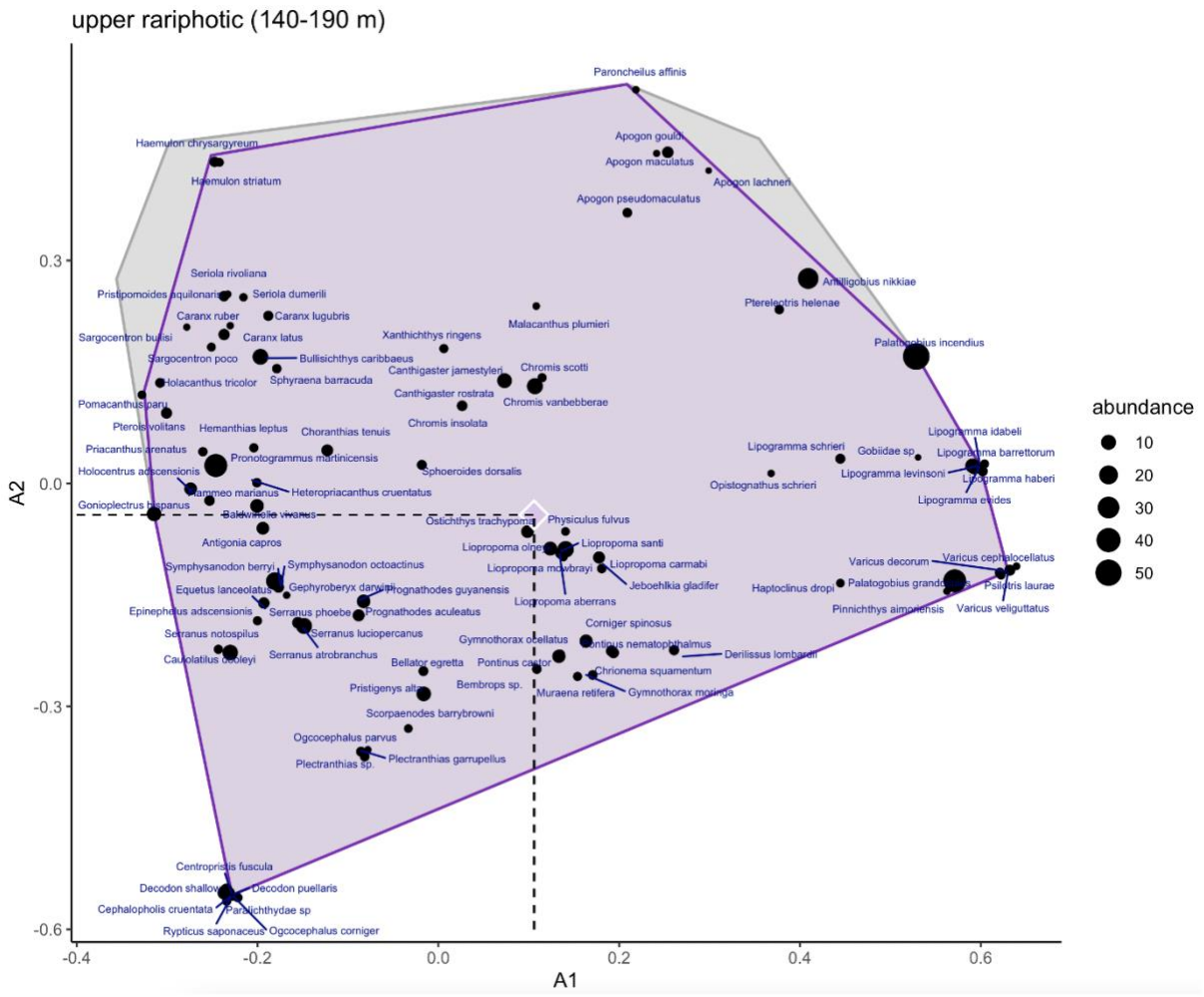

Figure SH: Species composing the trait space of upper rariphotic communities

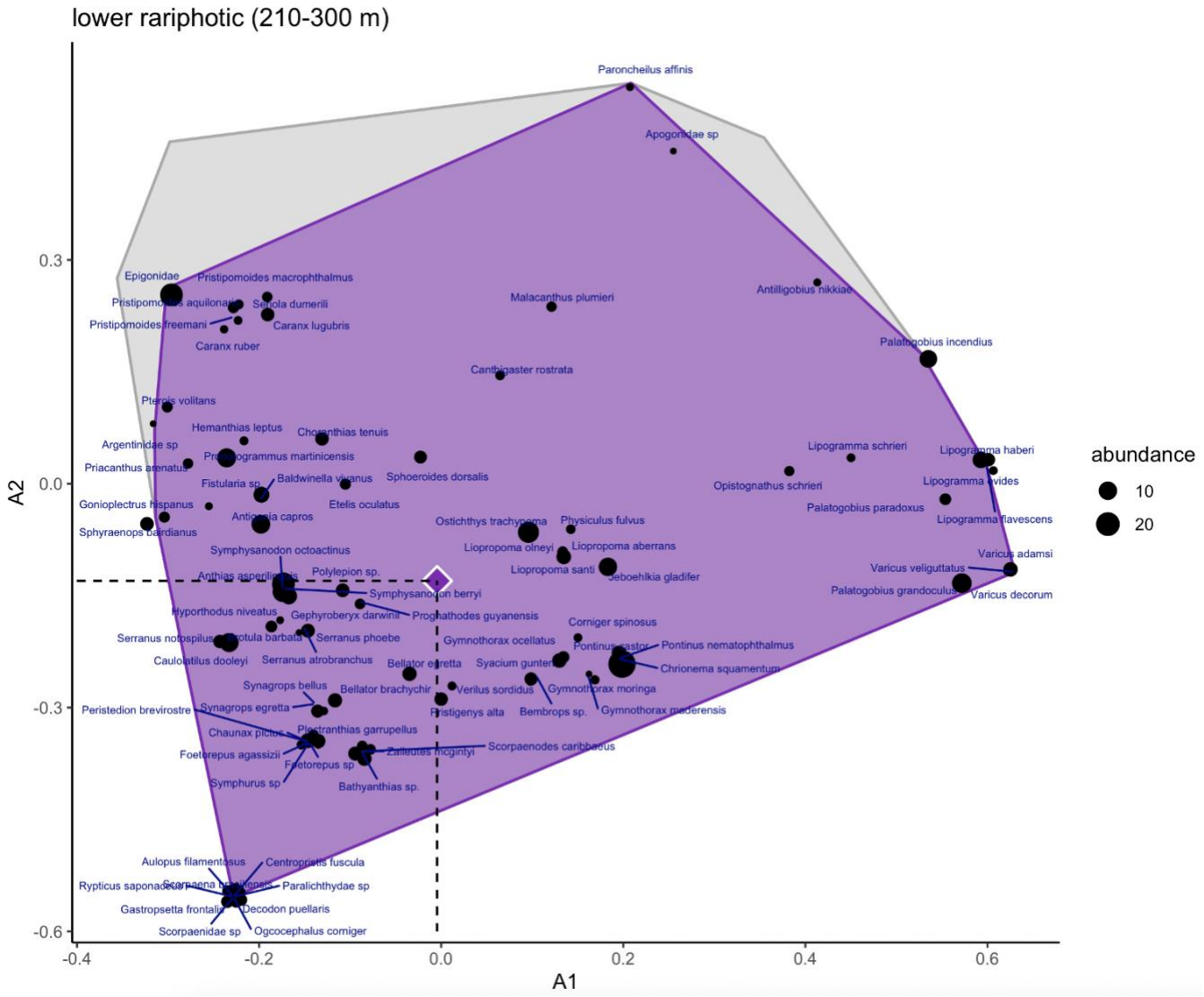

Figure SI: Species composing the trait space of lower rariphotic communities

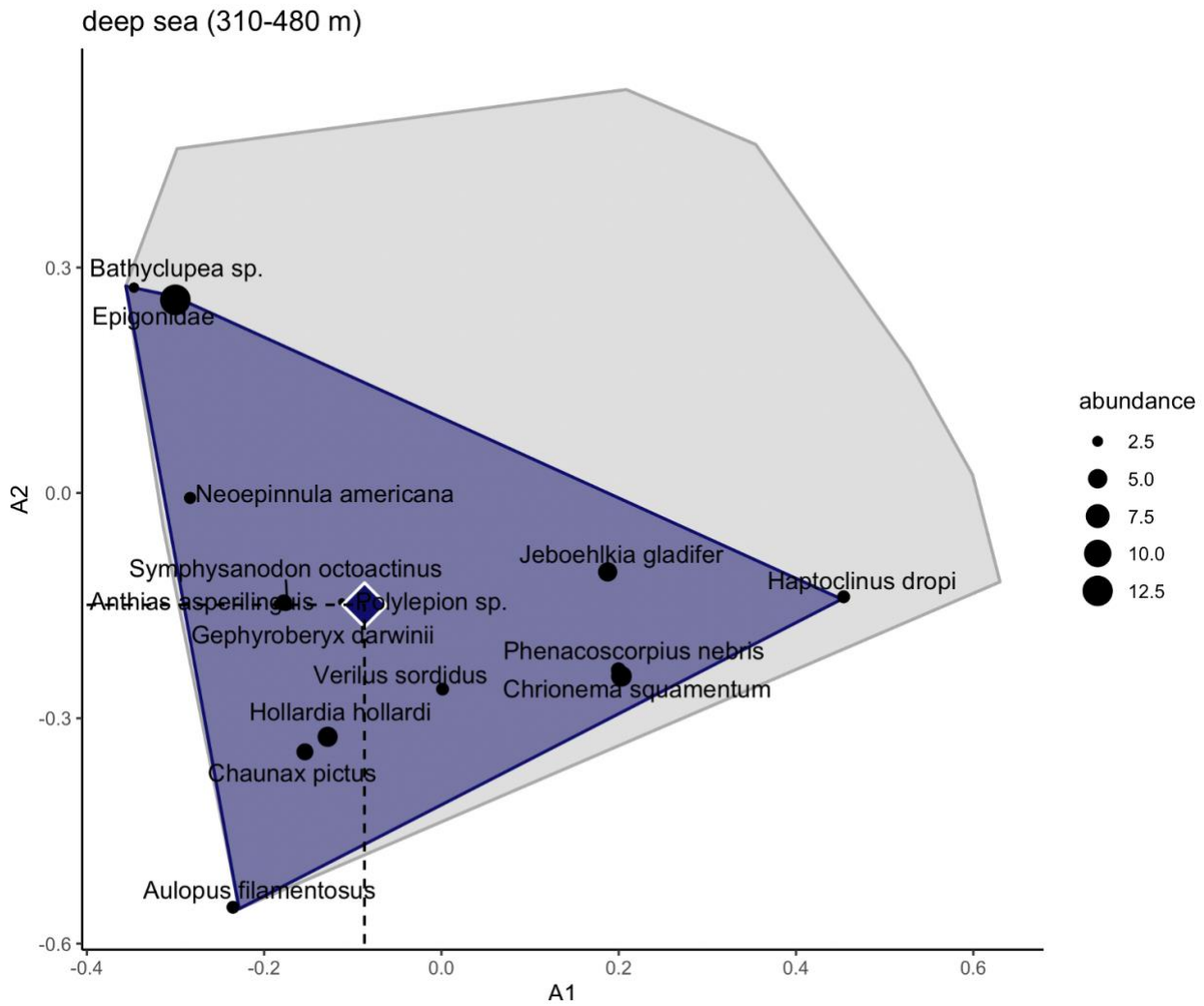

Figure SJ: Species composing the trait space of below-rariphotic communities

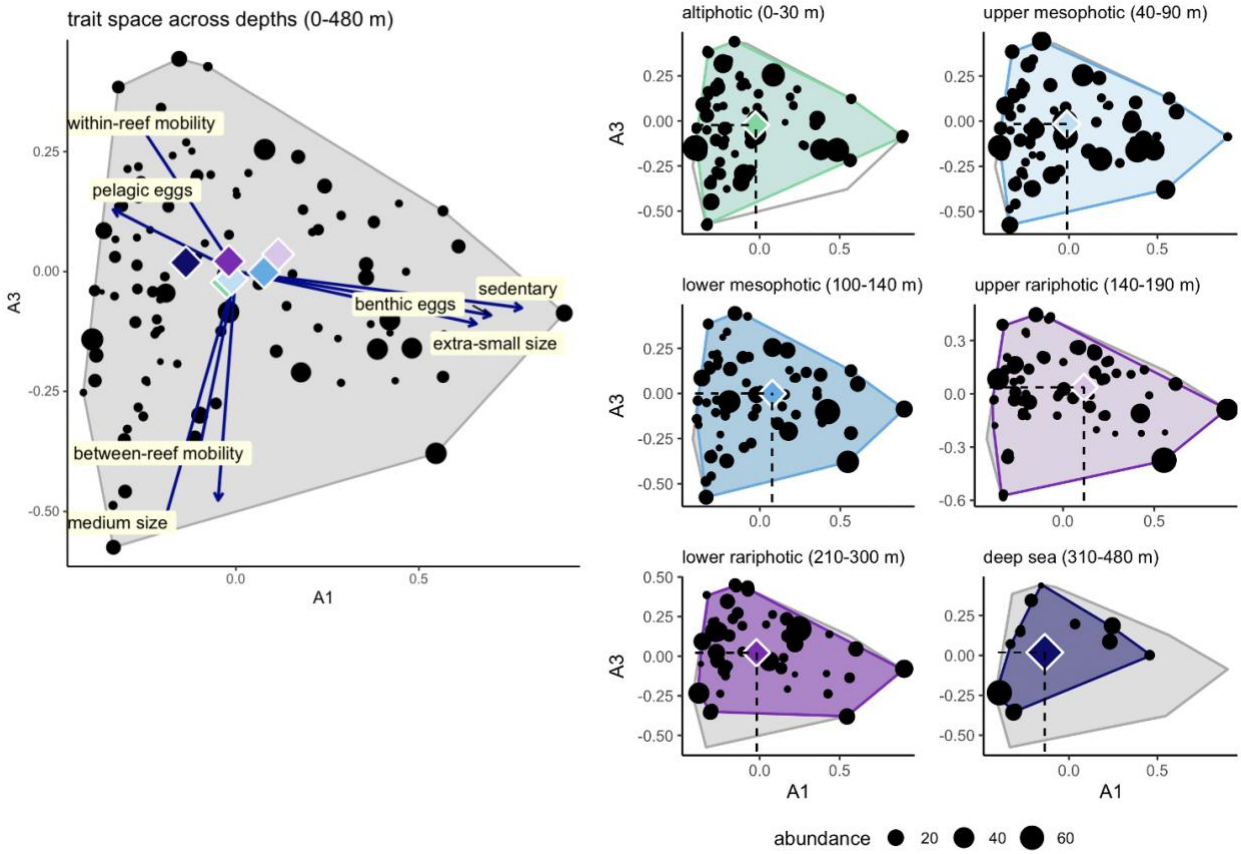

Figure SK: Trait space occupied by fish communities across depths represented along the first and third Principal Coordinate Analyses (PCoA) axes. Black points represent species' position in the trait space and size of points represents the relative abundance of these species. Colored diamonds indicate the trait centroid for each depth zone. Vectors (left plot) represent the correlation of traits to the two principal component axes.

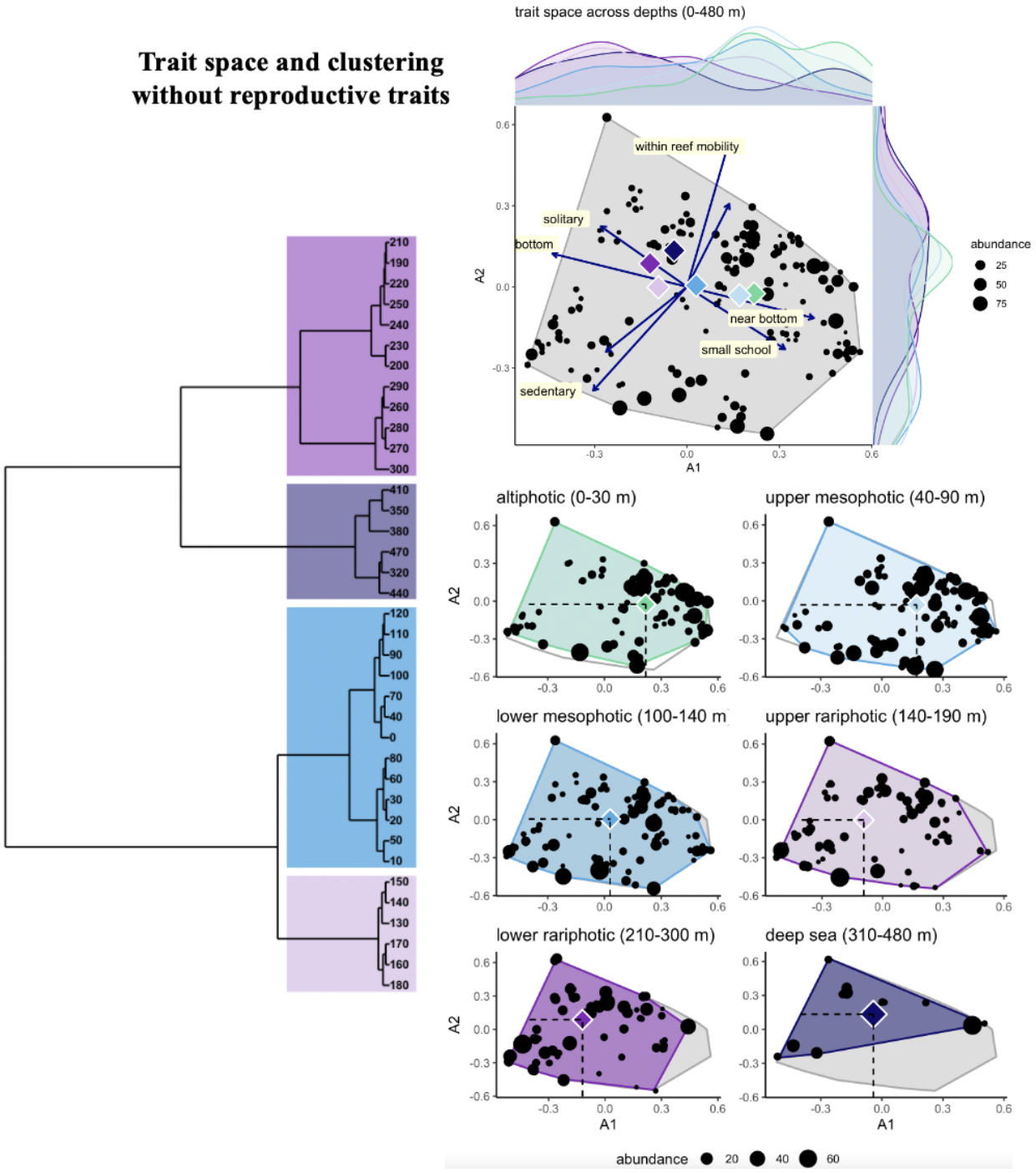

Figure SL: Hierarchical clustering (right) and Principal Coordinates Analyses (PCoA) of fish communities across depths based on all traits but reproduction. Black points represent species' position in the trait space and size of points represents the relative abundance of these species. Colored diamonds indicate the trait centroid for each depth zone. Vectors (top plot) represent the correlation of traits to the PCoA axes.

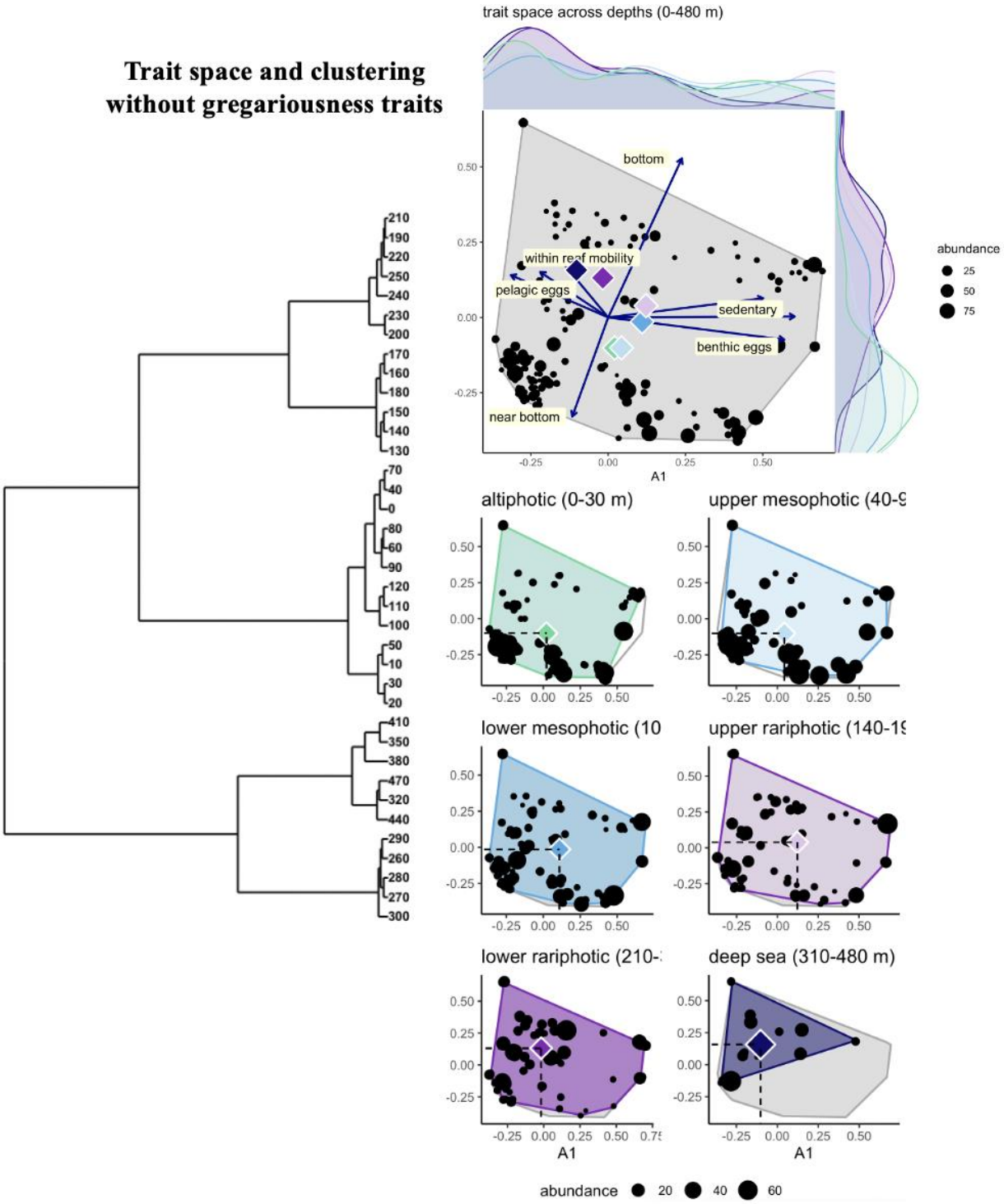

Figure SM: Hierarchical clustering (right) and Principal Coordinates Analyses (PCoA) of fish communities across depths based on all traits but gregariousness. Black points represent species' position in the trait space and size of points represents the relative abundance of these species. Colored diamonds indicate the trait centroid for each depth zone. Vectors (top plot) represent the correlation of traits to the PCoA axes.

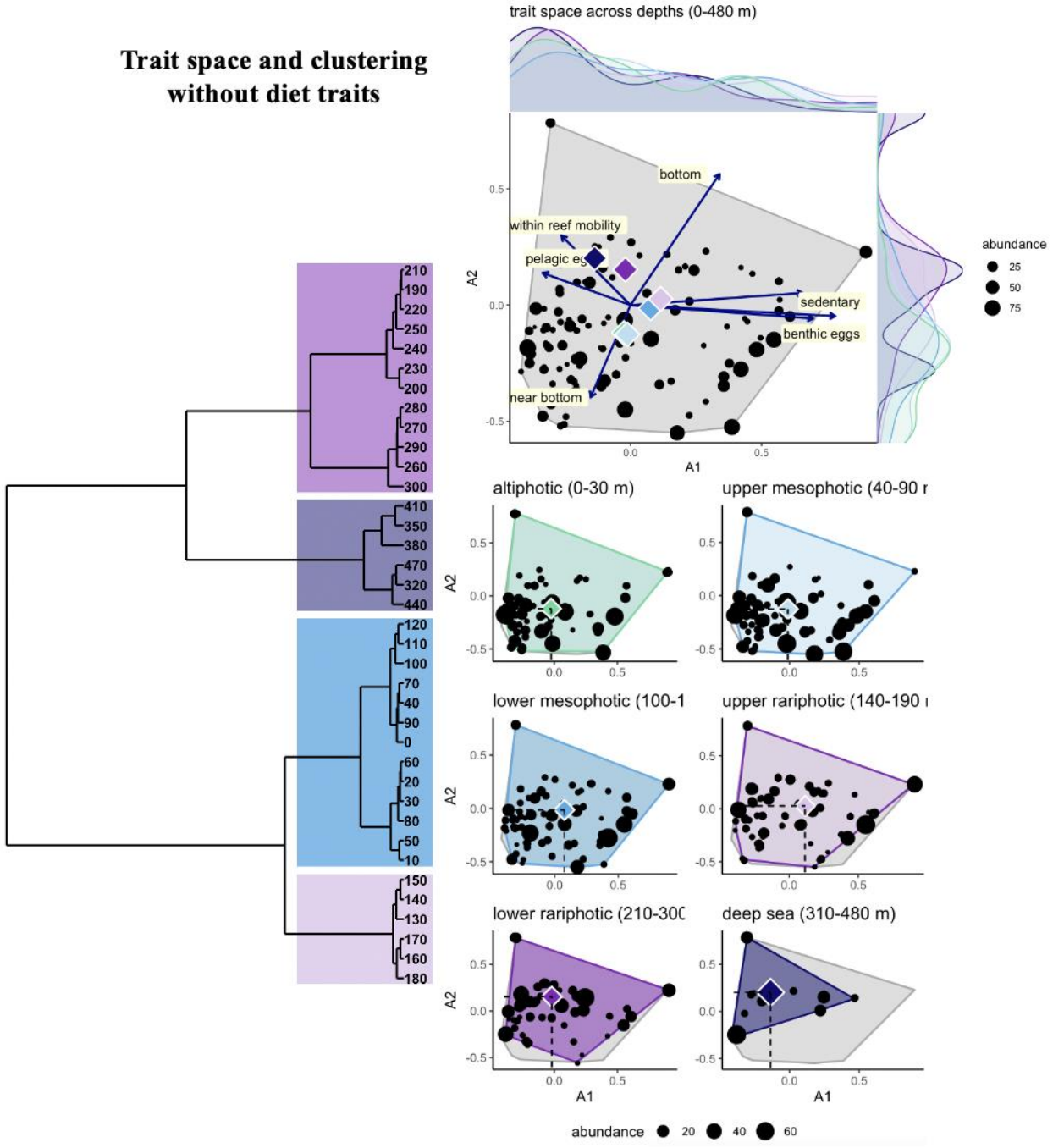

Figure SN: Hierarchical clustering (right) and Principal Coordinates Analyses (PCoA) of fish communities across depths based on all traits but diets. Black points represent species' position in the trait space and size of points represents the relative abundance of these species. Colored diamonds indicate the trait centroid for each depth zone. Vectors (top plot) represent the correlation of traits to the PCoA axes.