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Review

Ocean conservation boosts climate change mitigation and adaptation

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https://doi.org/10.1016/j.oneear.2022.09.002

SUMMARY

Marine protected areas (MPAs) are increasingly being promoted as an ocean-based climate solution. However, such claims remain controversial because of 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 the 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.

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.[1] Recent years have seen a growing focus on the ocean's central role in climate[2] 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 climate mitigation and adaptation.[3]

Considerable consensus exists on the cascading impacts of climate change on marine ecosystems and coastal communities,[2,4–6] but no such consensus exists on ocean-based climate solutions.[7] Most notably, although the potential of ocean conservation tools such as marine protected areas (MPAs) is widely recognized to deliver multiple positive ecological and social outcomes,[8,9] their ability to contribute to the resilience of marine social-ecological systems to climate change or to contribute to carbon sequestration remains highly controversial.[10–13] Although dogmatism drives part of these disagreements,[14] the underlying scientific challenge lies in the diverse and diffuse body of research that allows us to formulate a range of hypotheses on whether marine conservation can serve as a climate solution. Some argue that the increases in abundance, biomass, and biodiversity of fished populations occurring in MPAs[15–17] promote other ecological outcomes, such as reproductive output, genetic diversity, or ecosystem stability,[10] ultimately contributing to the adaptive potential of marine ecosystems to climate change.[18–20]

However, few studies have directly tested the effects of MPAs on climate change adaptative potential, and the existing literature shows contrasting results.[21,22] A great amount of literature has shown that MPAs failed to protect coral reefs from bleaching during heat waves.[23] In some instances, coral loss has even been shown to be greater in MPAs than in unprotected areas. This phenomenon, referred to as the "protection paradox,"[12] 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 because millions of livelihoods directly depend on fisheries for income and food security. Although MPAs have been shown to provide benefits to fisheries because of spillover of fish from protected to fished areas,[24] controversy remains regarding the overall costs and benefits to fishing communities.[25–27] Because coastal populations are among the most vulnerable to climate change,[1,2] it is paramount to identify solutions that will not further negatively impact their adaptive capacity.[28,29] However, no synthesis of the literature examining how MPAs impact social adaptive potential exists, casting doubt on whether marine conservation can be used as a holistic tool that benefits marine ecosystems and coastal communities.[30]

The 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.[13,31] Clarity regarding 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 vote counting and a meta-analytical approach. Vote counting (i.e., calculating the fraction of studies reporting positive, negative, or neutral outcomes) allows us to synthesize results from both qualitative and quantitative studies and to overcome some publication biases associated with meta-analysis. For these reasons, it is commonly used in social science,[25,32] as well as in ecology.[33,34] When sufficient quantitative data were available to perform meta-analysis, we also quantified the direction, magnitude, and uncertainty of MPA outcomes on climate pathways. Because previous analyses have shown that high levels of protection are required to achieve ecological[15] and social[35] 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. Meta-analyses showed that MPAs significantly increase carbon sequestration, coastal protection, biodiversity, and the reproductive capacity of marine organisms as well as fishers' catch and income. However, these benefits were only achieved under full or high levels of protection. Our study provides evidence that MPAs constitute an effective solution for climate change mitigation and adaptation of the intertwined components of social-ecological systems.

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[10,12,20,25,28] (Table S1). Two climate pathways contributed to climate mitigation (carbon sequestration and local acidity buffering) and 14 to climate adaptation (Figure 1). Social adaptation pathways were derived from the five pillars of social adaptive capacity[28]: assets, flexibility, agency, learning, and social organization, to which was added food security.[30] Ecological pathways were derived from climate adaptation pathways described previously:[10,12,20] 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 us to quantify aspects of the studied pathways not yet captured by the first two indicators (Table S2; Figure S4). The definition of each pathway and the units used to measure each indicator are detailed in Table S2. For two pathways (carbon sequestration and coastal protection), we also included all studies comparing exploited and preserved marine areas even when not officially labeled MPAs. This was done because the literature documenting the effect of preservation initiatives, comparable with MPAs, is abundant, whereas 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 (Figures 1B–1D), with most ecological adaptation pathways studied in Europe and most mitigation and social adaptation pathways studied in Asia (Figure S2). We found empirical evidence documenting the effects of MPAs on all climate pathways except acidity buffering, connectivity, and phenotypic plasticity (Figure 1). Eight climate pathways had sufficient quantitative data ($n > 3$) to perform a meta-analysis.

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 C ecosystems (mangrove, tidal marshes, and seagrass), which have already been recognized by the Intergovernmental Panel on Climate Change (IPCC) for C accounting schemes,[36] as well as sediments, macroalgae, and fish.[31,37] C sequestration was defined as organic C stored for over 100 years.[38] Mean effect sizes (log response ratios [lnRR], 95% confidence interval) indicated significant increases in C sequestration in preserved or restored seagrass ($\ln RR = 0.76 \pm 0.34$) and mangrove ($\ln RR = 0.75 \pm 0.14$) ecosystems in comparison with similar areas undergoing human pressure (e.g., thinning, anchoring, conversion to plantations). Similarly, sediments in untrawled seabed sequestered significantly more C than areas exposed to trawling ($\ln RR = 0.13 \pm 0.10$). Conservation had no effect on C sequestered by tidal marshes (Figure 2D), mostly because conversion of unprotected marsh into agricultural land increased C sequestered in plant biomass and in the soil.[39] Partial (e.g., thinning, anchoring) or full (e.g., clear cutting, excavating) degradation of mangroves and seagrass resulted in similar decreases of sequestered C, indicating that even low levels of human impact result in important C emissions (Figure 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 ($\ln RR = 1.10 \pm 0.58$),[16] which can serve as a proxy for C sequestration because a portion of that biomass undergoes exportation and is subsequently sequestered in the deep sea.[40] This is supported by several studies that calculated large impacts of fisheries on C sequestration from fish biomass removal.[31,41] However, this remains an indirect measurement of C sequestration, and more research is needed to quantify the exportation rates of organic C from fish biomass toward sediments.[42] Although macroalgae are increasingly being advocated as significant actors in marine C sequestration,[37,43] major knowledge gaps remain regarding how marine conservation affects their living biomass and, thus, their contribution to C sequestration.

Although 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 mangroves and macroalgae decreased it (Figure 3). Benefits to the adaptive potential of

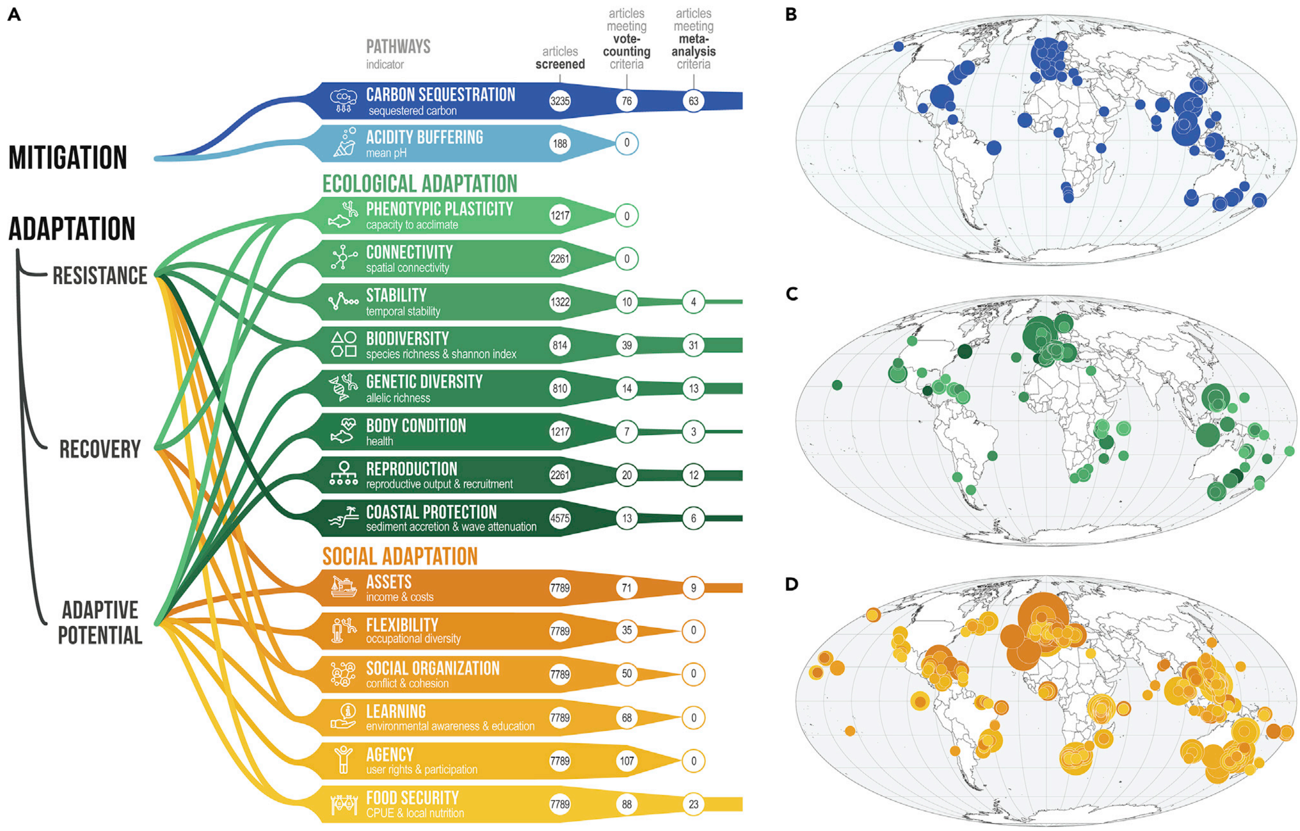

Figure 1. Pathways through which MPAs can contribute to climate change mitigation or adaptation, with quantitative and spatial assessment of available information

(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 the components of adaptation (i.e., resistance, recovery, and adaptive potential) to which they contribute. The number of articles found through our search queries and the number of articles that met the screening 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 the 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.

marine organisms could arise from exposure to greater pH fluctuations that occur in vegetated habitats, which has been shown to increase tolerance to acidification.[44] More research is required to support this hypothesis and assess whether conservation of vegetated habitats could benefit pH buffering or acidity tolerance.

CONTRIBUTION OF MPAs TO ECOLOGICAL ADAPTATION

We found that MPAs contribute to ecological adaptation by increasing biodiversity, reproductive output, and coastal protection compared with unprotected sites (Figure 2C). Species richness was higher in MPAs (lnRR = 0.20 ± 0.10), in agreement with previous regional[17] and global[45] meta-analyses, but the 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 increase the odds that ecosystem functions are maintained even after a stressor eliminates certain species,[46] a concept referred to as the insurance hypothesis.[47] 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 increased production of offspring.[48] In contrast, recruitment rates showed no significant increase, which could be explained by the higher predation rates on recruits experienced in MPAs.[49] Reproductive capacity is an important attribute of adaptation because it is linked to faster rates of population recovery[50] and increased larval dispersal distance, which, in turn, can promote populations' connectivity and ability to colonize new habitats.[48]

Preservation of mangroves and tidal marshes enhanced coastal protection through soil accretion rates of an additional 1.38 ± 0.88 cm $year^{-1}$ compared with degraded habitats. Coral reefs and seagrass can also contribute to coastal protection through wave attenuation (Figure 3), but no studies have assessed whether wave attenuation is enhanced when habitats are in an MPA. However, wave attenuation is linked to a habitat's structural complexity and vegetation density,[51,52] which suggests that habitats protected from physical disturbance would

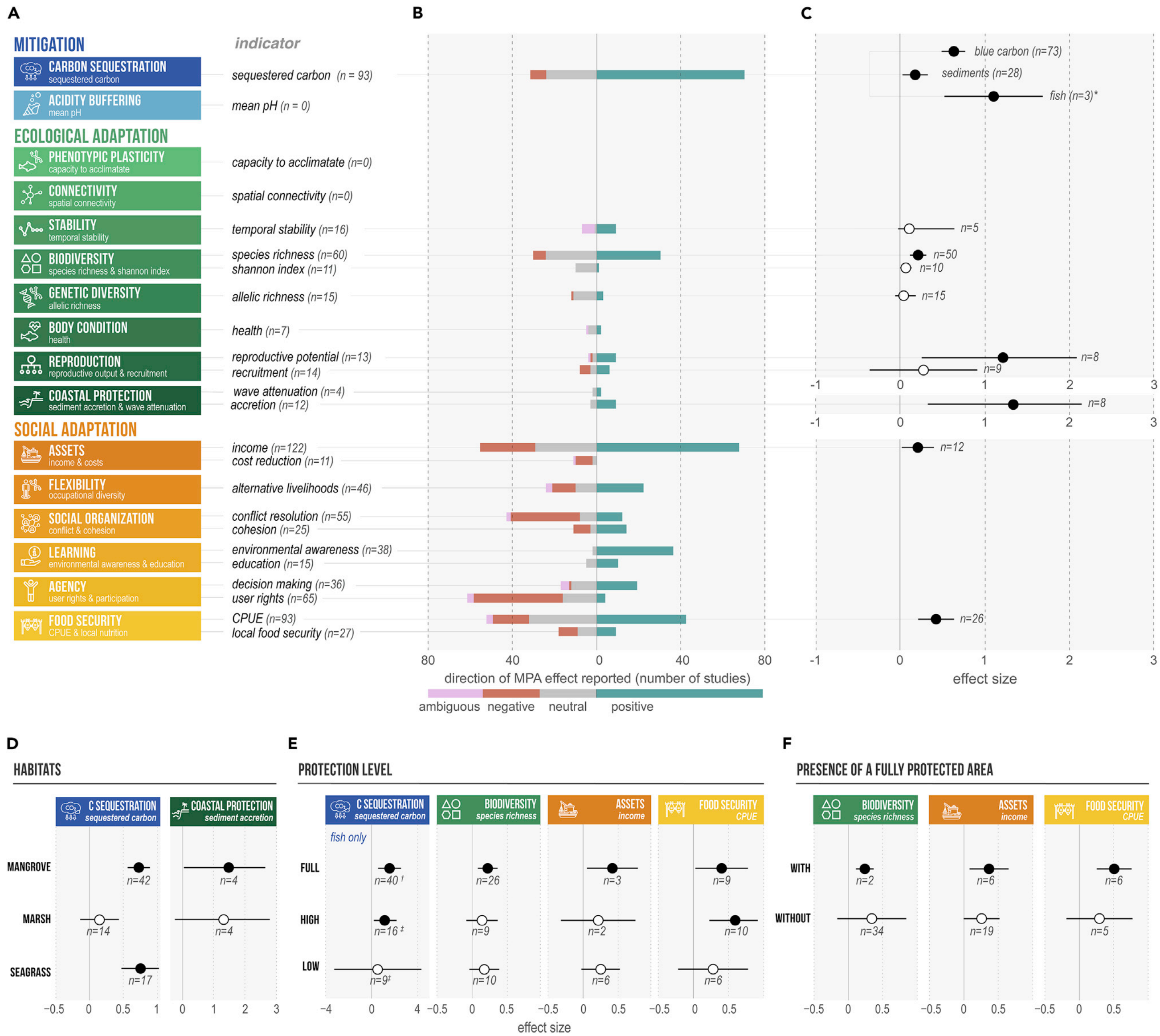

Figure 2. Effects of marine protected areas (MPAs) on climate change mitigation and adaptation pathways

(A–C) Climate pathways (A) and direction of reported MPA effects 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), the x axis indicates the log-transformed ratio of indicators between MPAs and controls. 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% confidence interval. Black dots indicate effect sizes that do not overlap zero and white dots those that overlap zero. Sample sizes (i.e., number of studies) of vote counting and meta-analysis results are indicated by n values. *In the case of C sequestration from fish biomass, the effect size was calculated from three previous meta-analyses, representing data from many more individual studies.

(D–F) 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 C sequestration (fish biomass only) are reported from Lester et al.[16] ‡Effects of high and low protection on C sequestration (fish biomass only) are reported from Zupan et al.[15]

perform better than degraded habitats. We found that MPAs increased ecosystem stability, but 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; Figures 2C and S7). This is consistent with the one previous regional meta-analysis[53] 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 (Figure 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.[54] The ability of MPAs to enhance connectivity constitutes

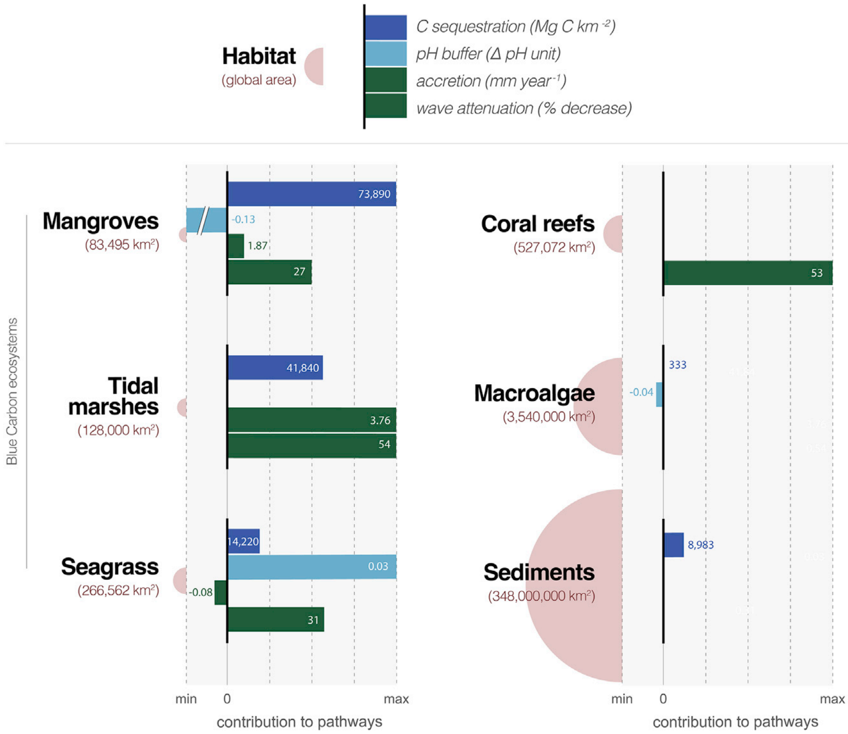

Figure 3. Contribution of marine habitats to climate pathways
Values in barplots indicate the capacity of marine habitats to contribute to C sequestration (mg C km^{-2}), coastal protection (accretion in mm year^{-1} and wave attenuation in % wave decrease), and acidity buffering (Δ pH unit). The height of the barplots represents the capacity of habitats to contribute to a given indicator relative to the maximum value reached by a habitat. For pH buffering, negative values indicate that the habitat decreases the average local pH. The spatial extent of habitats is indicated under each habitat's name and is represented by a half-sphere area that is log proportional to its global spatial area.

a major knowledge gap because connectivity is one of the most important pathways for adaptation to climate change by allowing recolonization of disturbed habitats, gene exchange, and climatic migration.[55]

CONTRIBUTION OF MPAs TO SOCIAL ADAPTATION

Among social adaptation pathways, food security and assets displayed sufficient quantitative data to perform a meta-analysis. MPAs significantly increased food security (lnRR = 0.43 ± 0.21; Figure 2C), measured using catch per unit effort (CPUE). Increases in CPUE arise from replenishment of fish populations in MPAs that can subsequently spill over into fishing grounds, benefitting local fisheries.[24] Increases in CPUE occurred when comparing fishing in and outside of MPAs, in the case of partially protected areas, and when comparing fishing near and far away from MPAs (Figure 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 (Figure 2F). Our results oppose those of a regional meta-analysis[56] that 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 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 potentially offset costs generated by 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 (Figures 2B, S3, and S4). 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.[25,32] 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, user rights were negatively affected by access and extraction restrictions imposed by MPA regulation, reducing local people's agency.[27,57] Increases in conflicts (59% of cases) arose from changes in spatial use of marine areas, potentially leading to tensions between different activity sectors; e.g., tourism operators and fishers.[58] However, MPAs increased social cohesion (56% of cases), likely resulting from a shared conservation vision and sense of purpose between stakeholders.[59] Such a discrepancy of MPA outcomes on conflict and cohesion suggests that impacts of MPAs on social organization are strongly context dependent.

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 (Figure 2E). In contrast, lower levels of protection generated no benefits. Increases in species richness and in fishers' income only occurred for fully protected areas, where no fishing is allowed. Increases in CPUE and C sequestration were also achieved by highly protected areas, where low-impact fishing is allowed. However, this was only the case when a fully protected area was also present in the MPA considered (i.e., a multi-zone MPA with one zone being a fully protected area).

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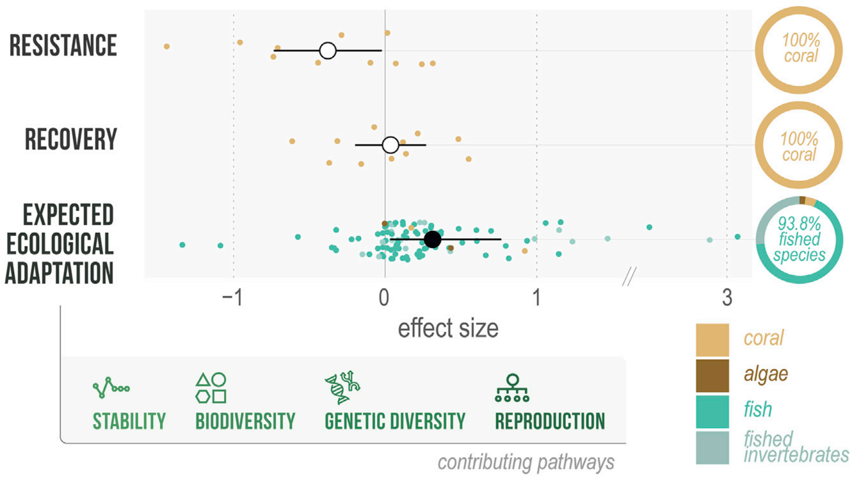

Figure 4. Disentangling confounding factors of the protection paradox
Effect sizes were calculated as natural log ratios of MPA and controls for resistance, recovery, and expected ecological adaptation of marine organisms. Values represent mean ± 95% CI. Black effect sizes indicate CIs that do not overlap zero, and 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. Donut diagrams on the right represent the distribution of individual effect sizes among taxa. Contributing pathways indicate the pathways from which individual effect sizes were aggregated to obtain the effect size of expected ecological adaptation.

All four climate pathways were positively correlated with MPA age (Figure 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 mangroves and seagrass. CPUE was positively correlated with MPA size (Figure S10), which can result from a greater proportion of mobile fish having their home ranges included in the MPA.[60] Level of protection, age, and size have already been established as important drivers and enabling conditions for MPAs to deliver positive ecological outcomes.[15,61] 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. The characteristics of each marine habitat influence its ability to contribute to climate pathways, and its spatial extent determines its 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., mangroves and seagrass; Figure 3) translate into a high mitigation potential per surface area but low mitigation potential at the 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 C pools into national greenhouse gas accounting would help make MPAs more actionable in climate change mitigation and including them into nationally determined contributions (NDCs).

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 to climatic stressors (lnRR = −0.38 ± 0.36) and no effect on their recovery from climatic stressors (lnRR = 0.04 ± 0.23) (Figure 4), which is consistent with previous findings[23] and referred to as the "protection paradox."[12] In contrast, we found a significantly positive effect of MPAs on expected ecological adaptation (lnRR = 0.31 (0.03–0.87)), calculated from all data points included in resilience-related pathways (i.e., 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 because all studies on recovery and resistance focused on corals, whereas most studies documenting adaptation pathways focused on fished species. Not only is the literature on conservation outcomes on resilience biased toward coral species, but it has also been shown to be further biased toward specific oceanic regions.[62] The ability of MPAs to enhance ecological adaptation results mostly from alleviation of fishing pressure, which represents a minor threat to corals in comparison with temperature rise and acidification.[63] In contrast, fishing pressure is currently the main threat to fished species,[64] 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, theoretical[65,66] and empirical[22,67] research suggests positive effects of MPAs on the resilience of fish populations. More research is required to test whether the enhanced adaptation pathways reported in this study effectively translate into enhanced resilience of fished species.

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 protection of climatic refuges such as upwelling sites.[68,69] 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.[70–72] Ensuring high protection levels in existing MPAs should be the priority to secure climate benefits to coastal social-ecological systems.

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. The outcomes of several social adaptation pathways, such as agency and learning, result from how local stakeholders are included throughout MPA establishment and management.[27,73] Involvement of stakeholders through co-management allows the identification of peoples' needs and minimization of negative social impacts, e.g., through the development of alternative livelihood options or conflict-resolution tools.[74] Positive perceptions of governance by local stakeholders has also been shown to increase support and compliance with MPA regulations,[75] which, in turn, allows ecological benefits to accrue.[76] This results in a positive feedback loop whereby perceived ecological benefits act as another incentive for communities to support MPAs[77] and allow 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;[78] involve local communities in MPA management and decision-making;[79] identify potential negative social outcomes of MPAs and find solutions to avoid, reduce, or compensate for them;[80] and monitor MPA social outcomes and adjust MPA governance accordingly.[73]

WHAT ROLE FOR OCEAN CONSERVATION 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 in 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.[81] When 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 large-scale dispossession of local communities from the landscapes and seascapes that sustain them,[82] and poorly implemented protected areas could fail to deliver the expected benefits, 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 United Nations Sustainable Development Agenda and the Paris Climate Agreement. Multiple opportunities now exist to leverage this scientific basis to guide public policy and private sector initiatives. First, there is considerable scope to expand the consideration and recognition of MPAs in national climate strategies, including NDCs and adaptation communications.[83] 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.[36] Second, because 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 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.

EXPERIMENTAL PROCEDURES

Resource availability

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Joachim Claudet (joachim.claudet@cnrs.fr).

Materials availability

This study did not generate new unique materials.

Data and code availability

All original code and datasets have been deposited at Zenodo under https://doi.org/10.5281/zenodo.7108799 and are publicly available as of the date of publication.

Identification of pathways

Pathways through which MPAs could contribute to climate change mitigation or adaptation were identified from the literature. Review articles on the ecological and social adaptive capacity of marine systems were screened, and the components of marine climate change mitigation and adaptation listed therein were attributed to climate pathways. Five reviews were retained,[10,12,20,25,28] 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. Definitions of social adaptation pathways were adapted from Cinner et al.[28]

Systematic literature review search strategy

To investigate the 16 pathways identified in the section "identification of pathways," 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 screen 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[25]
- For C sequestration[13,84,85]
- For resistance and recovery[23]

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 when the searches were performed are detailed in Data S1 (accessible through the Zenodo link provided in the ''data and code availability'' section). 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 MPAs, and the search string included all 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 as MPAs by regulating natural resource extraction. To allow a maximum of results to be found, the search string broadly included the names of the habitats of interest (Data S1; see ''data and code availability'' section), and the articles were selected when they compared preserved habitats with degraded controls (see ''screening criteria'' section).

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, and others were specific to pathways. Common screening criteria were as follows:

- The article provided primary data collected on the field or in a lab (models, reviews, and syntheses 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 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 as follows:

- 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 studies that were clearly irrelevant to our search. Studies that passed our title screening phase were exported from Web of Sceince in an Excel file with all their relative information (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).[86] This package allows us to screen abstracts without showing authors or the journal's title, limiting sources of bias in the selection process. Articles selected after abstract screening were downloaded, and their text was fully read to assess whether they were relevant to our search criteria.

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).

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 the same taxon, different religions within a community …) to avoid over-representing studies. When time series 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 closest to before MPA establishment was kept as the MPA ''before'' value.

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 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 in the MPA studied (km^2). Levels of protection were determined according to the regulation-based classification system for MPAs.[87] 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, and 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 the {sf} package to manipulate vectors, {maps} to create the background layer, and {tidyr} to manipulate datasets. The projection used was Mollweide.

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. The direction of outcomes was positive, negative, neutral, or ambiguous. ''Ambiguous'' was used when contradicting trends were reported by the article and when the article could not conclude how the MPA affected the pathway. Increases in positive indicators (e.g., participation, alternative livelihoods, and catch) were coded as positive (and negative for decreases), and increases in negative indicators (conflict, costs, mortality, coefficient of variation) were coded as negative (and positive for decreases).

When results were quantitative and associated with an error, the direction ''neutral'' was attributed when 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 were reported as positive). When two outcomes' proportions were closer than 5% to each other (e.g., 48% negative and 52% positive), "ambiguous" was attributed.

Additional screening criteria for the meta-analyses

Among studies that met our search criteria for vote counting, we identified those that 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 the 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 when more than three articles met our criteria for a given indicator.

Quantitative data extraction and preparation

Quantitative results were extracted from the main text, tables, and figures of articles and from supplemental material. Mean values and errors were extracted from figures using the online application WebPlotDigitizer v.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 were 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 deviation (SD). Mean values and variance were calculated when results were presented across categories irrelevant to our study (see "number of values extracted per study" section), and sample size was 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:

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

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

Calculation of effect size

All MPA outcomes (except in two cases; see below) were modeled as the natural logarithm response ratio of the indicator measured in the MPA and outside of the MPA.[88] For each study i, the MPA effect size ($\ln RR_i$) was calculated as the log ratio difference of the mean value of the indicator in ($\overline{X}_{MPA,i}$) and outside of ($\overline{X}_{control,i}$) the MPA (CI design) or after ($\overline{X}_{after,i}$) and before ($\overline{X}_{before,i}$) MPA establishment (BA design):

$$\ln RR_i = \ln\left(\frac{\overline{X}_{MPA,i}}{\overline{X}_{control,i}}\right) \text{ for CI designs.}$$

$$\ln RR_i = \ln\left(\frac{\overline{X}_{after\ MPA,i}}{\overline{X}_{before\ MPA,i}}\right) \text{ for BA designs.}$$

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

$$\ln RR_i = \ln\left(\frac{\overline{X}_{after\ MPA,i}/\overline{X}_{before\ MPA,i}}{\overline{X}_{after\ control,i}/\overline{X}_{before\ control,i}}\right)$$

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 follows:

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

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

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

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

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

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 $\overline{X}_{before\ MPA,i}$, $\overline{X}_{after\ MPA,i}$, $\overline{X}_{before\ control,i}$, and $\overline{X}_{after\ control,i}$, respectively, and $n_{before\ MPA,i}$, $n_{after\ MPA,i}$, $n_{before\ control,i}$, 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 us 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 follows:

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

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

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 the within- and among-study variance components.[89] Models were fitted using the {metafor}[90] package under R Core Team (2021).[86] Model heterogeneity, residual heterogeneity, degrees of freedom, and p values associated with 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.

Sensitivity analysis

To test the robustness of our meta-analysis results, we carried out a sensitivity analysis to detect (1) the presence of publication bias and of outliers using visual observation of funnel plots[91] (Figures S5.1–S5.6), (2) the sensitivity of our results to publication bias using Rosenthal's fail-safe number (N_{fs}),[92] (3) whether a different outcome could be obtained when correcting for publication bias using Duval and Tweedie's trim and fill test,[93,94] and (4) the impact of outlier removal on our results. For meta-analyses that did not have a significant result in the first place (Shannon index, recruitment and recovery), only the trim and fill test was performed.

Rosenthal's N_{fs}

Rosenthal's N_{fs} is an estimation of the number of additional non-significant effect sizes required for a significant meta-analysis result to become non-significant. This allows us to check the sensitivity of results to uncaptured studies. This risk is estimated to be high when N_{fs} is below the 5n+10, with n the number of data points in the meta-analysis.[92] 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 of 12 meta-analyses showed robust results of 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 C ecosystems.

Impact of outliers on results

Outlying effect sizes were identified through visual observation of funnel plots[91] (Figures S5.1–S5.6). The weight attributed to each effect size by the random-effects models was checked using forest plots (Figures S5.1–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 flaws or marked differences in experimental design of these studies were found, no points were excluded from our meta-analyses. 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).

Non-parametric data analysis

The indicators associated with genetic diversity and variability (allelic richness and coefficient of variation, respectively) were not associated with errors in the literature because of how these indicators are calculated. To provide quantitative results from those indicators, we performed non-parametric analyses using bootstrapping. Our bootstrapping analysis was weighted using the sample size associated with each value. MPAs were considered to have a significant effect on an indicator when the 95% confidence interval calculated through bootstrapping (n = 1,000 iterations) did not overlap zero.

Influence of moderators

Influence of moderators was 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, and habitat) could mediate MPA outcomes on climate pathways (Table S4). All analyses were carried out in R using the {metafor} package.[90]

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

C sequestration from fish biomass

The C sequestration pathway was investigated using keywords 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. Because those studies were not found through our dedicated literature search for C sequestration and because many synthetic studies and meta-analyses have already quantified the effect of MPAs on fish biomass, we based the value of this effect size on previous meta-analyses.

The effect of MPAs on fish biomass was calculated from three previous meta-analyses.[15,16,61] Those three meta-analyses were chosen because they used completely distinct datasets, were among the most cited publications for effects of MPAs on fish biomass, and, together, encompassed all types of protection levels and all oceanic regions of the world. For the effect of level of protection on fish biomass, we used values given in Lester et al.[16] for the effect of full protection, and values given in Zupan et al.[15] for the effects of low and high protection.

Capacity of habitats to provide climate benefits

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

We also performed a systematic search and meta-analysis following the methodology presented in the ''qualitative data extraction'' and ''quantitative data extraction'' sections 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; see ''data and code availability'' section). 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 (see ''data and code availability'' section).

Resistance, recovery, and adaptation potential values

Observed resistance and recovery were calculated through meta-analysis according to the methodology presented in the ''qualitative data extraction'' and ''quantitative data extraction'' sections. The search string and date of the systematic search as well as the indicators selected are detailed in Data S1 (see ''data and code availability'' section).

Expected ecological adaptation was calculated as the mean value of all effect sizes contributing to ecological adaptation, i.e., allelic richness (genetic diversity), species richness and Shannon index (biodiversity), temporal stability (stability), and reproductive output and recruitment (reproduction). The confidence interval was calculated by bootstrapping, using n = 1,000 iterations.

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.oneear.2022.09.002.

ACKNOWLEDGMENTS

Support for this study was provided by Pew Bertarelli Ocean Legacy. The views expressed are those of the authors and do not necessarily reflect the views of Pew Bertarelli Ocean Legacy.

AUTHOR CONTRIBUTIONS

This study was conceptualized by J.C.. The methodology for this was developed by J.C. and J.J. The systematic reviews and meta-analyses were carried out by J.J. with help from C.L.C. and M.L.G. under the supervision of J.C.. The original draft was written by J.J. and J.C., and reviews were performed by J.J., J.C., and R.B.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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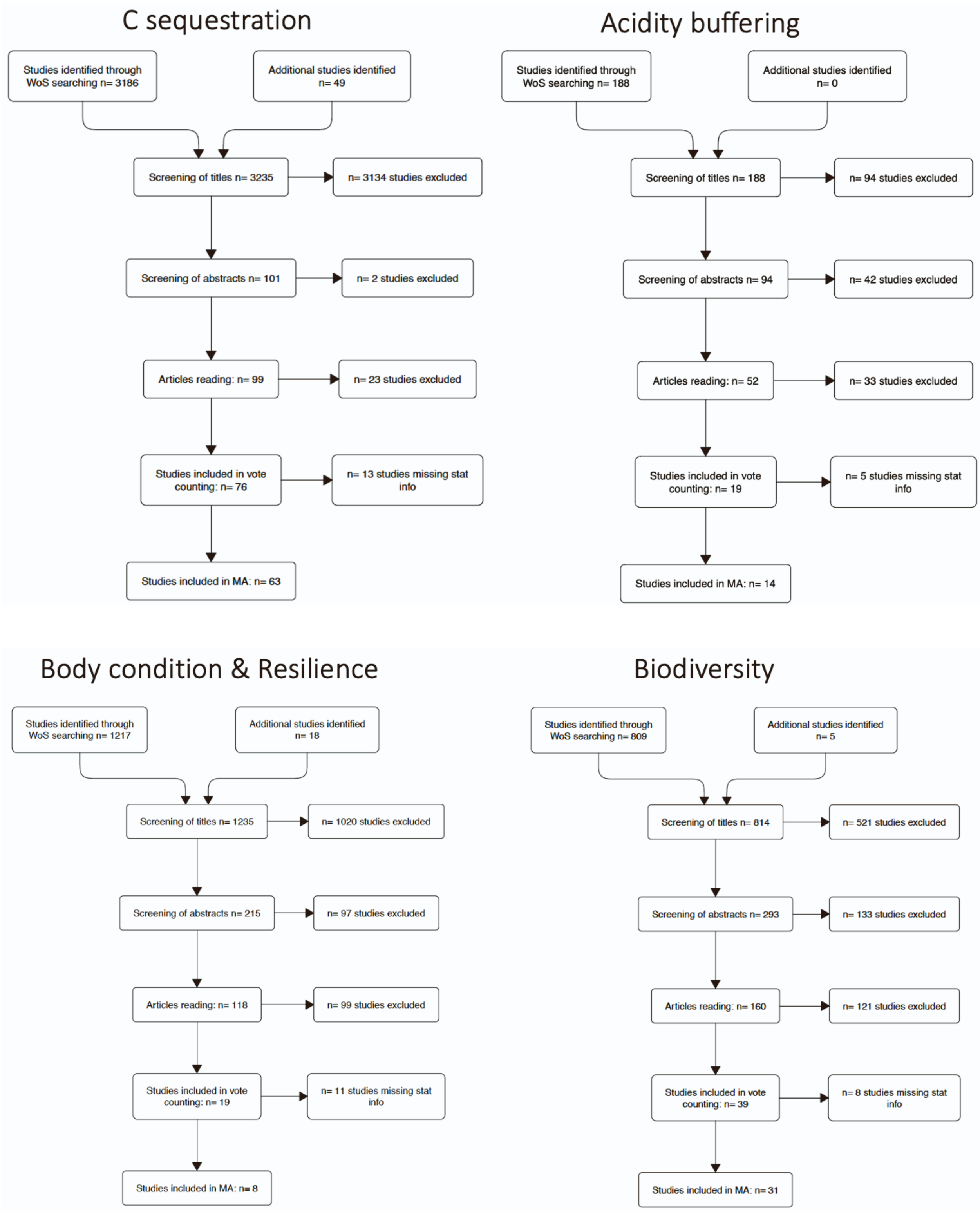
One Earth, Volume *5*

Supplemental information

Ocean conservation boosts climate change mitigation and adaptation

Juliette Jacquemont, Robert Blasiak, Chloé Le Cam, Maël Le Gouellec, and Joachim Claudet


C sequestration
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Screening of abstracts n= 101
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Articles reading: n= 99
n= 23 studies excluded
Studies included in vote counting: n= 76
n= 13 studies missing stat info
Studies included in MA: n= 63
Acidity buffering
Studies identified through WoS searching n= 188
Additional studies identified n= 0
Screening of titles n= 188
n= 94 studies excluded
Screening of abstracts n= 94
n= 42 studies excluded
Articles reading: n= 52
n= 33 studies excluded
Studies included in vote counting: n= 19
n= 5 studies missing stat info
Studies included in MA: n= 14
Body condition & Resilience
Studies identified through WoS searching n= 1217
Additional studies identified n= 18
Screening of titles n= 1235
n= 1020 studies excluded
Screening of abstracts n= 215
n= 97 studies excluded
Articles reading: n= 118
n= 99 studies excluded
Studies included in vote counting: n= 19
n= 11 studies missing stat info
Studies included in MA: n= 8
Biodiversity
Studies identified through WoS searching n= 809
Additional studies identified n= 5
Screening of titles n= 814
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Studies included in vote counting: n= 39
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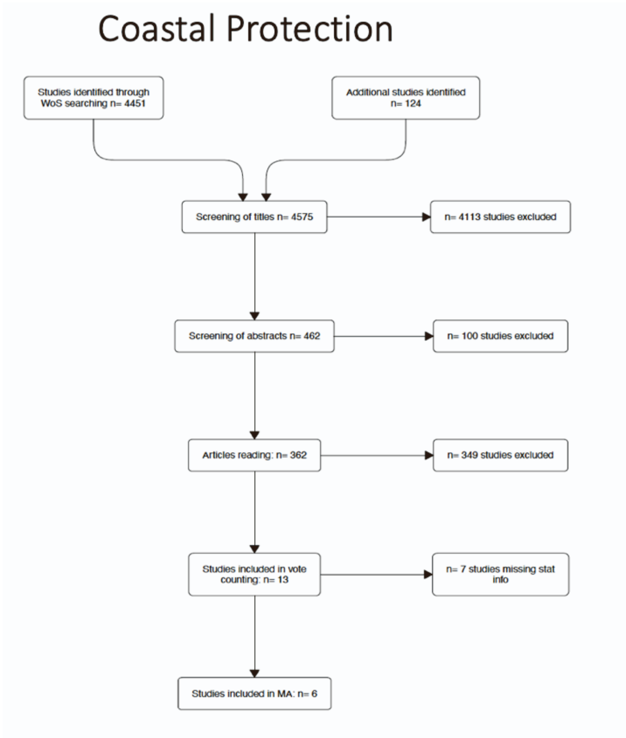
Studies included in MA: n= 31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Screening of abstracts n= 462
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Studies included in vote counting: n= 13
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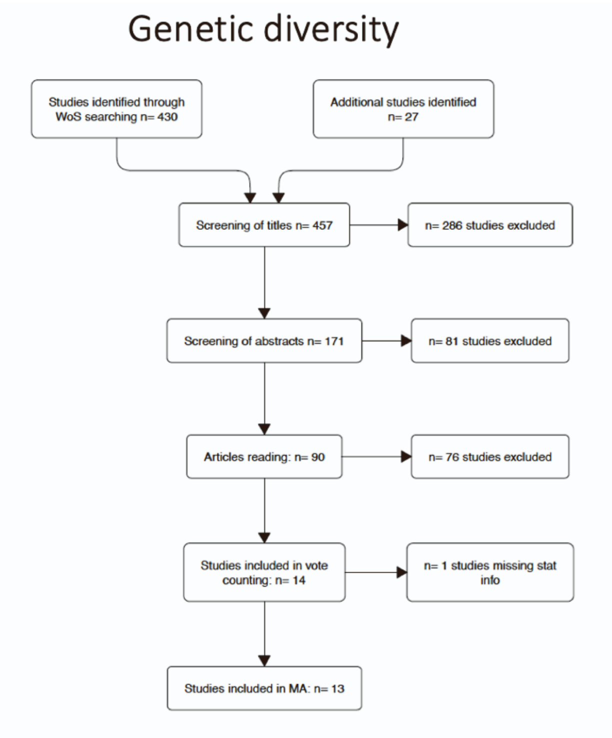
Studies included in MA: n= 6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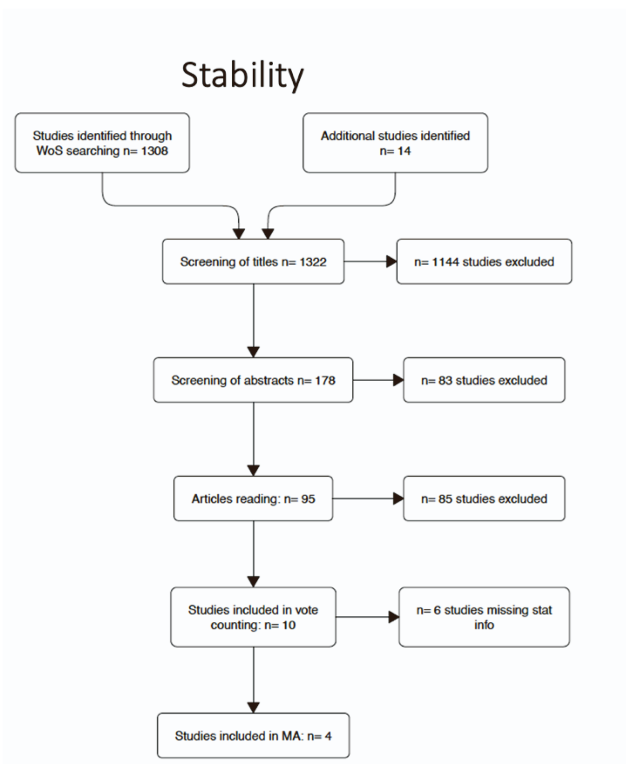
Stability
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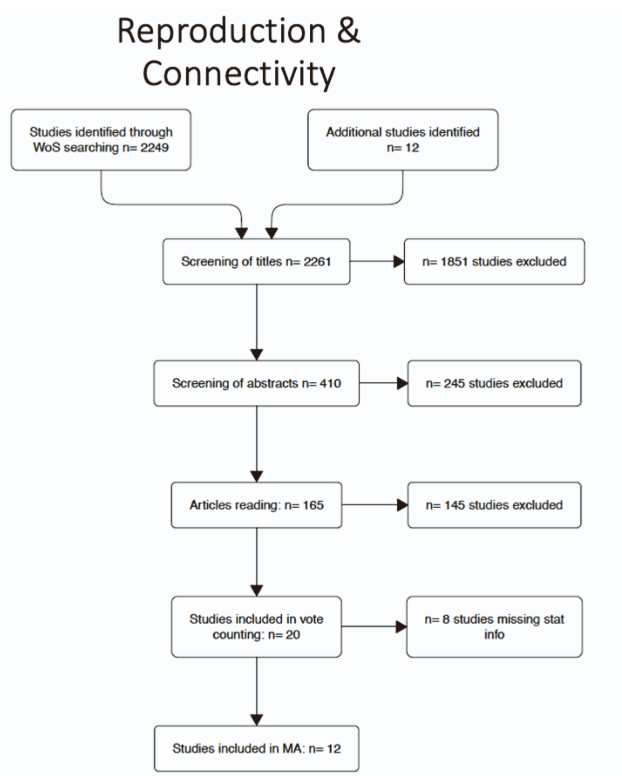
Reproduction & Connectivity
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Additional studies identified n= 12
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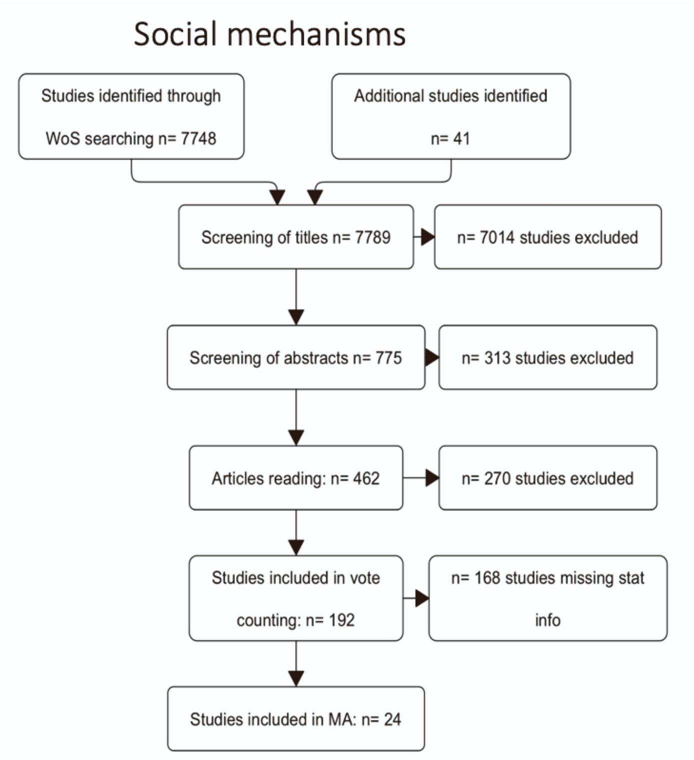


Figure S1. PRISMA plots detailing the selection phases of each systematic review carried out. PRISMA plots were obtained using the plot_PRISMA() function from the {metagear} package in R. Sample size (n=) indicate the number of studies selected or excluded at each phase. Related to Figure 1.

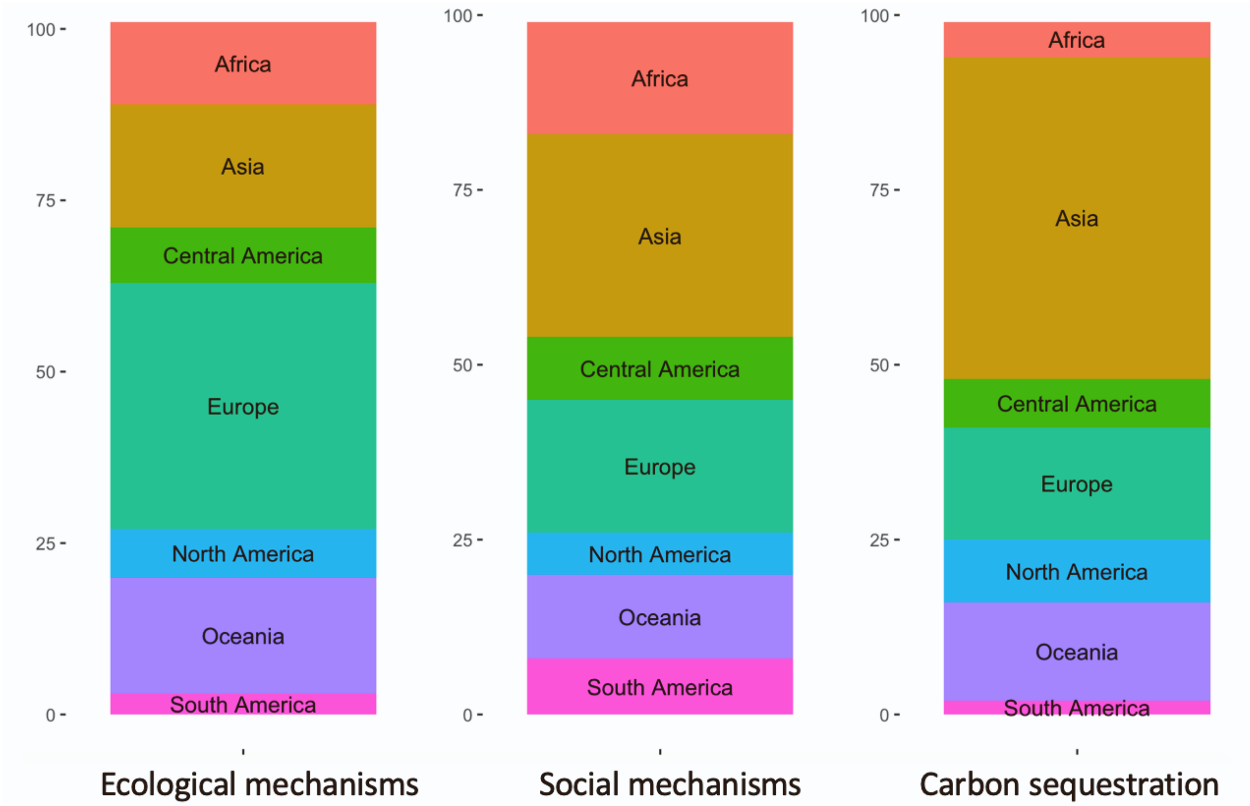


Figure S2. Distribution of studies included in our review among continents. Y axes represent %. Related to Figure 1.

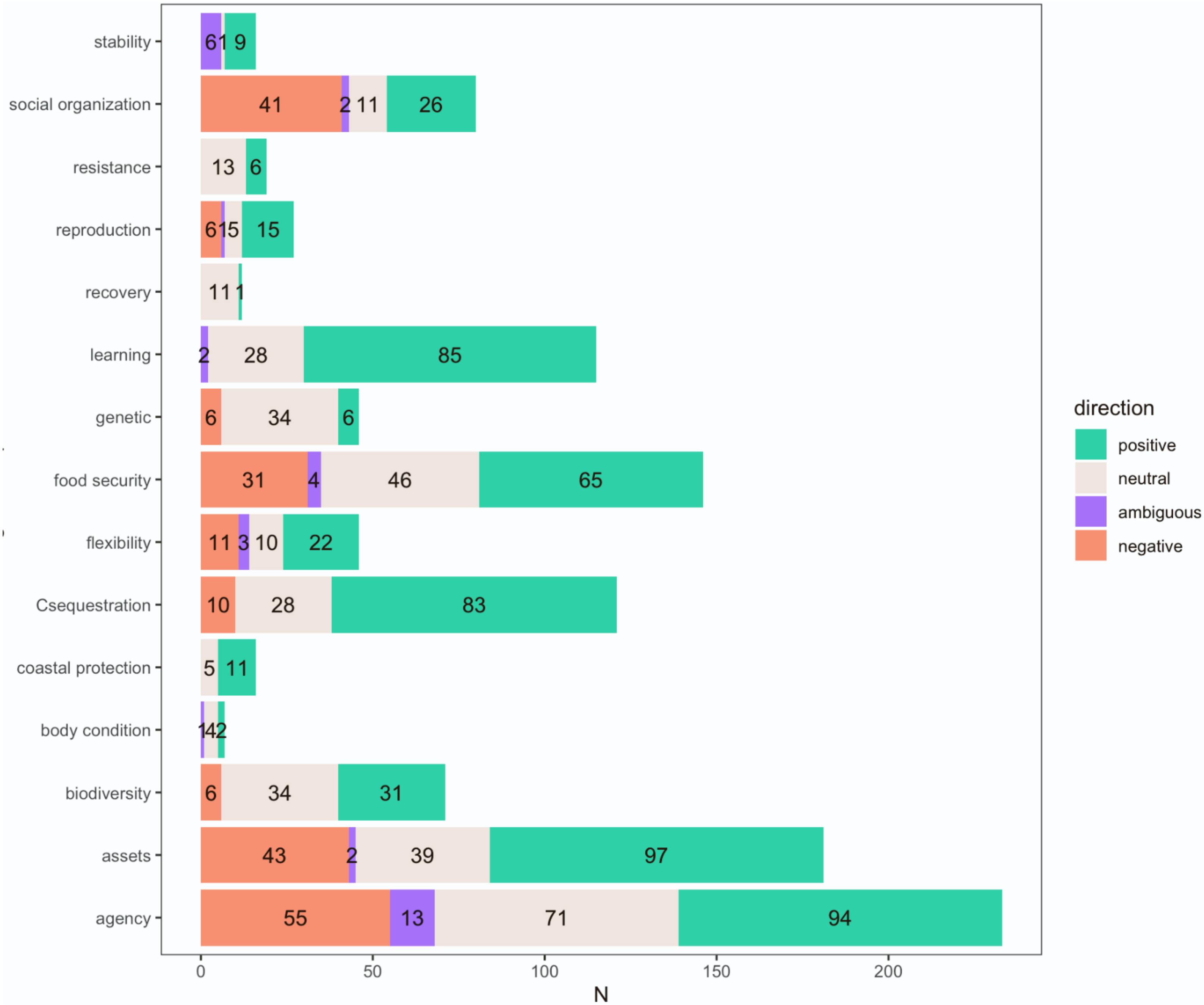


Figure S3. MPA outcomes on all studied mechanisms obtained through vote-counting. X axis indicates the cumulative number of data points (N) included in the vote counting for each pathway. Numbers in the barplots represent the number of data points of each direction (positive, neutral, ambiguous and negative).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

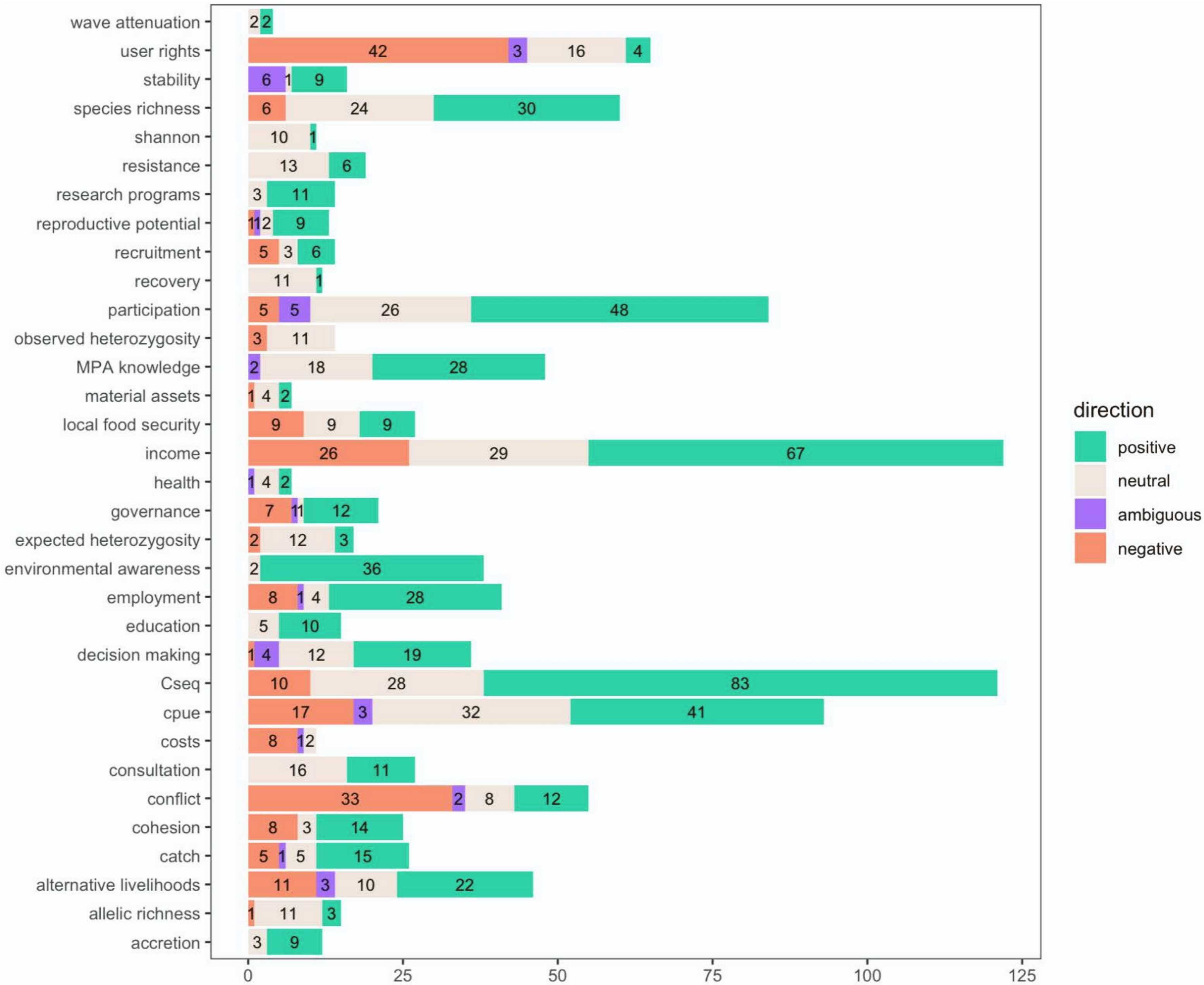
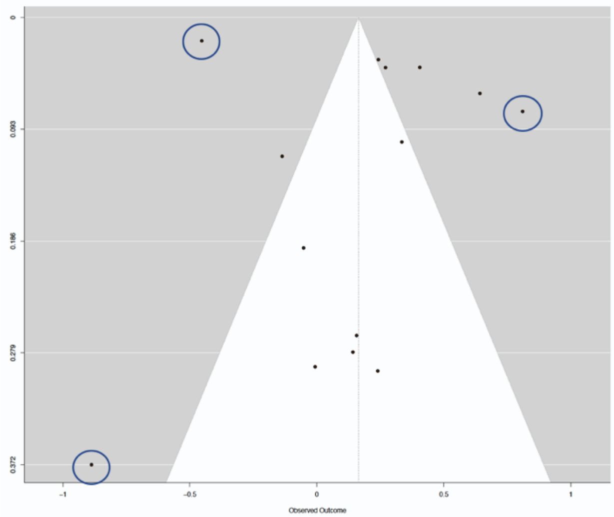
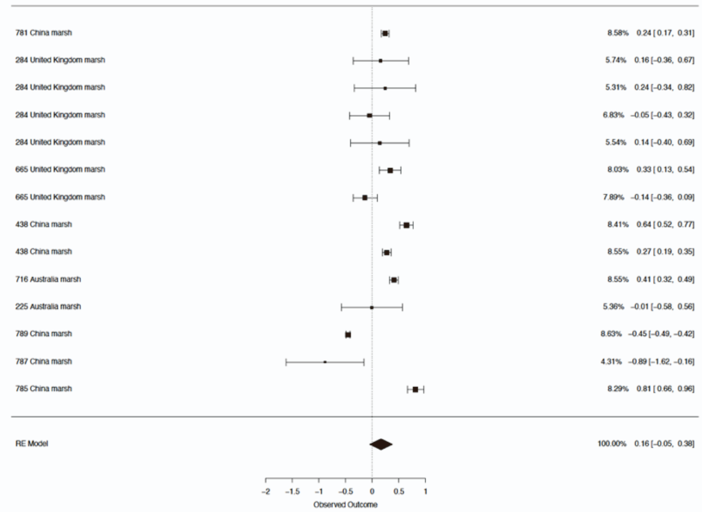


Figure S4. MPA outcomes on all studied indicators, obtained through vote-counting. X axis indicates the cumulative number of datapoints (N) included in the vote counting for each pathway. Numbers in the barplots represent the number of data points of each direction (positive, neutral, ambiguous and negative).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

Tidal marsh

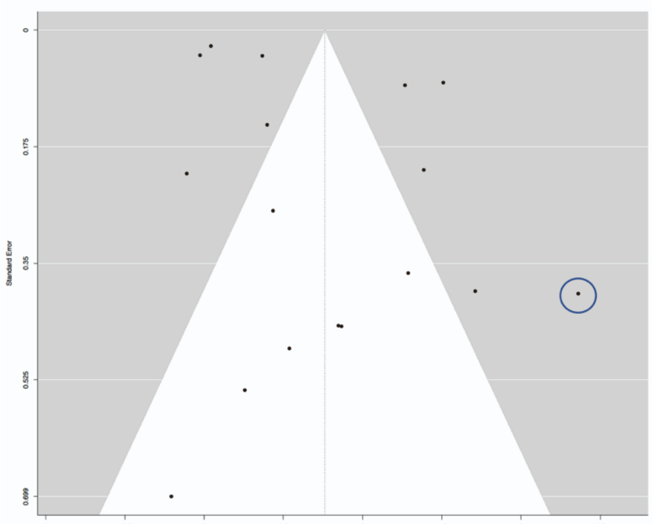


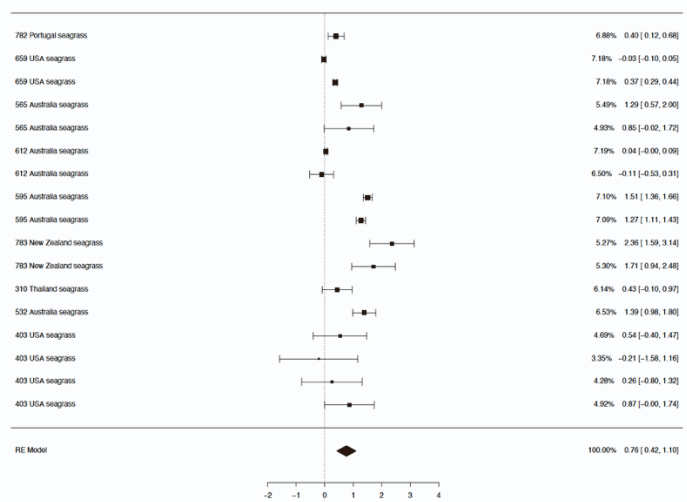



```
tau^2 (estimated amount of total heterogeneity): 0.1374 (SE = 0.0642)
tau (square root of estimated tau^2 value):      0.3706
I^2 (total heterogeneity / total variability):   97.51%
H^2 (total variability / sampling variability):  40.08

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

Seagrass

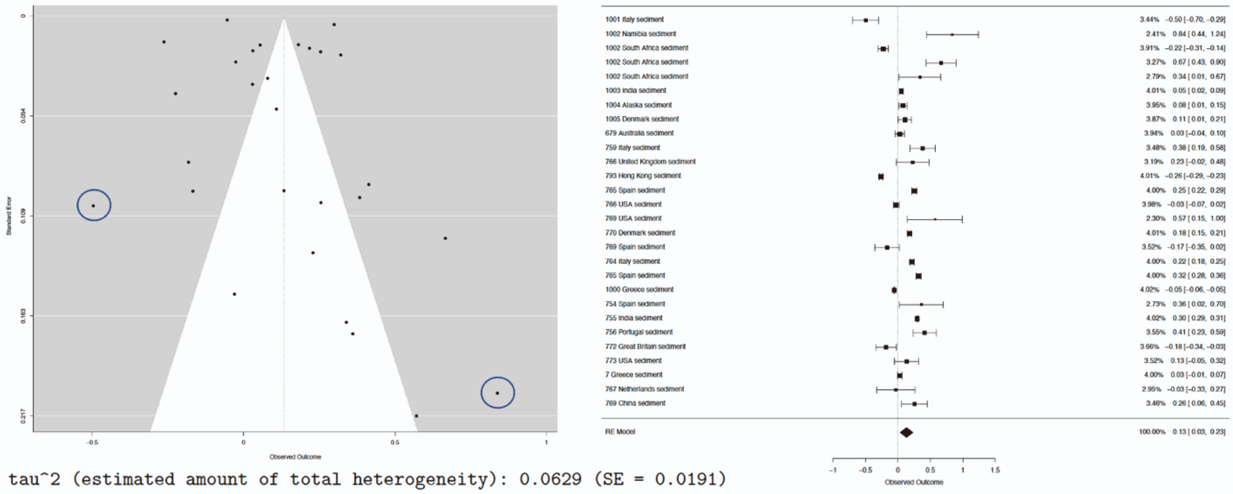





```
tau^2 (estimated amount of total heterogeneity): 0.4259 (SE = 0.1814)
tau (square root of estimated tau^2 value):      0.6526
I^2 (total heterogeneity / total variability):   98.49%
H^2 (total variability / sampling variability):  66.39

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

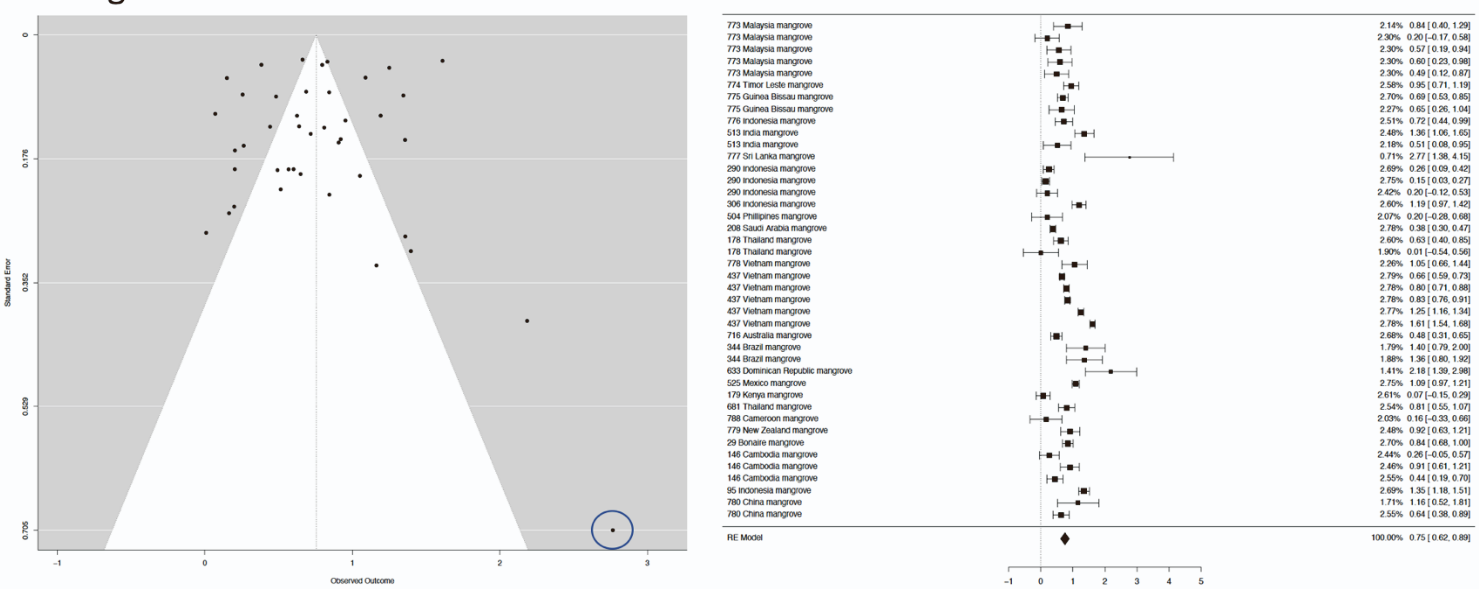
Sediment




```
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
```

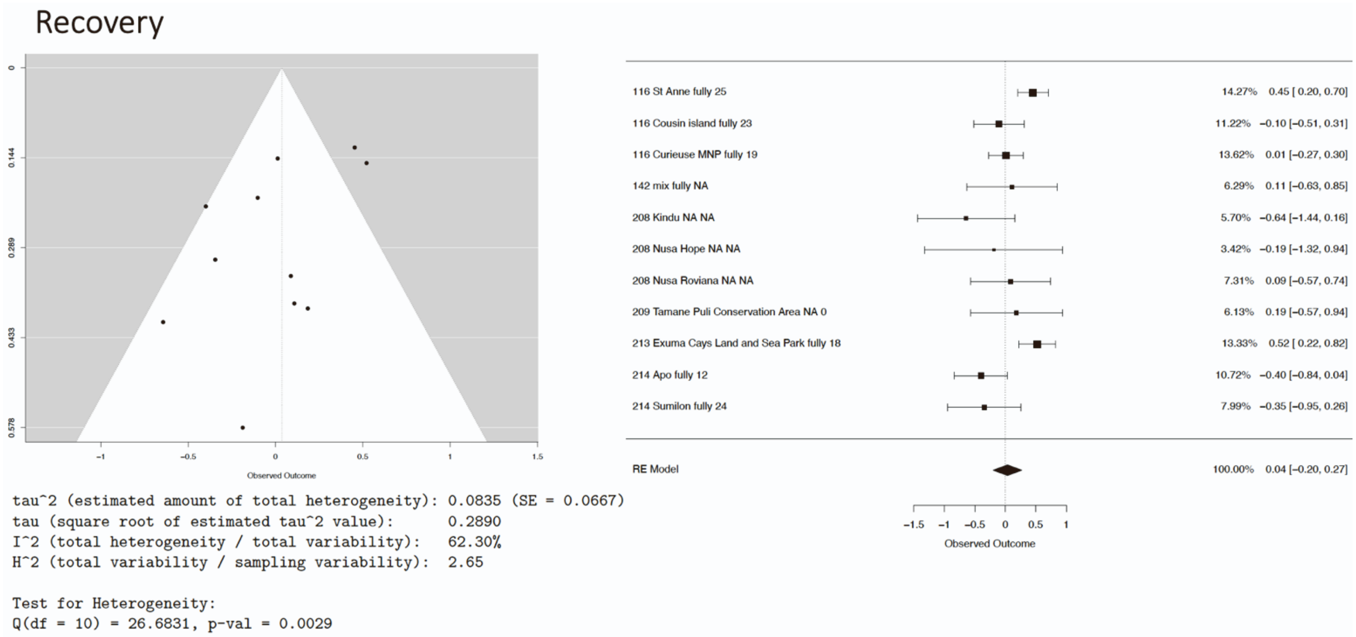
Mangrove




```
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
```

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.



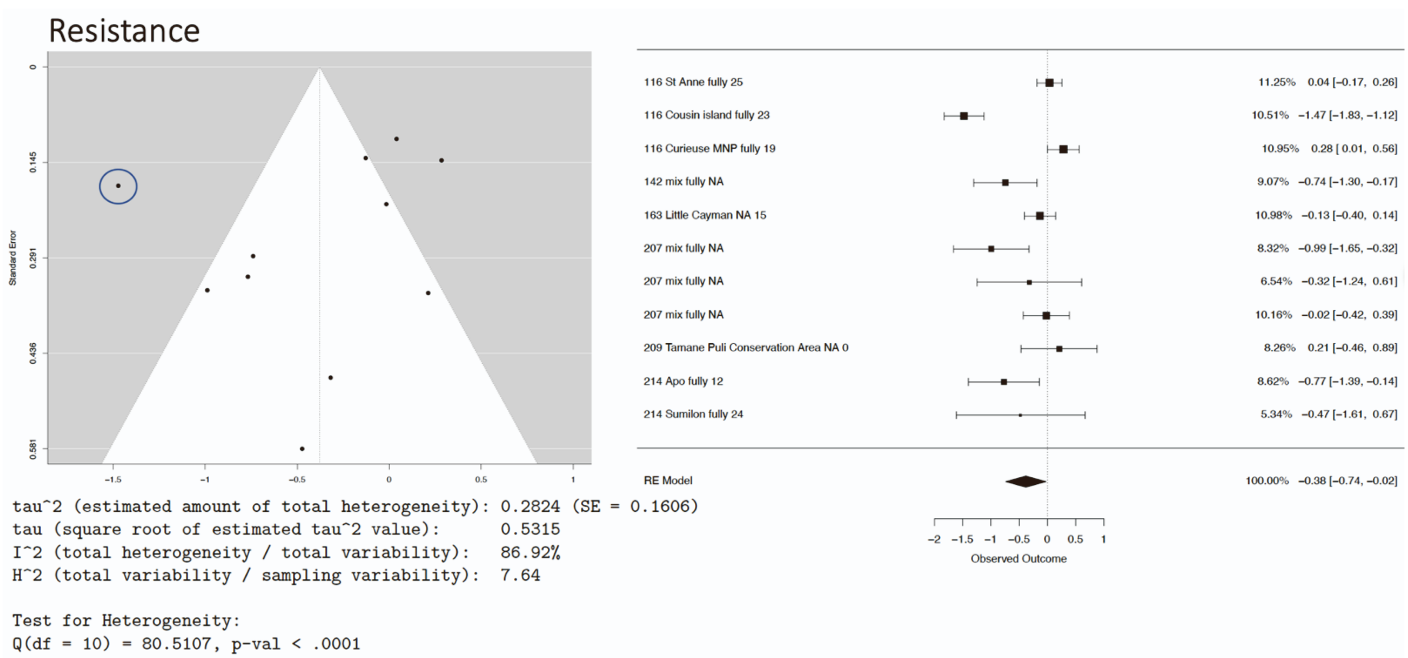
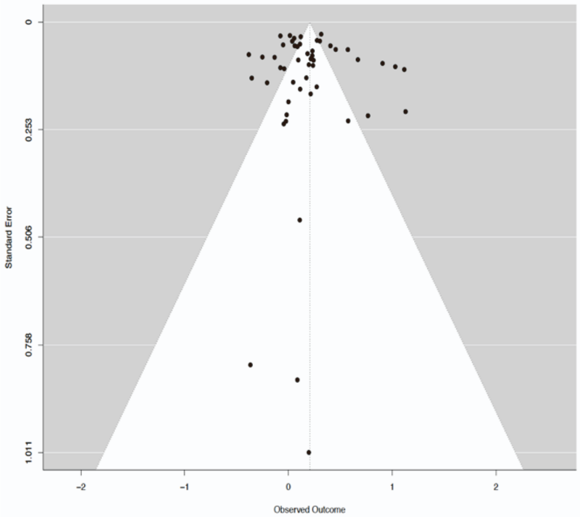
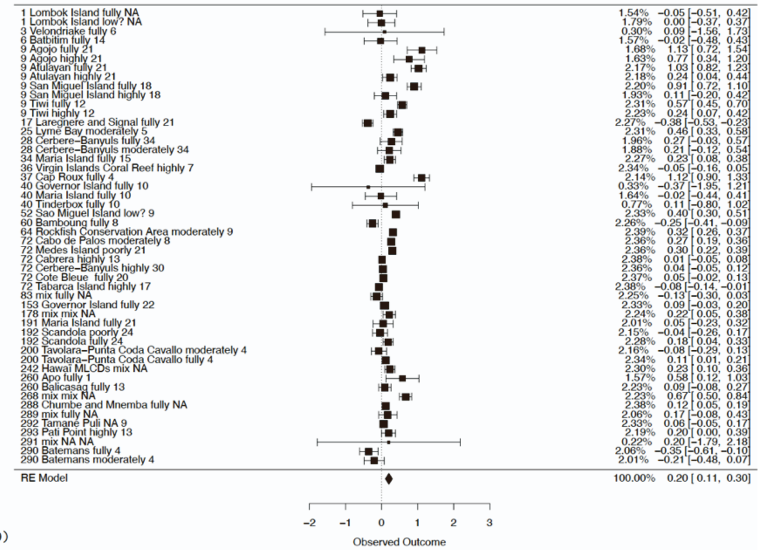


Figure S5.2. Funnel plots and forest plots of the effect sizes included in the resilience meta-analyses (from top to bottom: recovery and resistance indicators). Effect sizes circled in the funnel plots are identified outliers that were checked. Related to Figure 4.

Species richness

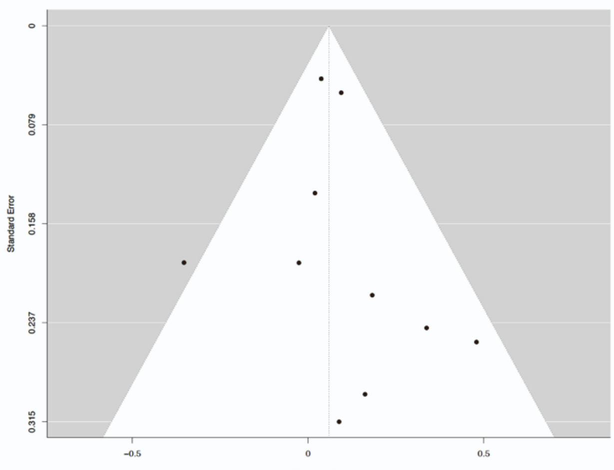


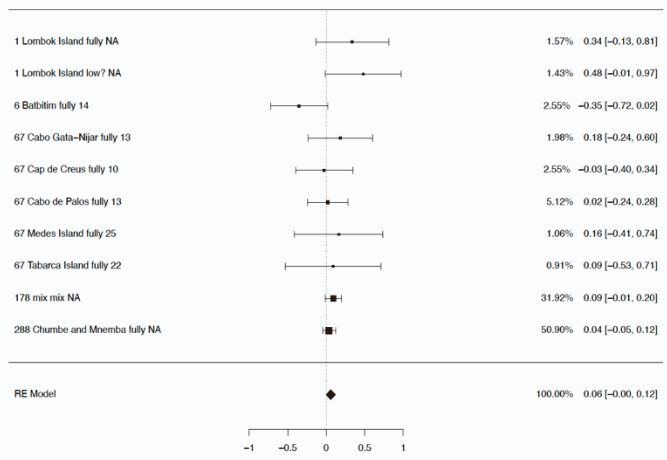



```
tau^2 (estimated amount of total heterogeneity): 0.1019 (SE = 0.0239)
tau (square root of estimated tau^2 value):      0.3192
I^2 (total heterogeneity / total variability):   95.64%
H^2 (total variability / sampling variability):  22.92

Test for Heterogeneity:
Q(df = 49) = 637.1608, p-val < .0001
```

Shannon Index






```
Random-Effects Model (k = 10; tau^2 estimator: REML)

tau^2 (estimated amount of total heterogeneity): 0.0000 (SE = 0.0031)
tau (square root of estimated tau^2 value):      0.0004
I^2 (total heterogeneity / total variability):   0.00%
H^2 (total variability / sampling variability):  1.00

Test for Heterogeneity:
Q(df = 9) = 10.3409, p-val = 0.3236
```

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.

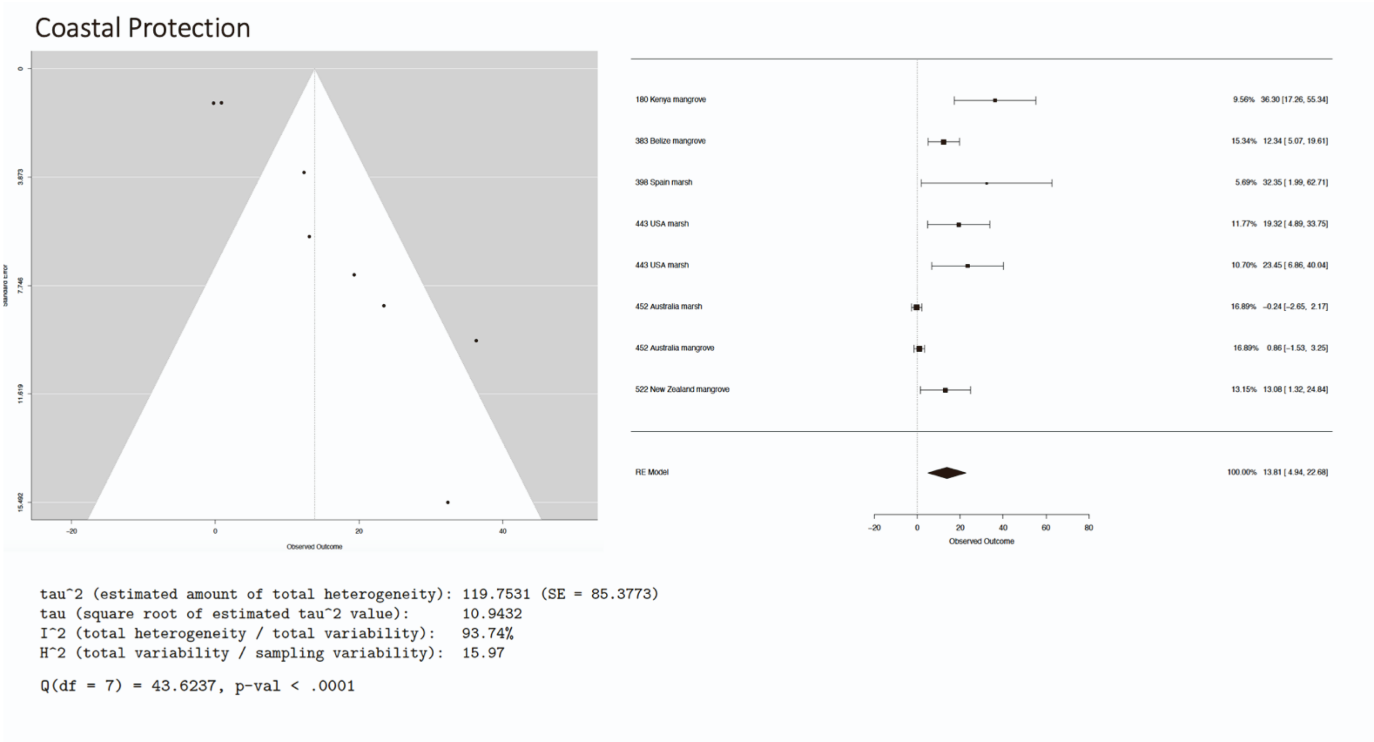


Figure S5.4. Funnel plots and forest plots of the effect sizes included in the coastal protection meta-analyses. Related to Figure 2.

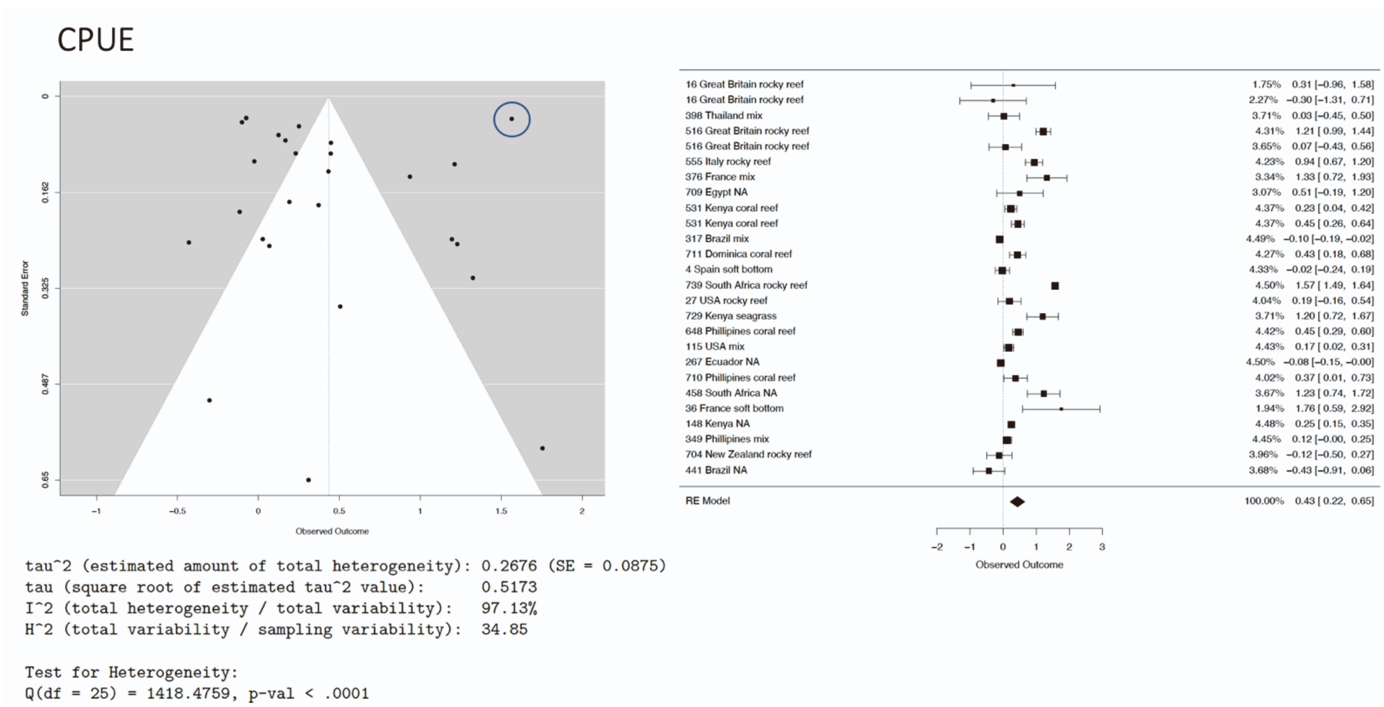


Figure S5.5. Funnel plots and forest plots of the effect sizes included in the CPUE meta-analysis effect sizes circled in the funnel plots are identified outliers that were checked. Related to Figure 2.

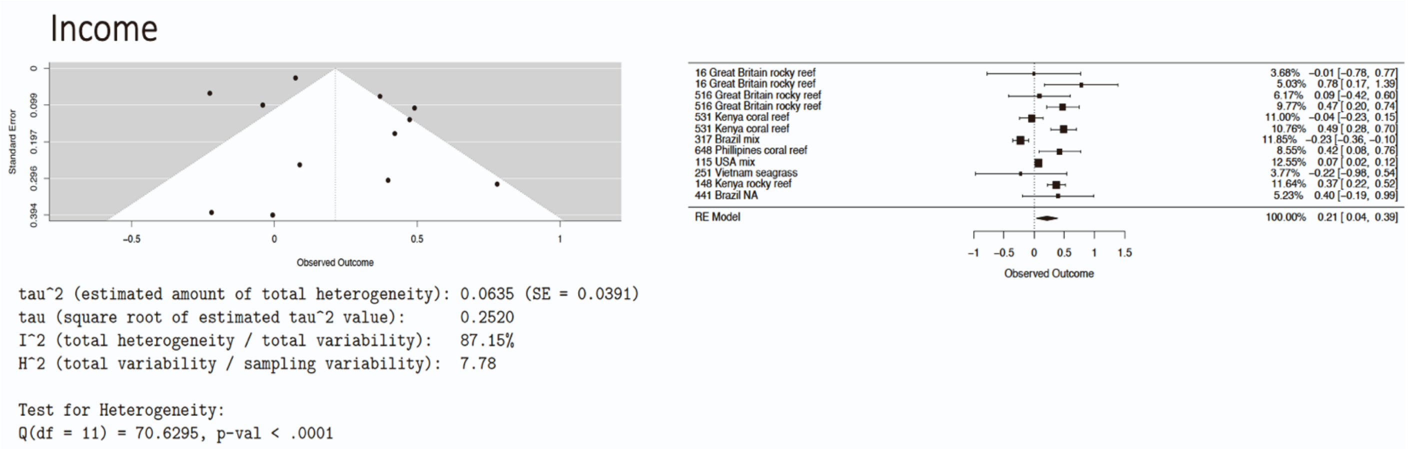


Figure S5.5. Funnel plots and forest plots of the effect sizes included in the CPUE meta-analysis effect sizes circled in the funnel plots are identified outliers that were checked. Related to Figure 2.

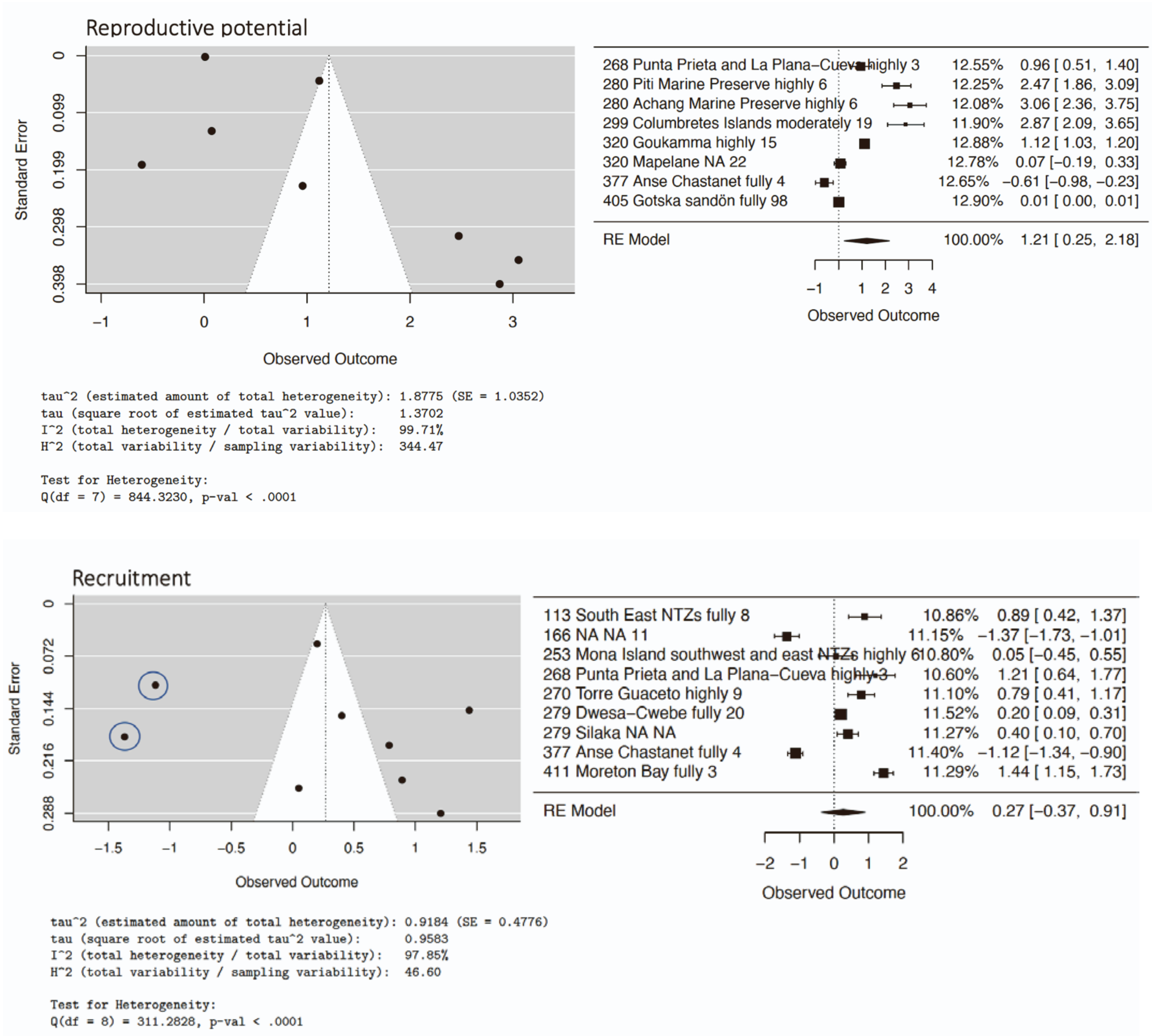


Figure S5.6. Funnel plots and forest plots of the effect sizes included in the reproduction meta-analyses (from top to bottom: reproductive potential and recruitment indicators). Effect sizes circled in the funnel plots are identified outliers that were checked. Related to Figure 2.

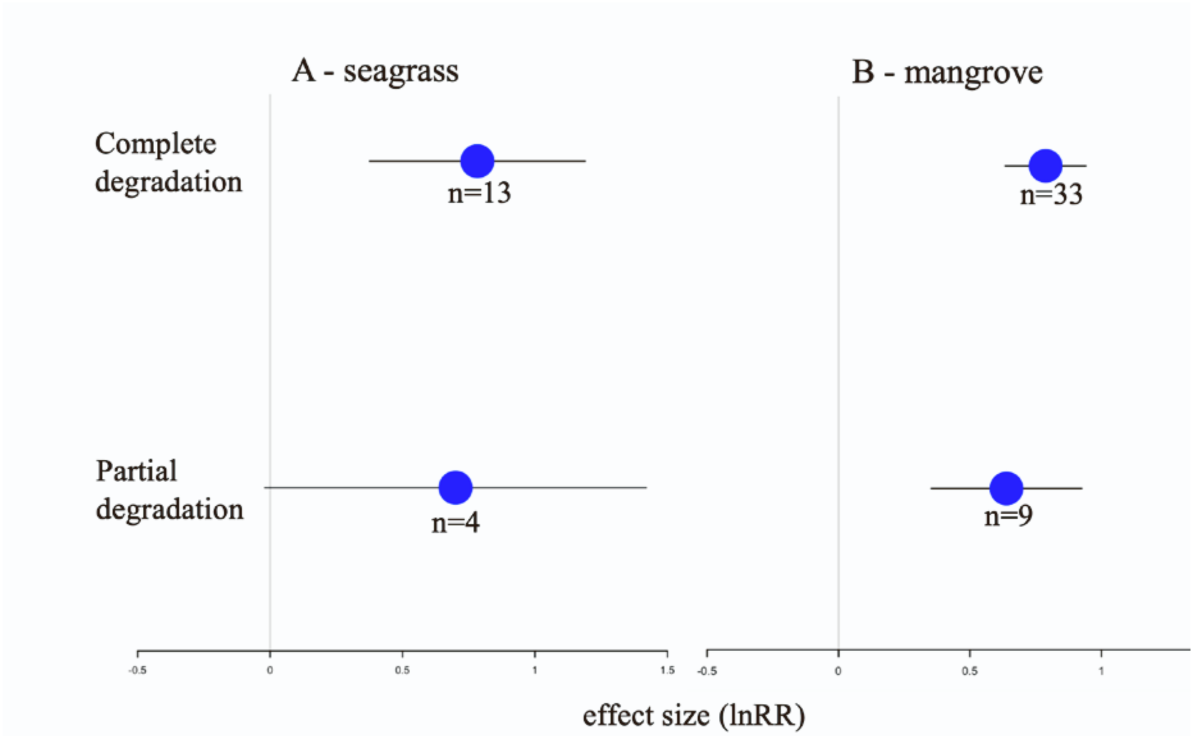


Figure S6. Effect of the level of degradation of habitats on the carbon sequestration benefits achieved from protection of seagrass (A) and mangrove (B). Error bars are 95% confidence interval. Sample size (n=) indicate the number of data point from which the effect size was calculated. Related to Figure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

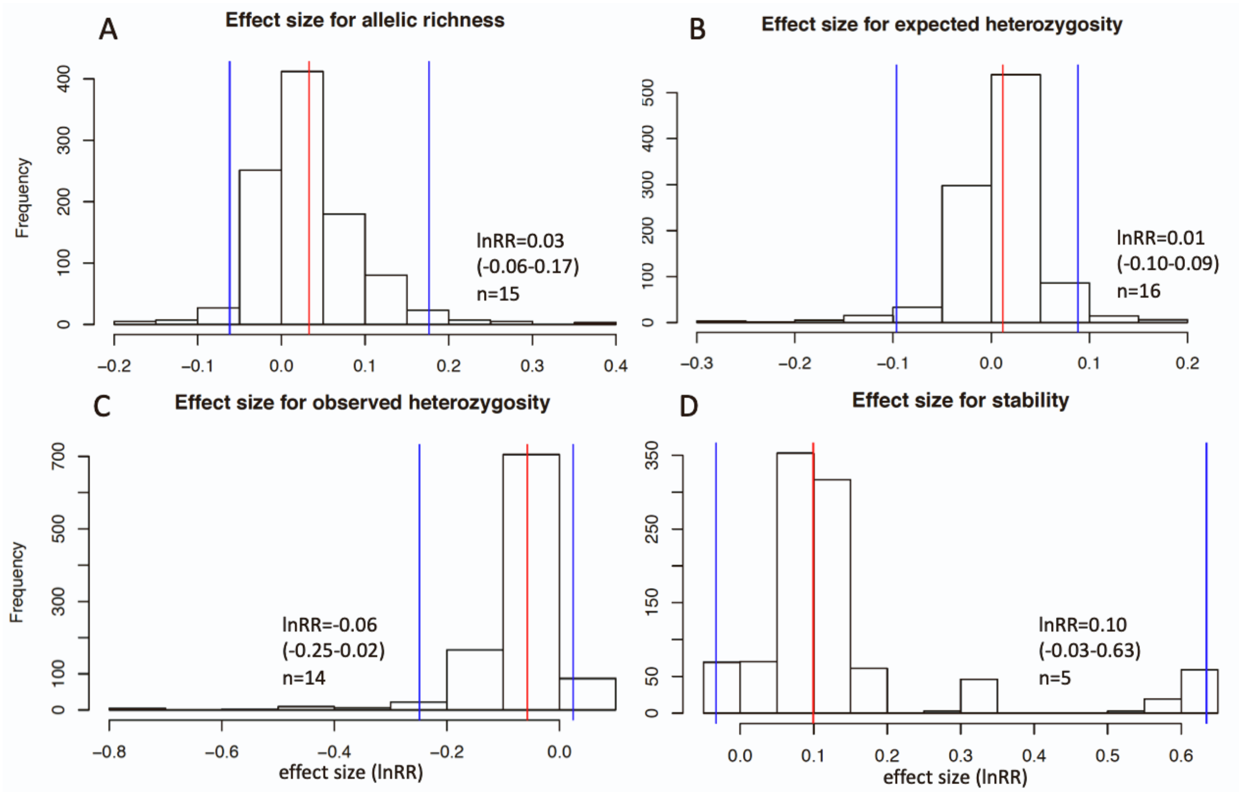


Figure S7. Effect size obtained by boot-strapping. Genetic diversity indicators (A-C) and stability indicator (D). Barplots represent the number of times each value of effect size was obtained out of 1000 iterations. The red vertical line represents the mean effect size value obtained, and the blue lines 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.

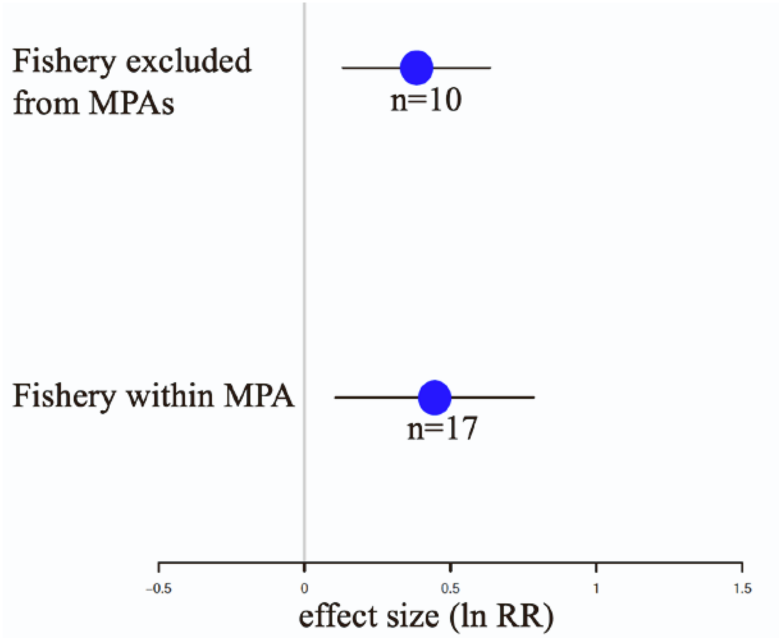


Figure S8. Changes in CPUE measured in fisheries excluded from MPAs and measured in fisheries allowed in MPAs. Effect size represent log ratios. Error bars are 95% confidence interval. Sample size (n=) indicate the number of data point from which the effect size was calculated. Related to Figure 2.

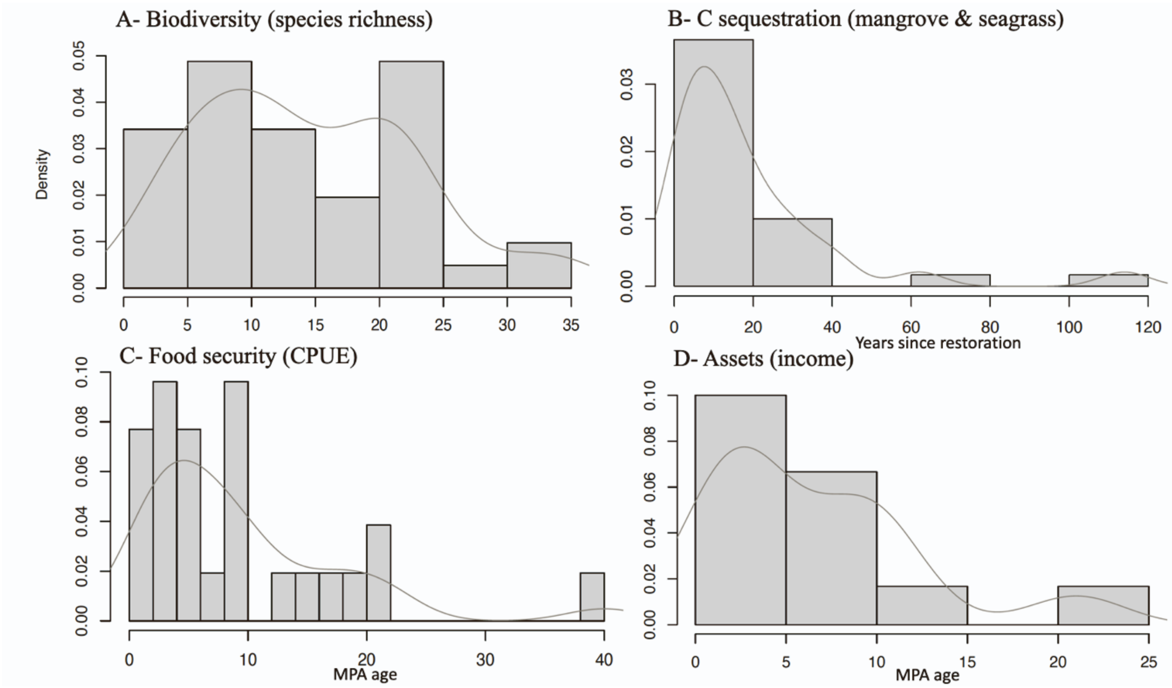


Figure S9.1. Distribution of the age of MPAs (log transformed) included in the meta-analyses on biodiversity, C sequestration, food security and assets.

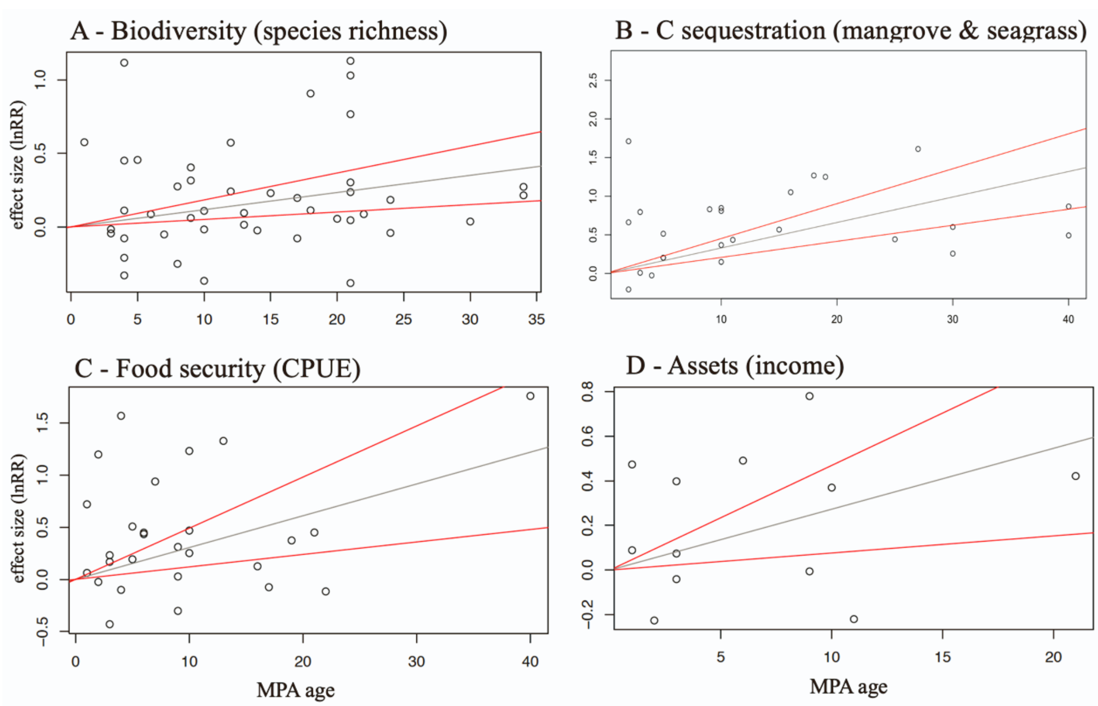


Figure S9.2. Effect of MPA age on biodiversity, carbon (C) sequestration, food security and assets. For C sequestration, only mangrove and seagrass C pools were included in the analysis. Gray line indicates the regression coefficient of the model, and the red lines the 95% confidence interval associated with the regression coefficient of the model. Dots indicate data points obtained from individual studies.

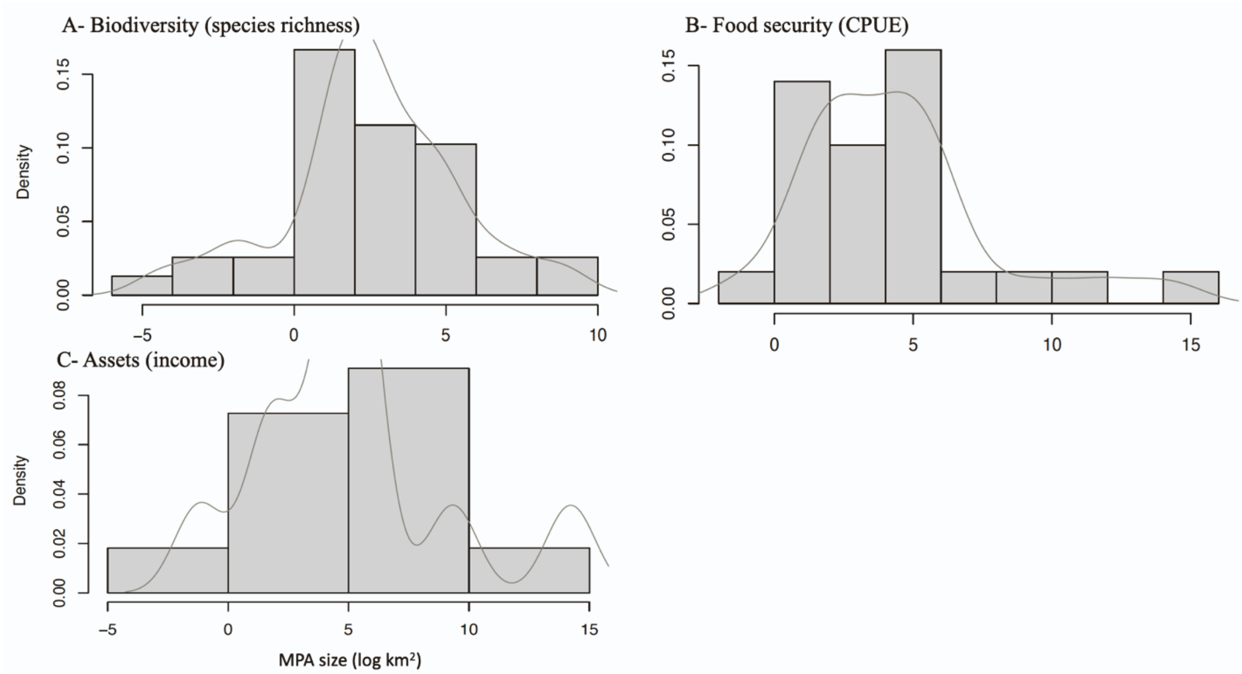


Figure S10.1. Distribution of the size of MPAs (log transformed) included in the meta-analyses on biodiversity, food security and assets.

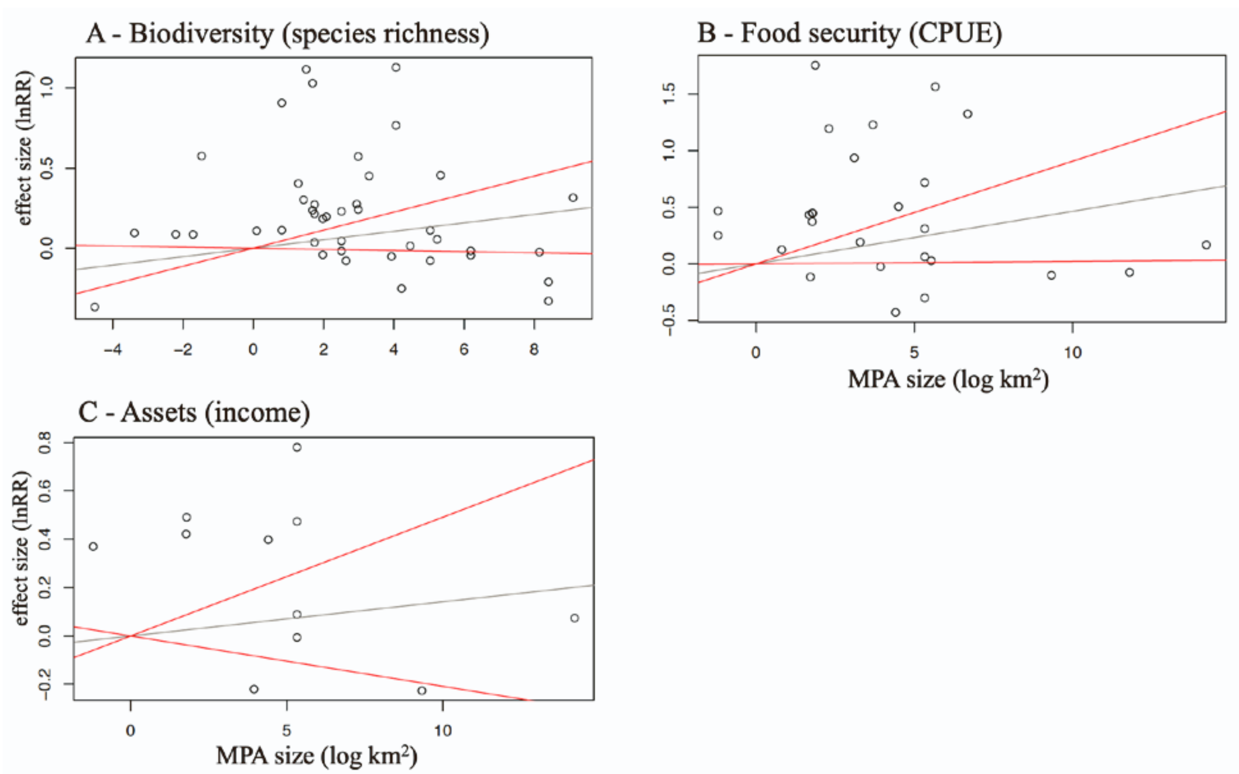


Figure S10.2. Effect of MPA size (log transformed) on biodiversity, food security and assets. Gray line indicates the regression coefficient of the model, and the red lines the 95% confidence. interval associated with the regression coefficient of the model. Dots indicate data points obtained from individual 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 metabolic, 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 offspring 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	ability to have free choice in responding to environmental change	user rights	increase or decrease of rights (binary)
				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 is the p value. Related to Figures 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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