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Drivers of ecological effectiveness of marine protected areas: A meta-analytic approach from the Southwestern Atlantic Ocean (Brazil)

Harildon M. Ferreira [a,*], Rafael A. Magris [a], Sergio R. Floeter [b], Carlos E.L. Ferreira [c]

[a] Chico Mendes Institute for Biodiversity Conservation, Ministry of Environment, Brasilia, Brazil
[b] Marine Macroecology and Biogeography Laboratory, Department of Ecology and Zoology, Federal University of Santa Catarina, Florianópolis, Brazil
[c] Reef Systems Ecology and Conservation Lab, Departamento de Biologia Marinha, Universidade Federal Fluminense, Rio de Janeiro, Brazil

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ABSTRACT

With the rapid global increase in the number and extent of marine protected areas (MPAs), there is a need for methods that enable an assessment of their actual contribution to biodiversity conservation. In Brazil, where MPAs have been designated to replenish biodiversity, there is a lack of regional-scale analysis of MPA impacts and the factors related to positive ecological change. This study aims to quantify the magnitude of the ecological effects of Brazilian MPAs and test whether some study and MPA characteristics (e.g., taxonomic group studied, exploitation level of species, MPA area, protection time, management effectiveness, level of connectedness, etc.) were underlying factors associated with their performance. We conducted a structured search in a database of scientific articles, selecting comparative studies of direct biodiversity metrics inside and outside MPAs offering different protection levels (i.e., fully- or partially-protected MPAs) or within MPAs with distinct zones. We then carried out a meta-analysis based on 424 observations found in 18 articles. Averaged across all studies, we found that MPAs had a 17% increase in the abundance of species, length of individuals, and community diversity. When compared to open-access areas, fully-protected MPAs increased biodiversity by 45%. However, MPAs offering partial protection had variable effects, ranging from significant positive to significant negative effects. MPA effects depended on the taxonomic group and exploitation level of species, with the strongest positive effects seen on exploited fish species and benthic invertebrates. Partially-protected MPAs that reported strong positive effects required long time of protection (>15years) and high level of connectivity. Conversely, fully-protected MPAs (i.e., no-take ones) could be effective even when small, under intense fishing pressure in their surroundings, and regardless of their level of connectivity. We used the Brazilian MPAs as a case study, but these results can contribute to a more comprehensive assessment of the association between ecological impacts of MPAs and drivers of conservation success, and offer key information to consolidate MPA networks that sustain biodiversity.

1. Introduction

Marine protected areas (MPAs) are the cornerstone of most conservation strategies worldwide and often recommended as a tool for protecting imperiled biodiversity (Di Minin and Toivonen, 2015; Lubchenco and Grorud-Colvert, 2015; McCauley et al., 2016). MPAs are expected to make a substantive contribution to biodiversity conservation such as helping species to restore their populations (e.g., Gaines et al., 2010) and maintaining ecosystem services (e.g., Leenhardt et al., 2015). Altogether, there are 25.3 million km^2 of marine areas covered by MPAs (Jantke et al., 2018). Because of recent international commitments to protect biodiversity such as the Convention on Biological Diversity - (CBD) and the Sustainable Development Goals (SDG), the establishment of new MPAs is likely to continue in the future. However, the growth in the global network of MPAs comes with increasing concerns regarding their conservation outcomes for biodiversity in the real-world context (e.g., Woodcock et al., 2017).

The success of MPAs in benefiting biodiversity growth and persistence is strongly contingent upon effective management. MPAs are financially challenging to be implemented and monitored (McCarthy et al., 2012), while enforcement efforts can be prohibitively expensive (Gill et al., 2017). Even for MPAs that are designed with management considerations in mind, they usually face implementation challenges such as limited political will and institutional capacity coupled with

* Corresponding author.
E-mail addresses: harildon.ferreira.bolsista@icmbio.gov.br, harildon@gmail.com (H.M. Ferreira).

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poor data and policy complexity (Ban et al., 2011; Davidson and Dulvy, 2017; Mills et al., 2020). Ultimately, the effectiveness of MPAs is also shaped by the level of compliance with MPA rules (Arias et al., 2015; Bergseth and Roscher, 2018), social impacts of MPAs (Jones et al., 2017; McNeill et al., 2018) and how governance principles are incorporated into the decision-making process (Bennett and Satterfield, 2018).

In the last decade, Edgar et al. (2014) demonstrated that the conservation benefits of MPAs accumulate with five key features: area, level of protection, age, level of enforcement, and isolation. Consequently, meta-analytic approaches to evaluate MPAs based on spatial response ratios have proliferated in the literature, usually measured as the ratio of density or biomass of species within protected relative to control, unprotected sites. The prevailing view is that fully-protected areas (e.g., no-take MPAs) enhance biodiversity to a greater degree than partially-protected ones (Giakoumi et al., 2017; Sciberras et al., 2013) and that effects of partially-protected areas increases when they are located in the adjacency of fully-protected MPAs and well enforced (Di Lorenzo et al., 2020; Zupan et al., 2018). Global patterns in the strength of ecological effects of MPAs have also demonstrated that fish species targeted by fisheries benefitted the most from protection (Di Lorenzo et al., 2020; Rojo et al., 2019). Despite the widespread expectation that large MPAs influence positively biodiversity, empirical evidence for this pattern is mixed (Giakoumi et al., 2017; Rojo et al., 2019). Other MPA parameters thought to be important, such as the presence of fishing activity near MPAs, the strength of management, and the occurrence of ecologically connected habitats within their boundaries, are missing for more comprehensive assessments. These facts highlight the need for a better understanding of the possible drivers of MPA performance.

In this study, a meta-analysis of published evidence is used to quantify the ecological effectiveness of MPAs of different categories of protection at a regional scale (Southwestern Atlantic Ocean; Brazil), and to examine how MPA characteristics correlate with the strength of effects from protection. We present a synthesis of studies assessing biodiversity along the Brazilian coast from 2001 to the present. To focus our investigation, we aim to identify specific study and MPA characteristics best correlate with any patterns in protection effects. The attributes from studies encompass the taxonomic group examined, its exploitation level, the metric used to measure biodiversity, and the distance of sampling points from MPAs boundaries. The attributes of the MPAs encompass MPA area, its management effectiveness, time of protection, the degree to which protected habitats connect with the surroundings at the seascape level, and the occurrence of fishing activity near the MPA boundaries. We broadly define ecological effectiveness of MPAs as the added benefit measured in biodiversity metrics (e.g., species abundance and biomass) over and above unprotected areas or areas under partial protection, and the resulting impacts on the respective metric.

2. Material and methods

2.1. Data compilation and extraction

We collected data through online databases to find research articles that could be used to investigate the ecological effects of MPAs in Brazil. For this search, we collected publications from Web of Science (All Databases; Thomson Reuters) on January 2020 using the combinations of the following keywords: "Brazil* AND ((marine protected area*) OR (marine reserve*) OR (marine no-take area*) OR (marine conserved area*))". This initial search resulted in 347 articles. The resulting articles were supplemented by a search of the reference lists of the articles acquired from the initial search. We carefully assessed each article to identify relevant publications following the inclusion criteria: (i) empirical study that used multiple locations (e.g., replicates for both within and outside MPAs) to measure biodiversity metrics (i.e., density, biomass of individuals per area, size of individuals, or species diversity); and (ii) study that explicitly reported sample sizes, means, and statistical measures of variation around the means (i.e., standard deviations, standard errors, or confidence intervals). We only included an article if the assessment had a sampling location deemed appropriate to use as a comparable reference for the protected sites under study. This resulted in a total of 18 articles for data extraction (see Supplementary material S1 for full reference list).

The 18 articles reported 424 valid observations assessing the effects of protection in 18 MPAs. We considered an observation every single biological measurement involving a comparison between inside and outside MPAs or within MPAs offering two different levels of protection in separate zones (full *versus* partial protection). Fully-protected MPAs (i.e., no-take zones) or fully-protected zones refer to areas where extractive activities are not allowed (i.e., corresponding to the IUCN categories Ia and b, II and III), while partially-protected MPAs (i.e., multiple-use ones) or zones refer to areas where extractive activities are permitted but are regulated, spatially and temporally, to a greater extent than areas outside these MPAs (i.e., corresponding to the IUCN categories IV, V, and VI). When possible, we extracted data directly from tables and the text of the articles. In cases the data was presented in a figure format, we used WebPlotDigitizer (Rohatgi, 2011) to extract them from figures. For articles reporting a time series, we only included the last data point, a standard practice in ecological meta-analysis (Magris and Ban, 2019). We extracted all biodiversity metrics where samples collected within MPAs were compared to samples outside MPAs or between zones within the same MPA. Thus, a study could have multiple observations if it analyzed multiple biodiversity metrics (i.e., abundance, diversity, and size of individuals) or more than one species or taxonomic group. If the article provided comparisons for more than one MPA, we also considered each one as a separate observation.

When a study provided both species-specific and multi-species measurements, we elected to include only the more specific ones to prevent double-counting. We included only results reported for the period after MPA establishment. Other studies had multiple observations sharing the same control. To avoid potential pseudo-replication, we treated these data in a specific way (see below). In each observation, we extracted data on (i) the biodiversity metric used (abundance, biomass, length, diversity), (ii) the information necessary to calculate an effect size, (iii) the geographical coordinates of sampling stations, and (iv) other study attributes possibly associated with response ratios (i.e., the taxonomic group assessed - algae, invertebrate, fish, or other vertebrate, and the exploitation status of species - targeted or non-targeted for fisheries). Targeted species for fisheries were assigned according to authors' information or peer-reviewed literature (Begossi and Richerson, 1993; Filho, 1992; Froese and Pauly, 2000).

2.2. Meta-analysis

We used a weighted random-effects meta-analysis to estimate the ecological effectiveness of MPAs (effect size), allowing for comparison between observations conducted in different regions and with different methodologies (Hedges et al., 1999). The effect size for each observation i was modeled as a natural logarithm response ratio (LnRR) and measured as:

$$LnRR = ln\left(\frac{Xt}{Xc}\right) \quad (1)$$

where Xt is the mean value for a quantified metric (e.g., abundance, diversity) when biological communities were protected and Xc is the mean value for a quantified metric when biological communities were outside MPAs (i.e., open-access areas). We replaced the mean value for the metric outside MPAs by the mean value for the metric inside partial-protection MPAs when comparing full *versus* partial protection levels. We also calculated the variance of the response ratio measured as:

$$V_{LnRR} = \left(\frac{SDt^2}{Nt \times (Xt)^2}\right) + \left(\frac{SDc^2}{Nc \times (Xc)^2}\right) \tag{2}$$

where *SDt* and *Nt* are the standard deviation and the sample size associated with the metric measured in the protected site, respectively, and *SDc* and *Nc*, the standard deviation and sample size associated with metric in the open-access site. Similarly to the LnRR calculation, we also replaced *SDc* and *Nc* by the corresponding information for the partial protection MPA or zone when this was the case. To improve the precision of effects, we used the inverse of variance-weighted model, such that observations with higher sample sizes were given more weight:

$$E_{LnRR} = \frac{\sum_{i=1}^{k} W_i LnRR_i}{\sum_{i=1}^{k} W_i} \tag{3}$$

where *LnRRi* and *Wi* are the effect size and weight (inverse variance) associated with each observation included in the analysis, respectively, and K is the number of observations. We used the 'metafor' package and the DerSimoniam-Laird estimator (DerSimonian and Laird, 1986; Viechtbauer, 2010) to calculate the overall effect sizes.

Thus, for all metrics, positive effect size (E_{LnRR}) values imply that the MPA positively affects biodiversity, while negative values imply a loss of biodiversity due to the presence of an MPA. Values around zero means there is no effect. We consider a mean effect size to be significant when its 95% confidence interval (CI) does not overlap zero. When data were presented for several treatments sharing the same control, we calculated a single effect size value as the average of individual effect sizes, and a variance that took into account the correlation among different treatments (Borenstein et al., 2009).

We synthesized the data for the ecological effect of MPAs using subgroup random effect models, to estimate the overall effects on each of our biodiversity metrics. To foster a deeper understanding of the ecological effects of MPAs, we analyzed the response ratios according to the protection level offered by MPAs, pooling data from different metrics, which resulted in three comparisons: full protection *versus* open access areas ($N = 122$ observations); full protection *versus* partial protection ($N = 143$ observations); and partial protection *versus* open-access areas ($N = 168$ observations). To compare the performance across all studied MPAs, we synthesized the effect size values within each MPA according to their respective management categories. We reported all results for the predictor analyses only when sufficient data was available ($k > 5$ observations).

We used four independent methods to examine whether publication bias occurs in the literature used. The first one was the most common method used for assessing publication bias, i.e., the funnel plot (Light and Pillemer, 1985). Because evaluating the plot asymmetry by visual inspection only can be subjective (Terrin et al., 2005), we also applied the Egger's test, which is based on a linear regression between the observed effect sizes and their standard errors (Egger and Smith, 1997). We also used the 'trim and fill' procedure, which provides an estimate of how the overall effect size would change if we were able to incorporate all missing studies and remove any funnel asymmetry (Jennions and Møller, 2002). Subsequently, we used a rank correlation test to evaluate the association between the standardized effect size and its sampling variance with Kendall's rank correlation coefficient (Begg and Mazumdar, 1994). Finally, we applied the most recently developed method to correct for the potential publication bias, the p-uniform. This method is based on the statistical principle that the distribution of p-values at the true effect size is uniform (null hypothesis). Since in the presence of publication bias not all statistically nonsignificant effect sizes get published, p-uniform discards nonsignificant effect sizes and computes p-values conditional on being statistically significant (van Assen et al., 2015). For publication bias analyses, we used the 'metaviz' (Kossmeier et al., 2020) and 'puniform' (van Aert, 2021) packages in addition to the 'metafor' package.

The summary effect sizes were back-transformed, so that they could be easily interpreted as the response ratio (RR) of metric obtained inside and outside the MPA or between two distinct zones offering different levels of protection:

$$RR = \left(e^{E_{LnRR}} - 1\right) \times 100 \tag{4}$$

This back-transformations process uses antilog to provide a geometric mean of the response ratios, which is known to underestimate the arithmetic mean (Rothery, 1988); however, this underestimation is generally very small (Hedges et al., 1999). Therefore, the percentage averages of the effect size reported here should be considered conservative estimates (Kroeker et al., 2013).

2.3. Predictor variables

Mixed effects models use predictors as a fixed effect and random effects to account for differences across studies assuming they do not share a common mean effect but that there is random variation among studies, in addition to within-study sampling variation (Borenstein et al., 2009). We performed mixed effects meta-analyses to investigate the potential influence of different predictors on the estimated effects of protection. In addition to study attributes, MPA characteristics included were: (i) area; (ii) protection time as the difference between the year of survey and the year of MPA establishment; (iii) management effectiveness, which describes the level of implementation of MPAs based on indicators such as MPA regulations, administrative capacity, level of threats faced by MPAs, and level of implementation of management plans; (iv) seascape connectivity as the extent to which protected habitats are interconnected with other habitats suitable for reef-associated species; and (v) level of fishing activity near the MPA boundaries. The effect of taxonomic groups and exploitation status of species were tested because previous studies have claimed that MPAs benefit some species more than others and serve as management tools for protecting particularly the fishing-target ones (Giakoumi et al., 2017). The effect of distance between protected and control sites, MPA area, protection time, and management effectiveness were tested because previous meta-analyses have suggested these factors were important to explain variation between MPAs offering full and partial protection (Sciberras et al., 2013; Zupan et al., 2018). The effect of connectivity was tested because previous study hypothesized that well-connected MPAs can enhance the effectiveness outcomes of protection (Magris et al., 2018). Lastly, the effect of fishing pressure surrounding MPAs has been tested because fishing mortality rates can affect the conservation success of MPAs (Di Lorenzo et al., 2020).

We collected data for each predictor from multiple sources. Information on MPA area and date of establishment were compiled from the dataset held by the Brazilian Ministry of Environment (MMA, 2020). The most recent overall score for the management effectiveness of each MPA were gathered from the dataset held by the national agency for biodiversity conservation (ICMBio, 2020), where the score values ranged from zero (considered to be poorly managed) to 100 (considered to be effectively managed). Distances between the sampling locations were obtained from the corresponding geographic coordinates and performed in Qgis 3.14 (QGIS, 2020). Based on a connectivity metric that combines physical attributes of the seascape (i.e., the spatial configuration of habitats) with information on the movement capability (i.e., estimates of typical reef's influence extensions) of reef-associated species (Magris et al., 2020), we mapped the level of connectedness between each MPA and the surrounding reef habitats. Threats posed by commercial fishing were expressed as the density of fishing activity detected in the adjacency of MPAs (in the unprotected area that was considered as control) and were captured by vessel monitoring systems (VMS) over 2015–2017 (Magris et al., 2020). The total area and connectivity metric associated with each MPA were log-transformed due to the large range of values.

We used two different approaches to explore the role played by predictors in explaining the differences in effect size, depending on the type of the predictor (if categorical or continuous). For categorical predictors, we examined the variation in the sensitivity of different taxonomic groups (i.e., algae, invertebrates, fish, and other vertebrates) to protection and the role played by MPAs in protecting fish species that are targeted or non-targeted to fisheries. To do so, we separated observations between these a priori defined subgroups and tested for differences among them. We carried out separate categorical meta-analyses using Q test to evaluate heterogeneity in effect sizes, which was compared against a chi-squared distribution (Gurevitch et al., 2001). We considered that a significant Q test statistic ($P < 0.05$) indicates a significant effect of the predictor on the mean effect observed.

For continuous predictors, we ran meta-regressions for each predictor individually based on intercept-only models to check whether these variables are associated with effect size differences (Harrer et al., 2019). To investigate whether comparisons involving different protection levels affected the strength of our effect size, each meta-regression is calculated using a mixed-effects model with a pooled estimate of *tau* (t^2), assuming that the true between-studies variance is the same for all subgroups (Borenstein et al., 2009). Differences between fixed-effect categories were determined using a Q-test on meta-regression coefficients.

To explore the contribution of the predictors, as well as all their possible combinations, and to have a better knowledge on how our predictors are related to effect sizes, we used the multimodel inference to produce multiple regression models representing alternative explanations for the found patterns. Prior to this procedure, we checked for collinearity among our predictors to make sure meta regression would be robust. The multiple models were compared using the corrected Akaike's Information Criterion (AICc) (Burnham and Anderson, 2007) and the package 'glmulti' (Calcagno and de Mazancourt, 2010). By using this approach, we determined the relative importance of each predictor as a way to build our multiple regression models. At each model, effect size was the dependent variable, the predictor variable or the predictors were the fixed independent variables, and observation number included as a random factor. To investigate the individual contribution of each predictor at improving the model fit, we compared the model including all predictors with the model without a given predictor (i.e., the reduced model). This comparison was examined for statistical significance using likelihood ratios test and the robustness of each model was also evaluated with a permutation test with 1000 interactions (Harrer et al., 2019).

Lastly, to perform investigations on the patterns of continuous predictor variables, we applied a Principal Component Analysis (PCA) to distinguish clustering between MPA management categories and predictors using the package 'psych' (Revelle, 2021). All statistical analyses were performed in R 4.0 (R Core Team, 2020) with RStudio IDE 1.3 (RStudio Team, 2020).

3. Results

3.1. Description of results

The 424 observations were made in 18 MPAs from the northern to the southeastern parts of the Brazilian coast and were thus well distributed across our study area (Fig. 1). Half of the studied MPAs (N = 8) were assigned as multiple-use MPAs (Table 1), with a total of 139 observations. While these MPAs frequently provide partial protection only, one of them (i.e., APA Costa dos Corais) had zones affording full protection at the time the survey was conducted. Seven MPAs were categorized as no-take ones with 236 associated observations. The two remaining MPAs were assigned as extractive reserves because they allow sustainable use of natural resources by small-scale communities while containing zones offering full (i.e., 13 observations) or partial protection (i.e., 36 observations). Most of the observations were conducted in coral (46.5%) or rocky reef (53.1%) environments. Just a few observations were not associated with reef habitats, such as soft-bottom substrata (0,2%) and pelagic environment (0,2%). The dataset of all observations was also biased towards studies with fish species (70.5%), and studies investigating biomass (30.4%) and abundance (59.0%). Few studies yielded observations on species diversity (3.1%), length of individuals (6.8%), and behavioral responses (0.7%). Egger's test, trim and fill procedures, Kendall's correlation tests, and the p-uniform method suggested that publication bias did not affect our effect size estimates (see Supplementary material S2 for more details on publication bias assessments); the only exception was for the comparison between full protection and open-access areas for the Egger's test.

3.2. Overall effects

Averaged across all observations, we found an overall positive significant effect of protection on marine biodiversity, with a 19% (±11%) increase in biodiversity (e.g., richness and abundance) in protected sites compared to unprotected or less protected areas (i.e., for the comparisons full protection versus partial protection) (Fig. 2a – "overall effect"). The weighted natural logarithmic response ratio (E_{LnRR}) was equal to 0.174, with an estimated 95% confidence interval (CI) of 0.099. The heterogeneity in the effect size was large, relative to a measurement error ($I^2 = 97.44\%$), indicating that there is significant among-study variation that needs to be further explored in the predictor analyses ($Q = 16{,}497.59$, $df = 423$, $p < 0.001$). When comparisons between fully- and partially-protected areas were excluded from the meta-analysis, effects of protection had similar magnitude to the overall effects on biodiversity (i.e., 17% ± 13% or $E_{LnRR} = 0.163 \pm 0.116$).

As expected, the effect of protection was most pronounced for the comparison between fully-protected and unprotected areas (i.e., open-access areas), which caused a 45% (±21%) increase in biodiversity ($E_{LnRR} = 0.375 \pm 0.144$) (Fig. 2a). Fully-protected areas also yielded smaller, but positive and significant results, when compared to partially-protected areas, with an increase in biodiversity of 22% (±23%) ($E_{LnRR} = 0.199 \pm 0.190$). When compared against open-access areas, partially-protected areas had no effect on biodiversity ($E_{LnRR} = 0.006 \pm 0.164$). All these three types of comparisons displayed significant among-study heterogeneity (Supplementary Table S2).

On average, protection led to an increase in the abundance of species ($E_{LnRR} = 0.194 \pm 0.13$), on the size of individuals ($E_{LnRR} = 0.152 \pm 0.141$), and in the diversity of species ($E_{LnRR} = 0.133 \pm 0.056$) (Fig. 2b). The protection also led to an increase in the biomass of the organisms, though these effects were not statistically significant ($E_{LnRR} = 0.155 \pm 0.276$). We did not report the results for behavioral responses due to the small number of observations available ($k = 3$). Only species diversity and behavioral responses did not display among-study heterogeneity (Table S2), probably due to a small number of studies.

Four no-take MPAs were considered ecologically effective with significant positive effects on biodiversity: (i) Abrolhos National Marine Park ($E_{LnRR} = 0.866 \pm 0.514$), (ii) Ecological Station Tupinambás ($E_{LnRR} = 0.405 \pm 0.255$), (iii) State Park Laje de Santos ($E_{LnRR} = 0.704 \pm 0.576$), and (iv) Biological Reserve Arvoredo ($E_{LnRR} = 0.379 \pm 0.166$). On the other hand, three multiple-use MPAs had significant negative effect sizes on biodiversity: (i) Environmental Protection Area Baleia Franca ($E_{LnRR} = -0.567 \pm 0.448$), (ii) Environmental Protection Area Recifes de Corais ($E_{LnRR} = -0.516 \pm 0.463$), and (iii) Environmental Protection Area Setiba ($E_{LnRR} = -0.473 \pm 0.408$). Conversely, one multiple-use MPA had significant positive effects on biodiversity (APA Tamoios, $E_{LnRR} = 1138 \pm 0.835$). Eight MPAs had positive but non-significant effects on biodiversity (Fig. 3).

3.3. The role of predictor variables

Taxonomic identity was a significant predictor for the comparisons involving full protection and open-access areas, and full protection versus partial protection (Supplementary Figure S2). Invertebrates was the only taxonomic group with a significant positive effect size for the

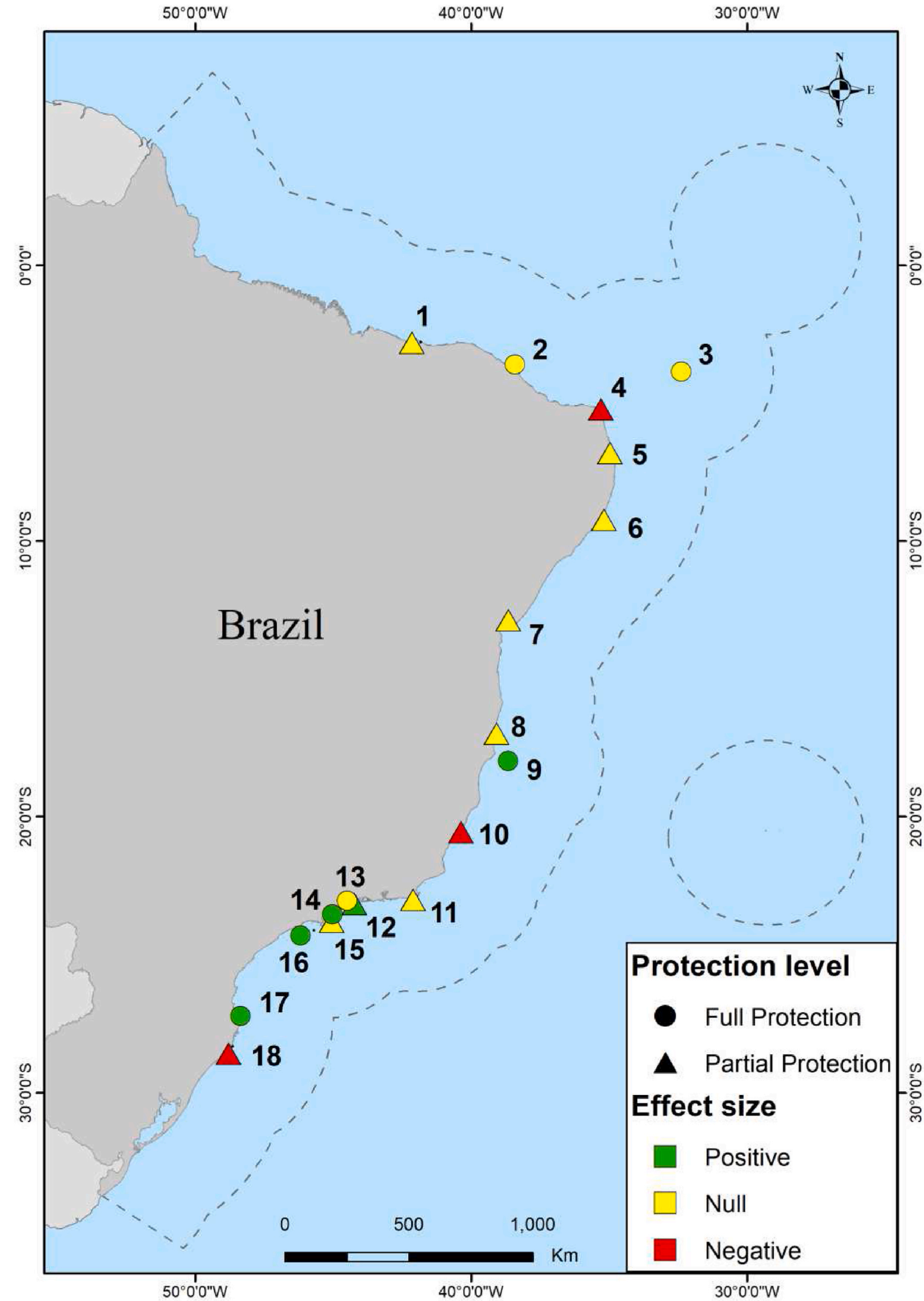

Fig. 1. Study area - Marine Protected Areas used in our analysis of ecological effectiveness classified according to the protection level afforded and their positive, negative, and neutral impacts on biodiversity. The number corresponds to MPAs described in Table 1 and the dotted line represents the boundary of Brazil's Exclusive Economic Zone.

Table 1
Main characteristics of Brazilian MPAs included in the meta-analysis. MPAs were placed into three broad categories according to their management intent: no-take areas, extractive reserves, and multiple-use. Because extractive reserves and multiple-use MPAs can have zones offering full or partial protection, we specified the type of comparison made within each MPA: FP refers to areas offering full protection; PP refers to areas offering partial protection; and OA refers to open-access areas outside MPAs and unprotected at the time of the survey. Please refer to Fig. 1 for the geographic location of MPAs.

MPA Name[a]	Year of establishment	MPA size (km^2)	Management category	Type of comparison		
				Treatment	Control	K
1. APA Delta do Parnaíba	1996	3138.0	Multiple use	PP	PP	02
2. PE Pedra da Risca do Meio	1997	332.0	No-take	FP	OA	13
3. PARNA Fernando de Noronha	1988	112.7	No-take	FP	PP	85
4. APA Recifes de Corais	2001	1800.0	Multiple use	PP	OA	27
5. APA Rio Mamanguape	1993	146.4	Multiple use	PP	OA	02
6. APA Costa dos Corais	1997	4135.6	Multiple use	FP	PP	14
				PP	OA	14
7. APA Baia de Todos os Santos	1999	800.0	Multiple use	PP	OA	15
8. RESEX Corumbau	2000	895.0	Extractive reserve	FP	OA	13
9. PARNA Abrolhos	1997	882.5	No-take	FP	PP	14
10. APA Estadual Setiba	1994	126.9	Multiple use	PP	OA	23
11. RESEX Arraial do Cabo	1997	516.0	Extractive reserve	PP	OA	36
12. APA Tamoios	1986	214.0	Multiple use	PP	OA	14
13. ESEC Tamoios	1990	86.6	No-take	FP	OA	10
14. APA Litoral Norte SP	2008	2360.5	Multiple use	PP	OA	19
15. ESEC Tupinambás	1987	24.6	No-take	FP	PP	21
16. PE da Laje de Santos	1993	50.0	No-take	FP	OA	11
17. REBIO Marinha Arvoredo	1990	178.0	No-take	FP	OA	82
18. APA Baleia Franca	2000	1561.0	Multiple use	PP	OA	09

[a] Acronyms at the front of MPA names are in accordance with SNUC (2000) as follows: Environmental Protection Area (APA), State Park (PE), National Park (PARNA), Extractive Reserve (RESEX), Ecological Station (ESEC) and Biological Reserve (REBIO).

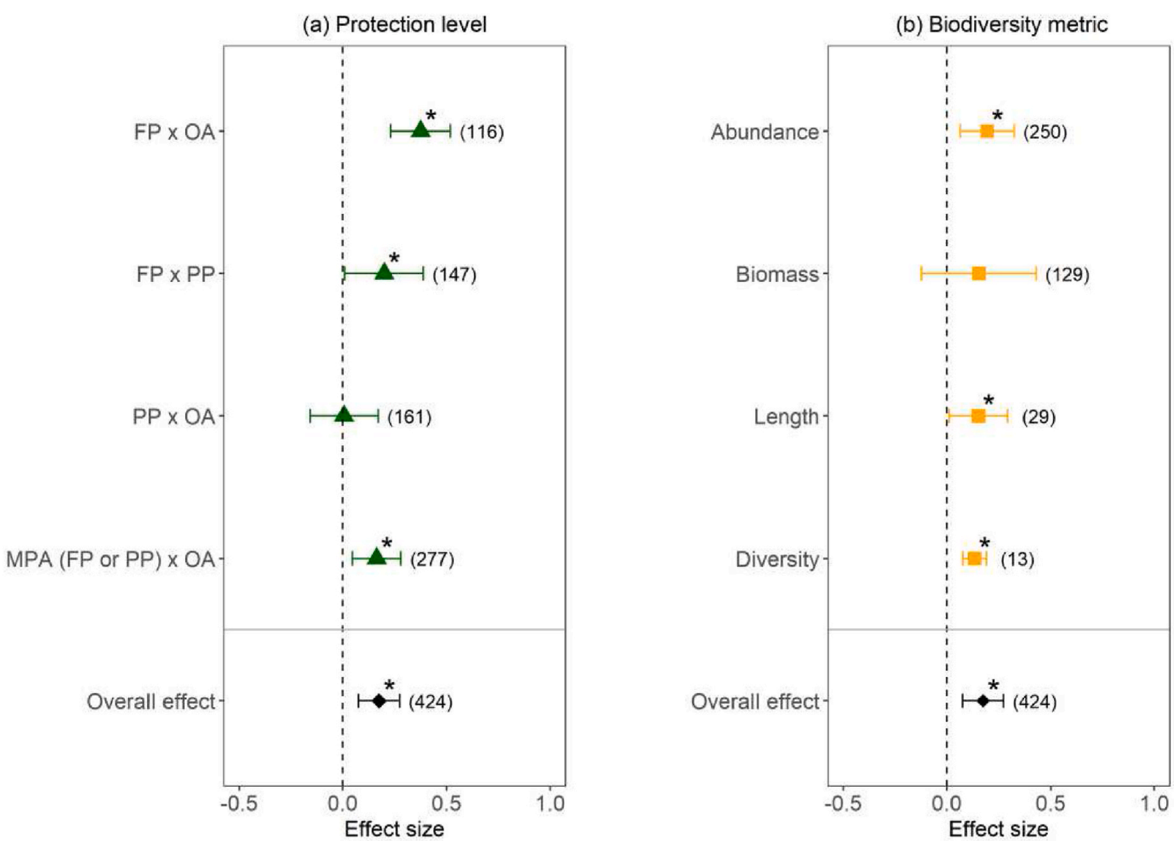

Fig. 2. MPA effect size - The mean effect sizes to estimate the ecological effects of protection by MPAs in Brazil according to the different protection levels afforded (a) and biodiversity metrics used (b). FP refers to full protection, PP refers to partial protection, OA refers to open-access areas. Error bars represent the 95% confidence interval. Sample size (k) for each ratio is shown in parentheses. Values greater than zero indicate a positive effect of protection, and values less than zero indicate a negative effect of protection. (*) The mean effect size is significant when the 95% CI does not overlap zero.

comparison between partial protection versus full protection (E_{LnRR} = 0.761 ± 0.384). Invertebrates and fish species had significant positive effects in the comparison between fully-protected versus open-access areas (E_{LnRR} = 0.262 ± 0.188 and E_{LnRR} = 0.431 ± 0.180, respectively). The effect of protection was non-significant for algae species in all comparisons. We evidenced significant positive effects of protection

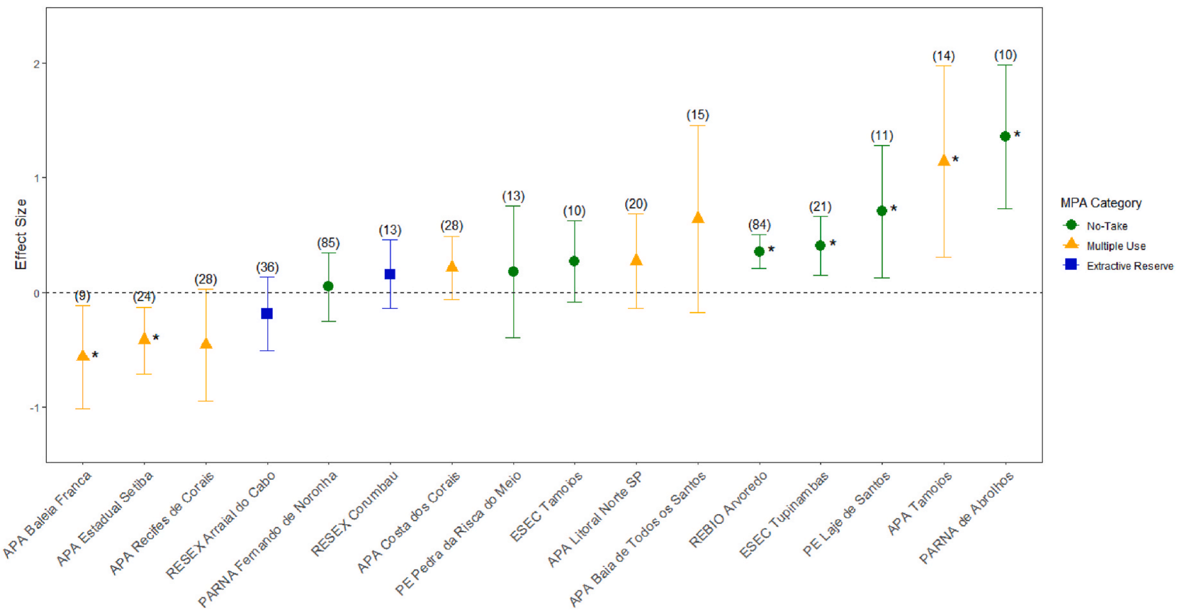

Fig. 3. Effect size across MPAs - The relationship between mean effect sizes (and their 95% confidence intervals) for each MPA and their management categories. Shape and colour of dots represent the management category of Brazilian MPAs. Sample size (k) for each ratio is shown in parentheses and values for MPAs with number of observations <5 were omitted. (*) The mean effect size is significant when the 95% CI does not overlap zero. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

for other vertebrates in the comparison between partially-protected and open-access areas ($E_{LnRR} = 0.369 \pm 0.920$). Considering the overall effect for the taxonomic group, without comparing between protection levels, the mean effect size was significant only for invertebrates (Table 2).

Because most studied effects of protection used fish species (N = 299 observations), we could assess whether targeted species are likely to be more benefited from MPAs and whether a specific biodiversity metric (abundance or biomass) is particularly sensitive to MPA presence. It was not possible to differentiate these impacts for length of individuals because of the small number of observations. The strongest effects of protection were documented for targeted fish species for both metrics and types of comparisons (Fig. 4 and Table 2). In addition, targeted species were the only group with significant positive effect size from protection when comparing fully-protected areas against partially-protected ones. The effect sizes on fishing-target species were always the most positive when compared to both all fish species and all taxonomic groups together (i.e., "overall effect" at Fig. 4). Non-targeted species did not show evidence of beneficial effects from protection. Lastly, there were no significant positive effects of protection when partially-protected areas were compared to open-access ones for both metrics.

Across all observations, the effect of protection on biodiversity metrics increased with protection time ($E_{LnRR} = 0.035 \pm 0.018$), with effect size becoming significantly positive for protection times longer than about 15 years (Fig. 5). Within types of comparisons, the effect of protection increased with time of protection for both the comparisons between partial protection versus open-access areas and full protection versus partial protection (Table 3 and Supplementary Figure S3). The comparison between fully-protected areas and open-access areas showed that there were consistent positive effects of protection, regardless of the time of protection.

The patterns of variation in effect sizes with seascape connectivity mirrored the pattern found for protection time, with effect sizes increasing at better connected protected seascapes ($E_{LnRR} = 0.058 \pm 0.040$). We found that the effects of protection increased at better connected MPAs in the comparison between partially-protected areas and open-access ones. We also found consistent positive effects of protection for the comparison involving fully-protected areas and open-access areas regardless of the level of connectivity (Figure S3).

Fishing pressure on the surroundings of MPA boundaries was a significant predictor of MPA effects on biodiversity metrics ($E_{LnRR} = 0.045 \pm 0.044$; Fig. 5), explaining a significant proportion of the variance in effect sizes. For the comparison full protection versus open-access areas, fishing pressure did not interfere in the mean effect sizes. Conversely, effects of protection varied with fishing pressure for the comparison between full protection versus partial protection (Table 3). When considering the entire dataset, we did not find a significant linear relationship between the distance of MPA to control areas and mean effect sizes (Fig. 5). However, we observed that effect sizes increased with distance in the comparison between fully-protected and open-access areas (Table 3 and Supplementary Figure S4).

Inspection of correlations suggested that any significant co-variation present among MPA predictors (e.g., time of protection and management effectiveness) would not warrant an immediate exclusion (Supplementary Figure S4). Specifically, we also observed that, while protection time and connectivity had positive relationships with effect size, management effectiveness and MPA area had positive and negative nonsignificant relationships, respectively (Supplementary Figure S5).

From the sixty-four models (i.e., 2^6 as there are six predictors) used in the multi-model inference, we identified that the best fit regression model included three predictors: time of protection, management

Table 2
Categorical predictors affecting the responses of biodiversity metrics to protection. The mean effect sizes for each class of categorical predictors are shown with the confidence interval (±95% CI) and the respective calculated p-value. (*) indicates the significant values.

Predictor	Estimate (±95% CI)	p-value	Heterogeneity		
			Q	df	p
Algae	−0.035 (±0.319)	0.83	5165.24	39	<.05*
Invertebrates	0.550 (±0.214)	<.05*	4173.76	76	<.05*
Other Vertebrates	0.369 (±0.368)	0.43	1031.76	7	<.05*
Fish	0.108 (±0.130)	0.10	5598.93	298	<.05*
Target	0.341 (±0.176)	<.05*	2169.27	128	<.05*
Non target	−0.098 (±0.245)	0.43	3165.17	136	<.05*

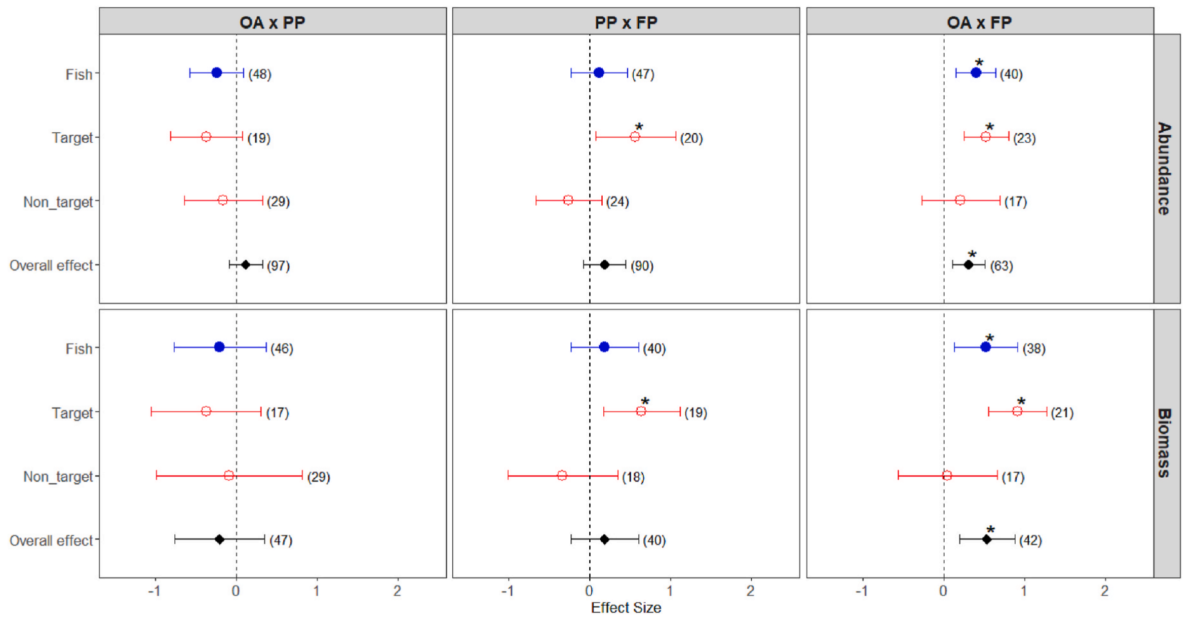

Fig. 4. Mean effect size of protection on fish species, comparing effects on species that are targeted and non-targeted for fisheries for different protection levels and biodiversity metrics (abundance and biomass). FP refers to full protection, PP refers to partial protection, and OA refers to open -access areas. Overall effect sizes are estimates for all species from all taxonomic groups. Error bars represent the 95% confidence interval. Sample size (k) for each ratio is shown in parentheses. (*) The mean effect size is significant when the 95% CI does not overlap zero.

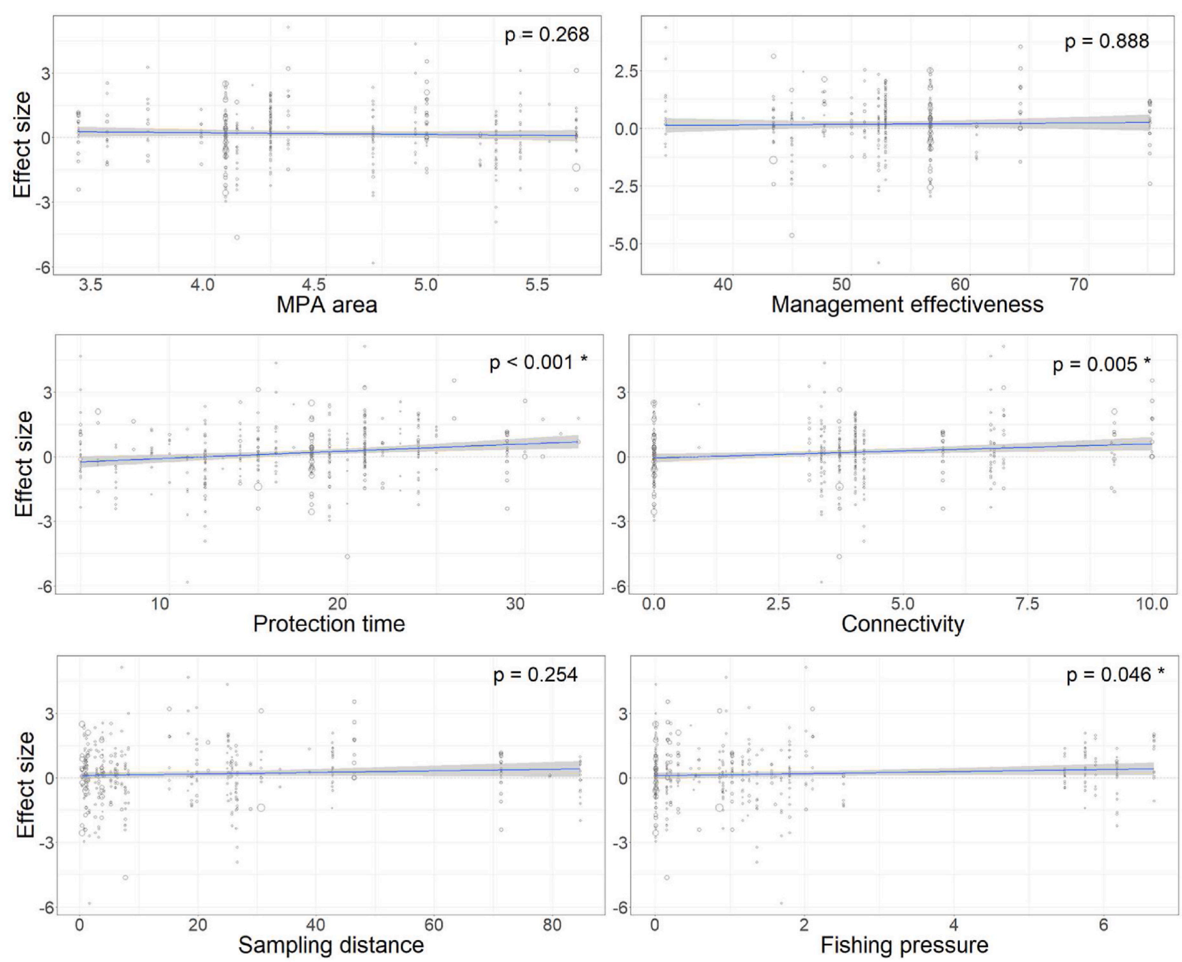

Fig. 5. Meta-regression plots showing the relationship of the effect sizes with the characteristics of the MPAs: log-transformed MPA size, management effectiveness scores, MPA age (years), the level of connectedness at the seascape level, the distance between the treatment and control points (in kilometers), and the fishing pressure in the control area. The size of the circles is proportional to the inverse of the effect size variation.

Table 3
Summary table showing tests of moderators (QM) from linear mixed models and residual heterogeneities (QE) that contrasted the response of biodiversity to protection levels provided by MPAs against predictor variables. The respective degrees of freedom (df) and p-values are also shown, where (*) indicates the significant values. FP refers to full protection, PP refers to partial protection, OA refers to open-access areas.

Predictor	Effect size for comparison type (±CI)			Moderator			Residual		
	FP x OA	FP x PP	PP x OA	QM	df	p-val	QE	df	p-val
Taxonomic group	0.214 (±0.39)	0.078 (±0.36)	−0.148 (±0.35)	32.4	6	<.05*	15699.8	418	<.05*
Exploitation status	0.617 (±0.28)*	0.351 (±0.29)*	−0.005 (±0.29)	25.2	4	<.05*	4794.6	261	<.05*
MPA area	0.204 (±0.85)	0.013 (±0.89)	−0.207 (±1.01)	21.3	4	<.05*	16036.3	420	<.05*
Protection time	−0.349 (±0.47)	−0.469 (±0.44)*	−0.420 (±0.30)*	32.0	4	<.05*	15920.0	420	<.05*
Management effectiveness	0.746 (±0.85)	0.635 (±0.93)	0.312 (±0.77)	19.3	4	<.05*	13089.5	349	<.05*
Connectivity	0.142 (±0.24)	0.011 (±0.22)	−0.252 (±0.23)*	30.3	4	<.05*	16194.1	420	<.05*
Fishing pressure	0.335 (±0.39)	0.196 (±0.18)*	−0.006 (±0.18)	21.1	4	<.05*	16191.2	420	<.05*
Sampling distance	0.316 (±0.20)*	0.147 (±0.19)	−0.088 (±0.19)	23.8	4	<.05*	14874.2	412	<.05*

effectiveness, and seascape connectivity. These predictors were included in the best-ranked models according to AICc, and thus considered the most important for affecting effect size predictions (Table 4). Although the apparent importance of management effectiveness, it is noteworthy to mention that the influence of this predictor could be potentially confounded because of the correlation previously identified between protection time and management effectiveness (see Supplementary Figure S4).

The comparison between individual contributions of each predictor to the model fit showed that connectivity, protection time, and sampling distance improved significantly the model regression, reducing the AICc of the original model. The likelihood ratio test revealed the seascape connectivity has a better fit performance. The robustness of this result was confirmed by permutation test (Table 5).

Lastly, the principal component analysis (PCA) revealed a clear separation between no-take MPA or zones (i.e., offering full protection), and those areas considered partially protected (i.e., multiple-use MPAs and extractive reserves) (Fig. 6). In general, no-take MPAs were associated with longer protection times (no-takes MPAs in Brazil are usually older than other MPA categories), with higher scores of management effectiveness, and surrounded by areas under high fishing pressure. No-take MPAs were also better correlated with positive effect sizes. Conversely, multiple-use MPAs and extractive reserves were bigger, had provided shorter protection times (MPAs at these categories are relatively younger), and were associated with lower management effectiveness scores. With few exceptions, most of these partially-protected MPAs were not well correlated with effect sizes. The first two axis components explained 58.47% of the variance of the observations. The predictors most associated with PC1 according to their respective loadings are protection time (0.88), distance sample (0.79) and management effectiveness (0.76). In relation to PC2, the largest loadings were found for connectivity (0.75) and MPA area (0.70) (Supplementary Figure S6).

4. Discussion

Our synthesis of 424 observations demonstrates that biodiversity metrics (species abundance, length of individuals, and diversity) in areas under protection is 17% higher, on average, than in unprotected areas.

Table 4
Relative importance of predictors as a result of the multi-model analysis, with respective coefficients of the average model with and 95% confidence intervals (CI) and p-value. (*) Indicates the significant value.

Predictor	Estimate (95% IC)	p-value	Importance
Protection time	0.049 (±0.025)	0.001*	99.63%
Management effectiveness	−0.015 (±0.019)	0.139	84.79%
Connectivity	0.027 (±0.053)	0.315	68.21%
MPA Area	0.071 (±0.214)	0.515	47.43%
Sampling distance	0.009 (±0.004)	0.676	40.72%
Fishing pressure	−0.001 (±0.019)	0.896	34.53%

Table 5
Results of the Likelihood Ratio Tests (LRT) for multiple meta-regression models, with respective values of freedom degree (df), significance (p-value) and ordered by corrected Akaike Information Criterion (AICc). The p-value (*P*) of the permutation test to assess robustness of the models are also shown.

Predictor	Likelihood Ratio Test				Permutation
	df	AICc	LRT	*p-value*	*P*
Connectivity	3	1078.014	9.278	0.002*	0.022*
Protection time	3	1086.892	15.940	<0.001*	0.002*
Sampling distance	3	1092.357	10.474	0.001*	0.007*
Fishing pressure	3	1097.291	5.541	0.018*	0.080
Management effectiveness	3	1101.383	1.449	0.228	0.846
MPA area	3	1101.840	0.991	0.319	0.781

The response to protection of biodiversity was disproportionally increased when comparing fully-protected MPAs with open-access areas (i.e., 45%). Our regional meta-analysis of the ecological impacts of MPAs on biodiversity also help shade light on the characteristics or conditions at which MPAs best explain biodiversity benefits. The results support the main hypotheses that partially-protected MPAs (i.e., multiple-use ones) are limited to benefit any biodiversity metric unless they have the following characteristics: (i) an age of usually fifteen years or older; and (ii) a high level of connectivity at the seascape level. On the other hand, we reveal that the ecological effects of fully-protected MPAs are noticeable, even for young ones, placed in relatively more isolated areas, and surrounded by intense fishing activity. Importantly, even though the ecological effects of MPAs are highly context specific, overall mean effect sizes demonstrate the predominance of neutral relationships between MPA area and biodiversity across the types of comparisons, at least for the range of MPA sizes studied here (i.e., 24.6–4135.6 km^2). Furthermore, we emphasize that protection time and seascape connectivity are the most influential predictors in determining positive effects on biodiversity. Moreover, while the MPA effects analyzed varied weakly with management effectiveness, this predictor was an indirect driver to changes in biodiversity, given that old MPAs are usually more effectively managed (e.g., Rojo et al., 2021).

Meta-analytical approaches are necessary for conservation planning and management to examine general trends in the effectiveness of MPAs at improving biodiversity conditions, synthesizing information on changes in biodiversity metrics as well as to understand ecological impacts arising from MPAs under different contexts even in the absence of baseline information. Although this need has been recognized conceptually for nearly twenty years (Halpern and Warner, 2003), rigorous meta-analyses that control for confounded baselines (e.g., Before-After/Control-Impact design) have proven elusive. The current emphasis on assessing differences between protected and adjacent controls has led to efforts to quantify MPA effects even if the observed biodiversity value is due to site-specific features before the onset of protection (Stewart et al., 2009). Our results suggest that this

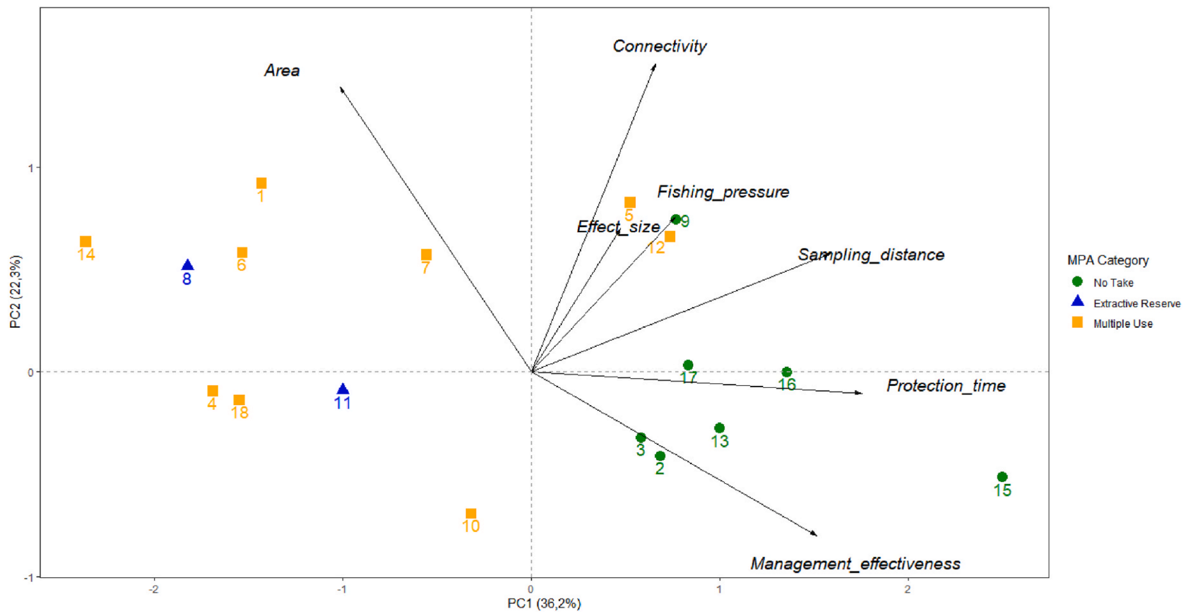

Fig. 6. Principal Component Analysis (PCA) applied to numeric predictors of MPA ecological effectiveness (MPA area, connectivity, fishing pressure, sampling distance, protection time and management effectiveness) classified according to their management categories. The numbers refer to the respective MPA names according to Table 1.

interpretation might be true because the comparison between fully-protected and open-access areas did not modify the mean effect sizes over time. However, it is important to note that fully-protected areas remained with positive and significant effect sizes even when MPAs were older, despite the potential large increase in threats surrounding these areas since their establishment (Halpern et al., 2015; Magris et al., 2020). Moreover, our results also indicate that partially-protected areas can improve biodiversity conditions over time, with positive benefits becoming prevalent for MPAs older than fifteen years.

Our results clearly indicated no-take MPAs as having higher biodiversity values for all metrics analyzed comparatively to unprotected areas, both for invertebrate and targeted fish species. This result is in accordance with previous studies (e.g., Floeter et al., 2006) in which heavily fished species were more benefitted from protection than lightly fished species. MPAs offering full protection against all extractive activities within their boundaries have been also widely supported as the best management tool to restore collapsed stocks (Di Lorenzo et al., 2020; Roberts et al., 2001; Zupan et al., 2018). In our analysis, seeking to quantify the ecological effects of MPAs on all species did provide evidence that MPAs can benefit other non-exploited species (e.g., invertebrates), even when allowing some human activities within their boundaries. Although it has been recently demonstrated that the impacts of fishing around no-take MPAs compromises significantly their conservation potential (Ohayon et al., 2021), our meta-analytical approach ascertained positive effects, suggesting that even small no-take MPAs can indeed contribute to recover exploited populations in fished areas.

Because we found an increase in the effect size as the distance between unprotected sites and fully-protected MPA boundaries became greater, we suggested that the increased biodiversity within these MPAs caused an outward export of individuals to surrounding unprotected areas. Two ecological processes might explain this outcome. First, larval output from MPAs can act to enhance the rate of population growth in other areas (Gaines et al., 2010), and provide recruitment subsidies to fished areas (Marshall et al., 2019). Second, spillover across the MPA boundaries can increase biodiversity in the surroundings (Di Lorenzo et al., 2020; Russ and Alcala, 2011). Previous work has shown that biomass export from MPAs occurs over small spatial scales - i.e., tens of km (Harrison et al., 2012; Ohayon et al., 2021; Russ and Alcala, 2011; Stewart et al., 2009). Consistent with these predictions, the impacts of MPAs on biodiversity were detected mostly over small distances from MPA boundaries, i.e., 10 km. However, it has been documented that the spatial extent of a spillover effect could extend beyond tens to hundreds of km, particularly for large, highly migratory pelagic predators of high trophic levels (Boerder et al., 2017; Bucaram et al., 2018).

Management measures and other correlated indicators (e.g., enforcement level) are intended to evaluate how well MPA management is working towards their objectives (Pajaro et al., 2010; Pomeroy et al., 2005). While these indicators can encompass biophysical, governance, and socioeconomic components, most of the evaluation approaches are based on composite scores that reflect perceptions of MPA staff regarding achievement of conservation outcomes (such as the one presented here, and also see Oliveira Júnior et al., 2021). Other stakeholders' perceptions of different factors can also influence attitudes, acceptability, and levels of support (Bennett, 2016; Sommerville et al., 2010), which in turn affect MPA effectiveness. Furthermore, management effectiveness of MPAs relies on users' compliance with regulations and patrol effort in enforcement activities (Arias et al., 2015), but this type of monitoring data is often lacking (Giakoumi et al., 2017). Our approach does not evaluate enforcement activity within MPAs based on monitoring data, and scores represent perceptions of conservation implementation of MPAs by managers only; further research is needed to understand which conditions are instrumental to MPA success based on MPA monitoring data through the application of more detailed assessment of management effectiveness.

In the absence of data on the distribution and abundance of species for a specific region, basic rules of thumb for MPA sizes derived from theory or other locations have been disseminated to afford greater or less protection to species (Sala et al., 2002; Shanks et al., 2003). Although large MPAs are typically favoured (e.g., Fox et al., 2012; McCook et al., 2009), there are also instances where smaller MPAs are preferred (e.g., Roberts et al., 2001). Recommendations for minimum MPA size have usually claimed that MPAs are effective when larger than 10 km^2 (Halpern and Warner, 2003). Our study has shown that, while no-takes MPAs with a size of 24.6 km^2 could be considered ecologically effective, large multiple-use MPAs with a size of 1500 km^2 were considered ineffective. Although design criteria regarding MPA size are intuitive approaches to support biodiversity (Magris et al., 2014), applying size rules cannot distinguish spatial heterogeneity in benthic habitat, nor can they account for connectivity between sites, which all affect the ability of MPAs to sustain biodiversity. Though conceptually simple, MPA size rules could be more reliable to evaluate conservation effectiveness as higher levels of documentation for ecological data with specific guidance emerge (Aued et al., 2018; Ferreira et al., 2004; Floeter et al., 2007; Morais et al., 2017).

An important limitation of our study is that the connectivity value of habitats protected by MPAs were quantified by estimating the potential dispersal distance of focal species and the structural position of each protected habitat relative to others (Magris et al., 2020). Although basic knowledge of regional oceanography was used to identify dispersal patterns of these species (Magris et al., 2016), a more robust strategy might be derived from employing biophysical modelling at the required scale of the connectivity processes. Despite improvement in connectivity modelling in the last decade (Kool et al., 2013) many regions lack spatially explicit connectivity information, and distance-based metrics informed by connectivity data have proved to be reasonable alternatives to data-heavy approaches (Goetze et al., 2021; D'Aloia et al., 2015). Due to data constraints, another limitation of our study is that we could not incorporate information on spatial patterns of artisanal fisheries, potentially leading to modify fishing activity in the surrounds of MPAs.

Identifying conditions at which MPAs affect biodiversity is a difficult task from empirical studies since each measurement can respond to influences at multiple scales (Di Lorenzo et al., 2020; Giakoumi et al., 2017; Sciberras et al., 2013; Zupan et al., 2018). Examining large-scale patterns of MPA effects is also inherently difficult because some studies might not aim to address this question (e.g., Aued et al., 2018; Morais et al., 2017), often leading to a high variability in the data compiled. For this reason, it is important to consider that factors other than MPA effects may vary between control and protected sites. In this study, over 83% of the study cases with measures of biodiversity values were direct measures of MPA effectiveness (e.g., Francini-Filho and Moura, 2008), and as such sites within and without of protection were selected as representative comparisons. While our data spans the southwestern Atlantic Ocean, larger datasets on MPA effects on biodiversity are slowly becoming available (e.g., Edgar et al., 2014) and may capture the long-term dynamics required to study causal relationships between biodiversity change and the time after MPA post-designation. Larger datasets would also allow repetition of taxa and biodiversity metrics, and consideration of further important explanatory variables like effects of disturbance events. There is a need of further empirical data to be gathered across latitudinal gradients with rigorous and consistent methods.

In general, time of protection and connectivity had the strongest impacts on MPA effects on biodiversity, consistent with expectations that longevity of conservation actions (e.g., Claudet et al., 2008; Edgar et al., 2014) and MPAs situated within a well-connected network (e.g., Goetze et al., 2021; Grorud-Colvert et al., 2014; Magris et al., 2018) are particularly important for successfully achieving conservation outcomes. These results are also in accordance with the pattern that effects of Brazilian MPAs are particularly discernible in top predators, long-lived species, which are economically-important for fisheries and have generation times on the order of 20 years (Floeter et al., 2007; Luiz and Edwards, 2011). On the other hand, the results do not conform the pattern that isolated MPAs confer more protection to biodiversity as suggested by a global meta-analysis (Edgar et al., 2014 but see Goetze et al., 2021); while we acknowledge that the level of isolation has not interfered in the ecological effectiveness of no-take MPAs.

5. Conclusion

Driven by global calls for the achievement of biodiversity goals, a new pattern of MPA design emerged in Brazil over the last few years, despite the fact that only 2.5% of Brazilian waters remains fully protected (Magris et al., 2020). An understanding of the MPA effects on biodiversity can inform the management of both the MPAs, and their drivers of effectiveness. Our study complements previous meta-analyses of the MPA effects on biodiversity by providing quantitative estimates of their net effects on marine biodiversity in Brazil and by exploring other drivers of ecological effectiveness (i.e., connectivity and fishing pressure). Our results conclude that fully-protected MPAs in Brazil are performing slightly poorer than MPA systems in developed countries (Giakoumi et al., 2017; Goetze et al., 2021), that partially-protected ones are performing a way worse than the global average (Sciberras et al., 2013), and that two predictors (i.e., time of protection and connectivity) play a strong role in enhancing the effects of partially-protected MPAs. The results also improve our knowledge of drivers associated with MPAs performance by identifying that no-take MPAs can be effective even when young, isolated, and surrounded by intense fishing. As the discipline of conservation planning advances, we would advocate the development and adoption of conservation assessments based on empirical data to help improve our understanding of the efficacy of MPAs in benefiting biodiversity.

Authorship contribution statement

HMF: Conceptualization, Formal analysis, Investigation, Data Curation, Writing – review & editing. RMA: Conceptualization, Supervision, Writing – original draft, Writing – review & editing. SRF: Data providing, Writing – review & editing. CELF: Data providing, Writing – review & editing.

Declaration of competing interest

RAM is a paid employee for the agency responsible for the implementation of protected areas in Brazil. The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2021.113889.

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