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# Integrated conservation planning for coral reefs: Designing conservation zones for multiple conservation objectives in spatial prioritisation



Rafael A. Magris<sup>a, b, \*</sup>, Robert L. Pressey<sup>b</sup>, Morena Mills<sup>c, d</sup>,  
Daniele A. Vila-Nova<sup>e</sup>, Sergio Floeter<sup>e</sup>

<sup>a</sup> Chico Mendes Institute for Biodiversity Conservation, Brasilia-DF, 70.670-350, Brazil

<sup>b</sup> Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University Townsville, QLD, 4811, Australia

<sup>c</sup> Centre for Biodiversity and Conservation Sciences, The University of Queensland, Brisbane, Queensland, 4072, Australia

<sup>d</sup> Department of Life Sciences, Imperial College London, Buckhurst Road, Ascot, Berkshire, SL5 7PY, United Kingdom

<sup>e</sup> Marine Macroecology and Biogeography Lab, Universidade Federal de Santa Catarina, Florianópolis, SC, 88010-970, Brazil

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## ABSTRACT

Decision-makers focus on representing biodiversity pattern, maintaining connectivity, and strengthening resilience to global warming when designing marine protected area (MPA) systems, especially in coral reef ecosystems. The achievement of these broad conservation objectives will likely require large areas, and stretch limited funds for MPA implementation. We undertook a spatial prioritisation of Brazilian coral reefs that considered two types of conservation zones (i.e. no-take and multiple use areas) and integrated multiple conservation objectives into MPA planning, while assessing the potential impact of different sets of objectives on implementation costs. We devised objectives for biodiversity, connectivity, and resilience to global warming, determined the extent to which existing MPAs achieved them, and designed complementary zoning to achieve all objectives combined in expanded MPA systems. In doing so, we explored interactions between different sets of objectives, determined whether refinements to the existing spatial arrangement of MPAs were necessary, and tested the utility of existing MPAs by comparing their cost effectiveness with an MPA system designed from scratch. We found that MPAs in Brazil protect some aspects of coral reef biodiversity pattern (e.g. threatened fauna and ecosystem types) more effectively than connectivity or resilience to global warming. Expanding the existing MPA system was as cost-effective as designing one from scratch only when multiple objectives were considered and management costs were accounted for. Our approach provides a comprehensive assessment of the benefits of integrating multiple objectives in the initial stages of conservation planning, and yields insights for planners of MPAs tackling multiple objectives in other regions.

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\* Corresponding author. Chico Mendes Institute for Biodiversity Conservation, Brasilia-DF, 70.670-350, Brazil.

E-mail address: [rafael.magris@my.jcu.edu.au](mailto:rafael.magris@my.jcu.edu.au) (R.A. Magris).

## 1. Introduction

Marine protected areas (MPAs) are increasingly viewed as an important spatial management tool within a suite of policy alternatives to address rapid declines in coral reef biodiversity (Mumby and Steneck, 2008). Where properly implemented, MPAs have proven to be effective tools for reef conservation, with documented empirical evidence of their benefits (Mumby and Harborne, 2010; Harrison et al., 2012; Olds et al., 2013). However, uncertainty remains over strategies to optimise MPA spatial design for conserving biodiversity in the long term and maintaining wider ecosystem functions (McCook et al., 2010). There is also an increasing recognition that many MPAs are ineffective at addressing a diverse set of conservation objectives (Watson et al., 2014). Optimising the diverse roles expected from MPAs and their effective implementation is therefore a current central concern of conservation planning.

Quantitative conservation objectives (sometimes referred as targets in the conservation literature) are the foundation for conservation planning (Game et al., 2013), and their formulation is a key step in applying scientific insights to achieve desired MPA outcomes (Pressey et al., 2015). The formulation of objectives can accommodate representation of biodiversity patterns (e.g. ecosystem types), while also addressing ecological and threatening processes related to the long-term maintenance of biodiversity, such as larval connectivity and global warming (Pressey et al., 2007). Despite processes being increasingly incorporated into decision-making strategies in recent years (Magris et al., 2014), most marine planning exercises typically develop objectives that represent only static elements of biodiversity (e.g. Green et al., 2009; Tulloch et al., 2013). However, representation objectives for biodiversity alone are probably insufficient to guarantee biodiversity persistence if an MPA system is composed of widely spaced, separate MPAs in which the maintenance of viable populations is limited by lack of connectivity. Similarly, conservation objectives that do not account for projected sea-surface temperatures might not support coral reef species in adapting to rapid global warming. Clearly, improving MPA design for persistence, complementing the longstanding focus on biodiversity representation, is essential to ensure adequate protection of coral reef systems over the next century.

In this study, we seek to address two influences on biodiversity persistence, which are particularly important for fostering coral reef conservation, but not yet well developed or interpreted in conservation planning: connectivity related to larval dispersal and global warming. Several studies have proposed approaches to designing well connected MPA systems for coral reefs (e.g. McCook et al., 2009; Beger et al., 2010; Magris et al., 2015b) and to maintaining functioning of these ecosystems under global warming (e.g. Chollett et al., 2014; Makino et al., 2014; Magris et al., 2015a). However, an assessment of the synergies between potentially competing objectives requires an integrated approach that investigates whether there is spatial coincidence between areas required to protect them, and seeks to maximize this coincidence. Beyond addressing aspects of possibly conflicting objectives in conservation planning, another challenge is therefore to integrate multiple sets of objectives. This integration can result in extensive proposed MPA systems that are financially challenging to implement in a real-world context with limited conservation funding (McCarthy et al., 2012). However, MPA systems composed of a mix of management regimes (hereafter “MPA zones”) could help the feasibility of integrated planning by reducing opportunity and management costs associated with no-take areas. Marine planning that accounts for variability in MPA zones to accommodate multiple sets of objectives could therefore provide planners and policy-makers with more flexibility, higher social acceptance, and a greater likelihood of implementation.

Here, we apply an MPA zoning approach to develop an integrated planning framework that links MPA design for different sets of conservation objectives to implementation costs. We address four main aims:

1. To enhance the process of framing conservation objectives for representing biodiversity pattern, maintaining connectivity, and strengthening resilience to global warming;
2. To assess the achievement of combined sets of conservation objectives by an existing system of MPAs with different zones, intended to protect Brazilian coral reefs;
3. To design an expanded MPA system that allocates multiple zones to achieve three sets of objectives simultaneously as a refinement of the existing MPAs, while also testing the extent to which planning for single sets of objectives incidentally achieves other sets not explicitly targeted;
4. To provide a method that assists planners to develop multi-objective MPA systems and demonstrate the value of developing integrated approaches from the outset of MPA planning.

We focus on coral reefs because they are ecosystems for which connectivity and resilience to global warming objectives can be defined in detail, and because of their heavy reliance on spatial management.

## 2. Methods

### 2.1. Conservation planning definitions

Conservation prioritisation involved several stages of analysis: assembling input data on biodiversity pattern, connectivity, and global warming; formulating the respective objectives; undertaking a gap analysis; and application of conservation planning software to develop scenarios. For these analyses, we resampled all features into 176 reef cells of  $10 \times 10$  km that

served as our planning units (the same resolution as that of our connectivity data, the coarsest-resolution dataset used in this study; [Appendix A](#)). The planning-unit size reflected a good compromise between the available data and extent of the study area. [Table 1A](#) defines key terms.

## 2.2. Conservation features

### 2.2.1. Biodiversity pattern

Biodiversity data comprised information on ecosystem types, functional biodiversity, and threatened and endemic fauna ([Table 1B](#)).

The ecosystems were 23 non-overlapping spatial classes derived from high and very high spatial resolution (4–30 m) satellite imagery ([Appendix A1](#)). By protecting examples of a full range of reef types, we assumed that our prioritisation would include elements important for structuring biodiversity patterns over large geographic gradients. Spatial delineation of ecosystems was constructed using boundaries of ecoregions, geomorphologic types (including fine-scale features), bathymetry data, and tidal zone discrimination.

Data on functional biodiversity and threatened and endemic fauna were based on range distributions of 405 reef-fish species. We chose reef-fish species as features because they play important roles in coral reef ecosystems through regulation of food webs and nutrient cycling ([Mouillot et al., 2014](#)), and represent the most studied marine group with consequent relatively robust distribution data along the Brazilian coast ([Vila-Nova et al., 2014](#)). For each reef-fish species, we gathered information on functional traits relevant to its habitat requirements and ecological vulnerability ([Halpern and Floeter, 2008](#)), including: body size (maximum body length), maximum depth, and trophic category. We then mapped the range distribution for each of the 79 functional fish groups defined by unique combinations of traits, following [Halpern and Floeter \(2008\)](#). The protection of the full range of functions performed by fish species is vital to ensure the long-term functioning of ecosystems ([Mouillot et al., 2014](#)). Although delineation of functional diversity patterns might produce shortfalls in the representation of any single species, we did not intend to perform an exhaustive species-based prioritisation here (see [Klein et al., 2015](#) for an example). Rather, we aimed to illustrate the potential of conservation planning to incorporate and develop objectives for functional groups, given recent calls that MPA planning should pay serious attention to ongoing loss of functional roles ([Mouillot et al., 2014](#); [D'agata et al., 2016](#)).

To explicitly account for those species with greatest conservation need and to acknowledge the prominent role of geographic range size in determining risk of extinction ([Harnik et al., 2012](#)), we also used modeled species distributions for two groups of fish: 32 species listed as facing extinction risk according to the Brazilian government; and 47 endemic species listed by [Vila-Nova et al. \(2014\)](#).

### 2.2.2. Connectivity

We used spatial data on demographically significant dispersal links between reef cells to depict connectivity ([Magris et al., 2015b](#)). Connectivity is defined here as the likelihood that, for a particular species, larvae originating at a source coral reef are capable of reaching neighboring reef cells. Connectivity was modeled considering the amount of coral reef in each cell and bio-physical factors relevant to larval dispersal (e.g. oceanic currents and maximum pelagic larval duration). The model accounted for four different species, which captured a range in dispersal potential: two with low dispersal abilities (i.e. a brooder and a broadcast spawning coral) and two with high dispersal abilities (i.e. a snapper and a surgeonfish). The resulting asymmetric connectivity-probability matrices were used to produce spatially explicit metrics (i.e. outflux, betweenness centrality, and local retention) for each species and each reef cell. Further details on the parameterization of larval dispersal simulations can be found in [Magris et al. \(2015b\)](#).

For the two species representing low dispersal abilities (the brooder and the broadcast coral), we defined conservation features related to connectivity by stratifying our study area into three strata (i.e. northeastern, central, and southern coast). This was because our previous study ([Magris et al., 2015b](#)) observed major breaks in the connectedness for those species and we wanted to ensure sufficient replication of important reefs for short-distance dispersers. By combining three connectivity metrics for each of two strongly dispersing model species across the entire study area (6 features) and three metrics for each of two species for three separate strata or subregions (18 features), we obtained 24 conservation features for connectivity ([Table 1B](#)). Our connectivity features were related to replenishment of larvae, increased potential recovery, and capacity of reefs to be self-sustaining, all known to address requirements for promoting population replacement.

### 2.2.3. Global warming

Although there is a vast suite of features relevant to improved coral reef resilience in times of global warming ([McClanahan et al., 2012](#)), our targeted features focused on temperature variability to delineate thermal-stress regimes and determine areas most likely to be resilient to disturbances induced by climate change ([Magris et al., 2015a](#)). By using measures of chronic and acute thermal stress and combining historical and projected data sets ([Table 1B](#)), we mapped the exposure of Brazilian reefs to nine thermal stress regimes identified across the study area that warranted conservation attention in conservation planning. The chronic and acute measures of stress were based on rate of sea-surface temperature rise and degree heating weeks (DHWs), respectively, and captured not only mortality levels of stress, but also sublethal effects that impair ecosystem

function (e.g. capacity to grow, repair, or reproduce). The thermal stress regimes corresponded to six types of thermal refugia (i.e. regimes containing varying levels of historically and/or future stable conditions but with limited bleaching stress levels; regimes 1–6 in Fig. S5) and three types of regimes potentially impacted by thermal disturbance (i.e. regimes subjected to past or future thermal disturbances and thus more likely to contain thermally tolerant species; regimes 7–9 in Fig. S5).

All the regimes were factored into our analysis of conservation priorities, specifically because they reflect the variability in the mechanisms associated with avoidance of climate disturbances, mitigation of cumulative stresses, ability of individuals to respond adaptively to thermal stress, and future resistance to warming (Magris et al., 2015a). Our thermal-stress regimes were intended to aid the development of climatically representative system of MPAs.

### 2.3. MPA data

We focused on an MPA system spatially coinciding with coral reef ecosystems and containing two zones: (i) no-take (IUCN categories I to IV); and (ii) multiple-use (IUCN categories V and VI). The existing no-take MPAs and multiple-use MPAs covered nearly 32% and 37% of the coral reef area, respectively (Magris et al., 2013).

### 2.4. Formulation of conservation objectives

Rather than using uniform percentages as objectives, we refined our conservation objectives to account for differences between features in management requirements and vulnerability to threats. Table 2 summarises our objectives for groups of conservation features within each set of objectives and the methods involved in their formulation.

#### 2.4.1. Biodiversity pattern

Details about assignment of objectives to features comprising biodiversity pattern are in Appendix A4. A summary of the approach follows.

Representation objectives for ecosystem types and functional groups ranged from 10 to 30% of their distributions, depending on the spatial extent of each ecosystem within the study area and the combination of biological traits within each functional group (Fig. 1). For ecosystem types, we set area-based objectives by linear interpolation, in which the maximum

**Table 1**

Terms and targeted features. Definitions of terms (A) and descriptions of conservation features (B).

A	
Term	Definition
Targeted feature	Species, ecosystem types, or functional groups that indicate aspects of biodiversity pattern and process-related variables related to connectivity and global warming
Conservation objective	Quantitative statement of the minimum amount of a feature that needs to be conserved in a particular type of MPA; this term is often referred as a target in the conservation planning literature, but avoids the confusion of “target” also being used to refer to features that need conservation
Set of objectives	A group of conservation objectives for features of a particular type; this study distinguished three types, related to representation of biodiversity patterns, connectivity, and global warming
Reef cells	Square grid cells containing coral reefs that could be potentially be selected for protection (also referred to as planning units)
MPA zones	Types of MPA defined by management intent and intended level of protection (e.g. no-take or multiple-use areas)
Scenarios	Systems of MPAs that achieve one or more sets of conservation objectives
B	
Set of objectives	Targeted features
Biodiversity pattern	<ul style="list-style-type: none"> <li>- Ecosystem types</li> <li>- Functional groups: groups of species that have the same functions in the ecosystem, providing similar ecosystem services, and described by unique combinations of functional traits (i.e. maximum depth, maximum body size, and trophic category), all known to influence responses to threats and to influence conservation requirements</li> <li>- Endemic species: species with occurrence restricted to the Brazilian Province</li> <li>- Threatened species: species included within the Critically Endangered, Endangered, or Vulnerable categories in the National Red List</li> </ul>
Connectivity	Combinations of four modeled species (i.e. two with low and two with high dispersal abilities) and three connectivity metrics: <ul style="list-style-type: none"> <li>- outflux - related to the source strength of a reef cell and its ability to sustain the populations of surrounding units through its outgoing connections in larval supply</li> <li>- betweenness centrality - related to the ability of stepping-stone reef cells to control flux of larvae, and help spread risk against disturbances</li> <li>- local retention - associated with the degree to which a given reef cell is self-sustaining in larval supply</li> </ul>
Global warming	Thermal-stress regimes, which combine historical (1985–2009) and projected (2010–2099) variability in sea-surface temperature and metrics of acute (i.e. bleaching/mortality level of heat stress) and chronic stress (impaired capacity to grow, repair, or reproduce): <ul style="list-style-type: none"> <li>- Thermal refugia regimes - reef cells facing the lowest chronic stress for both historical and projected conditions or the lowest acute stress, considering either historical or projected anomalies, but still facing chronic warming</li> <li>- Disturbed regimes - reef cells currently facing either the highest chronic or acute stress, or projected to be exposed to the highest level of acute stress</li> </ul>

**Table 2**

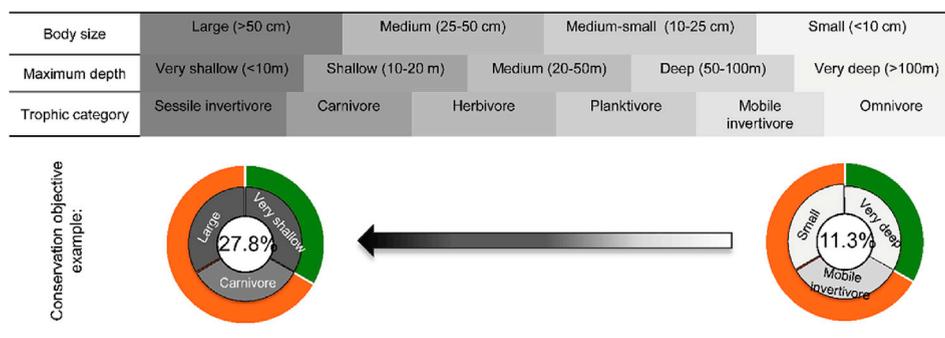
Summary of conservation objectives used for the gap analysis and development of scenarios. Our objectives were set as percentages of the extent of each conservation feature. For each group of conservation features, the upper and lower boundaries of objectives and methods involved in their derivation are given. *N* represents the number of conservation features in each group.

Set of objectives	Targeted features	Upper and lower boundaries of our conservation objectives	Method involved in formulation
Biodiversity pattern	Ecosystem types ( <i>N</i> = 23)	10–30% of each ecosystem type within MPAs; 3–10% of each ecosystem type within no-take zones	Linear interpolation between maximum and minimum spatial extents
	Functional groups ( <i>N</i> = 79)	11.3–27.8% of the spatial extent of each functional group within MPAs; 4–9% within no-take zones	Vulnerability of each functional trait to threats
	Endemic species ( <i>N</i> = 47)	10–100% of species range within MPAs; 3–67% of species range within no-take zones	Linear interpolation between maximum and minimum range sizes
	Threatened species ( <i>N</i> = 32)	30–100% of species range within MPAs; 10–67% of species range within no-take zones	Linear interpolation between maximum and minimum range sizes, complemented by conservation status
Connectivity	Source reefs ( <i>N</i> = 8)	80–90% of normalised values within no-take zones	Amounts equal to the sum of values across reef cells belonging to the top tercile for outflux
	Stepping stone reefs ( <i>N</i> = 8)	50–90% of normalised values within no-take zones	Amounts equal to the sum of values across reef cells belonging to the top tercile for betweenness centrality
	Self-persistent reefs ( <i>N</i> = 8)	70–90% of normalised values within no-take zones	Amounts equal to the sum of values across reef cells belonging to the top tercile for local retention
Global warming	Thermal refugia reefs ( <i>N</i> = 6)	50–100% of total extent of reef cells assigned to all types of thermal refugia regimes (see Fig. S5 for definitions) within no-take zones	Framework provided by Fig. 5 of Magris et al. (2015a)
	Thermally-disturbed reefs ( <i>N</i> = 3)	30% of total extent of reef cells assigned to thermally-disturbed regimes (see Fig. S5 for definitions) within multiple-use zones	Framework provided by Fig. 5 of Magris et al. (2015a)

objective corresponds to those ecosystems with the smallest extent and the minimum objective to those with largest extent. For functional diversity, we scaled our objectives so that larger objectives were associated with biological traits that reflect increased vulnerability and greater likelihood of population declines. For instance, functional groups comprised of large-bodied and corallivorous fish species associated with shallow habitats are disproportionately more affected by reef degradation than others (Bellwood et al., 2004; Genner et al., 2010; Mouillot et al., 2014), and thus had larger objectives.

For threatened and endemic species, the objectives were inversely scaled with the species' range sizes and incremented according to their conservation status (Guilhaumon et al., 2014; Venter et al., 2014). The representation objective for endemic and non-threatened species was 30% of range for those with restricted distributions and 10% for widespread species, and interpolated log-linearly for species with intermediate distributions. Objectives were then increased for threatened species, interpolated according to distributions and status as above, and further incremented for species that were both endemic and threatened (*n* = 7). Critically endangered species had objectives of 100%, irrespective of range size.

Given the differential ecological effectiveness of different types of MPAs, we assigned a portion of our overall biodiversity objectives to be met by no-take zones only (i.e. a zone-specific objective), the ecological benefits of which have been already well documented (Halpern and Warner, 2002; Harrison et al., 2012). A zone-specific objective was set as one third of the



**Fig. 1.** Formulation of conservation objectives for functional groups. Functional traits (body size, maximum depth, and trophic category) for 405 fish species were summarized according to a gradient reflecting their vulnerability to threats (represented by shades of gray) with species that are larger, associated with shallower habitats, and greater dependence on coral for food facing more threat and having more demanding objectives (dark gray). Examples of conservation objectives (bottom row) are shown for the upper and lower boundaries as percentages of distributions (inner circles) – i.e. 11.3 and 27.8%, respectively. The proportions of the objective required as no-take or multiple-use zones are illustrated by the outer circle: green indicates coverage required by no-take MPAs, i.e. – one third of the overall objective, and orange the remaining objective, optionally required to be achieved by no-take or multiple-use. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

overall objective within no-take zones for each ecosystem type, functional group, species that were both endemic and non-threatened, and species that were both non-endemic and threatened. For species both threatened and endemic, the zone-specific objective was then increased to two thirds of the overall objective within no-take MPAs. The most demanding zone-specific objective was assigned to critically endangered species with restricted ranges (100% of the overall objective within no-take zones).

#### 2.4.2. Connectivity

Similar to features for biodiversity pattern, we treated connectivity as a feature to be represented. We computed a cumulative distribution curve for the values of each connectivity feature and used the top one-third reef cells for each of the three connectivity metrics to derive our objectives. The connectivity objectives were defined by calculating the percentage that top-ranked reef cells contributed to the total values of each metric. For example, the reef cells falling in the upper tercile for the conservation feature defined by the combination of surgeonfish and betweenness centrality accounted for 60 percent of the total value of that combination, and were likely the central priority areas for maintaining a connected MPA system for that species. Thus, 60% became the objective for this feature (Appendix A4). Given uncertainties surrounding the effectiveness of multiple-use areas in supporting connectivity through larval export to subsidize fished areas, we required our conservation objectives for connectivity to be met only in no-take zones.

#### 2.4.3. Global warming

Objectives for global warming specified amounts in both no-take and multiple-use zones following Magris et al. (2015a). In this approach, zone-specific objectives were defined considering historical or future ecosystem states of each of the nine thermal-stress regimes. For instance, areas facing a low level of historical thermal stress or least affected by projected stress are more likely to retain a naturally functioning ecosystem that brings benefit or environmental services such as the replenishment of local populations in the surroundings via larval dispersal. These areas therefore qualified for strict protection by no-take zones. Conversely, areas exposed to a certain level of thermal stress or projected to face stressful conditions in the future might be degraded or contain disturbance-tolerant species only. These areas should be targeted for mitigation of threats not related to global warming by management in multiple-use MPAs. Furthermore, the percentage objectives were based on the relative importance of protecting sites under specific thermal-stress regimes (Côté and Darling, 2010; Selig et al., 2012; van Hooijdonk et al., 2015). For historical and future thermal refugia, as an example, the conservation objective was 100% coverage within no-take areas. The objectives were set as 100, 50, or 30% of coverage within a specific zone.

### 2.5. Gap analysis

We applied a gap analysis to assess how well the existing MPAs achieved objectives for biodiversity pattern, connectivity, and global warming. Once we developed the feature-specific conservation objectives, we measured the extent to which each feature was covered by both no-take and multiple-use MPAs zones and compared that amount with the respective objective. We did this based on the spatial overlap (in %) of each reef cell within the study area with the boundaries of each MPA zone. Levels of achievement were capped to a maximum value of 100%. For each group of features (biodiversity pattern, connectivity, global warming), we recorded the frequency distribution of achievement levels across features, then averaged the achievement of objectives across features ( $Obj_a$ ):

$$Obj_a = \frac{\sum_{i=1 \dots N}^i \left( \frac{P_i}{Ob_i} \right) \times 100}{N} \quad (1)$$

where  $P_i$  is the proportion of conservation objective  $Ob_i$  achieved for feature  $i$ , and  $N$  is the total number of conservation features.

### 2.6. Costs

We estimated two sets of costs: one was a layer of cell-specific costs to be used in spatial prioritization, defining the cost of including each reef cell within an MPA; and the second was the configuration-specific cost of implementing alternative MPA systems, considering size and the configuration of the MPAs. The second set of cost values could be derived only when the configuration of proposed MPAs was known.

To develop our layer of cell-specific costs, we first defined a coastal development index (Rowlands et al., 2012) as a proxy for opportunity or management cost (Appendix A5). In the case of opportunity costs, the index was scaled to correlate with fishing pressure, reflecting the finding that opportunity costs are higher when MPAs are closer to coastal communities (Klein et al., 2012; Mazor et al., 2014). In the case of management costs, the index was re-scaled to indicate the current proximity to coastal infrastructure as a measure of impediments to conservation management. For example, if the objective was to select MPAs while minimising the costs of enforcing and maintaining MPAs, then one suitable cost would be a measure of how remote they were from urban areas. Although, in principle, proximity to the coast as a surrogate for opportunity cost and distance from the coast as a surrogate for cell-specific management costs might tend to cancel one another out, there was one

factor that called for the use of both estimates: different conversion factors were used to adjust both types of cost between no-take and multiple-use zones.

Second, both measures of cell-specific costs needed to be adjusted between the different zones. To differentiate the cell-specific opportunity costs of no-take and multiple-use zones, we reviewed fishery restrictions imposed by management plans of existing MPAs containing coral reefs in Brazil. By using fishery statistics from governmental reports, we then calculated the relationship between the opportunity cost of multiple-use and no-take MPAs. On average, we found that the opportunity cost of partial protection was 0.29 of that of no-take (a cost to all fisheries) and used this number a multiplier for the cell-specific cost related to forgone fishing (Appendix A5). To differentiate the cell-specific management costs of no-take and multiple-use zones, we extracted budget information from published management plans of existing MPAs in Brazil. On average, we found that no-take zones were 2.3 times more costly, per unit area, to manage than multiple-use zones. This is because no-take zones pose more restrictions, which result in higher levels of noncompliance with zoning regulations, and require more enforcement by authorities (Gerhardinger et al., 2011). Thus, we used 2.3 as a multiplier for the estimate of the cell-specific management cost of no-take zones.

The calculation of the total cost of MPA implementation was based on scenario outputs (see section below). The cell-specific component of total cost reflected the summed cost of reef cells selected by Marxan with Zones' best solution (i.e. selected reef cells that meet the conservation objectives at the lowest cost). Estimates of configuration-specific management costs were based on linear models relating budgetary information on implementing existing MPAs to their areas, a major driver of per-unit-area management costs (Gravestock et al., 2008; Ban et al., 2011). The annual configuration-specific management costs of MPA systems were therefore estimated from known costs of managing no-take and multiple-use zones modified by sizes of individual MPAs identified for each zone (Appendix A7).

## 2.7. Conservation scenarios

We considered eight conservation scenarios to explore alternative MPA configurations: (i) expanded MPA systems that complement the existing MPAs and achieve each set of objectives individually and all three simultaneously ( $N = 4$ ); and (ii) MPA systems that ignore the existing MPAs, and achieve each set of objectives individually and all three simultaneously ( $N = 4$ ). To generate these scenarios, we used Marxan with Zones (Watts et al., 2009), a conservation planning tool that allows for zone-specific objectives (Appendix A6). Our formulation of zone-specific objectives meant that we did not need to stipulate different levels of zone effectiveness as inputs for the software. Given that existing MPAs constrain the total coral reef area available for further protection to fully achieve objectives in the expanded scenarios, we allowed existing multiple-use zones to be upgraded to no-take areas where necessary to ensure all objectives were achieved. Our goal was not to support solutions for on-ground conservation, but to investigate potential implications of multiple objectives for coral reef management in hypothetical MPA systems.

We calculated the total cell-specific and configuration-specific management costs for each scenario to test whether the expansion of existing MPA systems would be more costly than designing MPA systems from scratch. For analyses focused on biodiversity, connectivity, and global warming objectives separately, we measured the incidental achievement of all other objectives. We used the same calculation of percentage achievement of objectives as in Eq. (1) for the gap analysis. We then used ANOVA to evaluate differences in the incidental achievement of objectives for each paired comparison of sets of objectives for both expanded MPA systems and MPA systems designed from scratch.

To investigate spatial differences in the distribution of priority areas between scenarios designed to achieve all sets of objectives, both considering and ignoring existing MPAs, we compared the selection frequencies from Marxan with Zones (i.e. how often each reef cell was selected for an indicated zone) across 100 runs for each reef cell. We also evaluated how the spatial refinement of existing MPA systems could accommodate each set of objectives and all objectives together. In this analysis, we did not incorporate any release of MPAs or increase in the extent of activities allowed (i.e. MPA downgrading). Accounting for this aspect of MPA dynamics would require a more thorough understanding of the ecological effectiveness of MPAs since their establishment.

## 2.8. Benefit-cost ratios

Our final aim was to estimate the benefit-cost ratios of different conservation scenarios in relation to direct and incidental benefit of planning for each set of objectives separately and all combined as well as the additional cost required to achieve the portions of objectives not met by existing MPAs.

We used the reef cells identified by Marxan with Zones' best solution and calculated the benefit  $B$  of a given scenario as the summed direct (for all features targeted) and incidental objective achievement (for all features not considered in that scenario):

$$B = \sum_{1 \dots N}^i Obi - Obi_{ex} \quad (2)$$

where  $Obi$  is the incidental or direct achievement of the objective for each feature  $i$  and  $Obi_{ex}$  is the current level of achievement for feature  $i$ .

The total cell-specific cost,  $O_c$ , was obtained by summing the total cost for each zone and scenario as in the prioritisations. The benefit-cost ratio for cell-specific costs  $BO$  was the overall benefit divided by the proportional increment or reduction in the cell-specific cost for a given scenario in relation to existing MPA zones:

$$BO = \frac{B}{M_{OS}/M_{Oex}} \quad (3)$$

where  $M_{OS}$  is the total cell-specific cost for a given scenario and  $M_{Oex}$  is the total cell-specific cost of existing MPAs.

The total configuration-specific cost,  $M_c$ , was calculated as in the section above, and the total scenario benefit-cost ratio for configuration-specific costs ( $BM$ ) was the overall benefit divided by the proportional increment or reduction in the annual management costs in relation to existing MPA zones:

$$BM = \frac{B}{M_{cS}/M_{cex}} \quad (4)$$

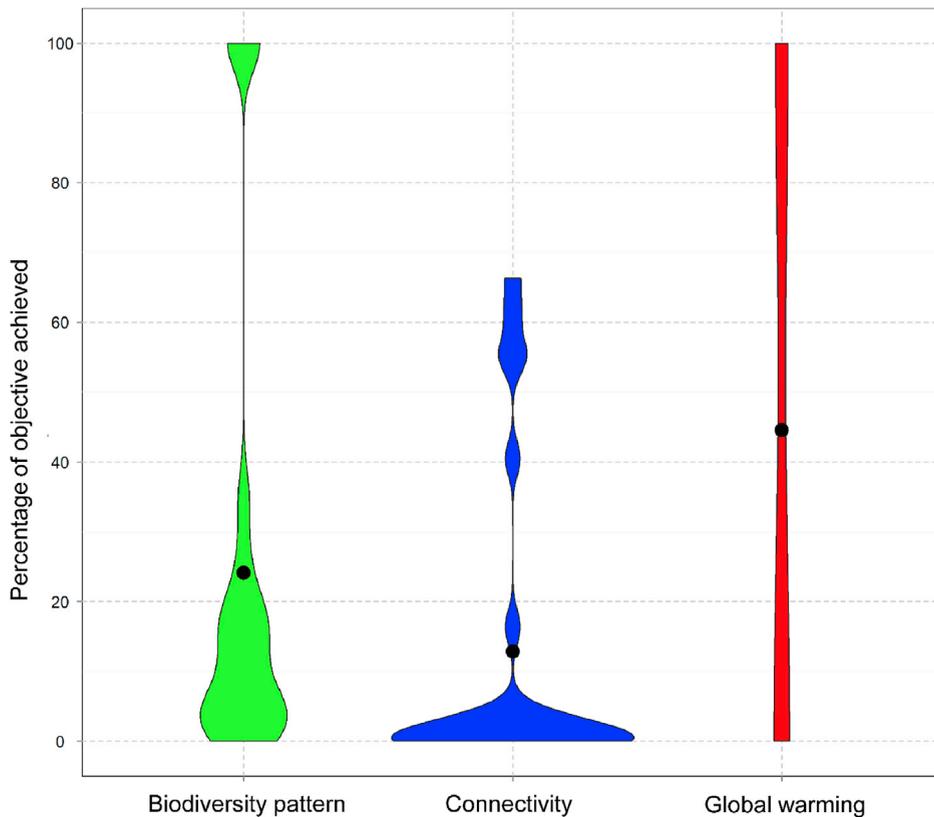
where  $M_{cS}$  is the total configuration-specific cost for a given scenario and  $M_{cex}$  is the total configuration-specific cost of existing MPAs.

All data analyses used R 3.1.3 statistical programming and ArcGIS 10.

### 3. Results

#### 3.1. Gap analysis for existing MPAs

Achievement of objectives in existing MPAs varied strongly between the three sets of objectives (Fig. 2). For biodiversity pattern, the achievement of objectives in MPAs averaged 24.8% (median 24%). Values were lower for connectivity and higher



**Fig. 2.** Percentages of objective achievement by existing MPAs for biodiversity pattern (green), connectivity (blue), and global warming (red). Violin graphs show the density of features against percentage achievement (as an illustration of frequency distributions), and black dots display the means. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

for global-warming objectives (means of 12.8% and 44% achieved, respectively). About 16% of biodiversity features (i.e. 29 features) met both their overall and zone-specific objectives in existing MPAs. Conversely, 77% of biodiversity features achieved no overall or zone-specific objectives. Separating the results by subsets of biodiversity features (Appendix B), ecosystems and threatened species had the best overall representation (means of 48 and 42%, respectively) despite species under legal protection having more demanding objectives.

Connectivity (Fig. 2) was marked by a concentration of 18 out of 24 features with low achievement (less than 10%) of objectives in existing MPAs and 65% maximum achievement. Betweenness centrality received the lowest level of protection out of all three metrics, with about 2.5% achievement. The objectives of 12 connectivity features were completely missed.

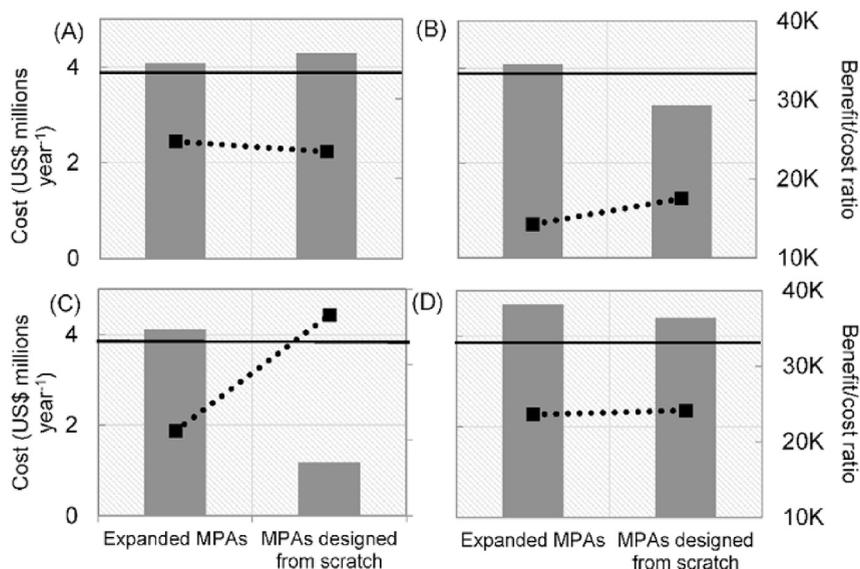
For the nine global-warming features, the distribution of objective achievement was polarised, around either 0% or 100% (Fig. 2). Out of all thermal refugia types, only one (historical thermal refugia projected to face increased stress in the future) fell within existing no-take MPAs. All of the remaining thermal refugia were outside MPAs or were covered by multiple-use zones that did not contribute to the achievement of objectives requiring coverage by no-take MPAs. On the other hand, reef cells projected to face disturbances related to global warming and requiring mitigation interventions by multiple-use MPAs largely occurred within established no-take MPAs, with their objectives being fully achieved.

### 3.2. Comparisons between scenarios

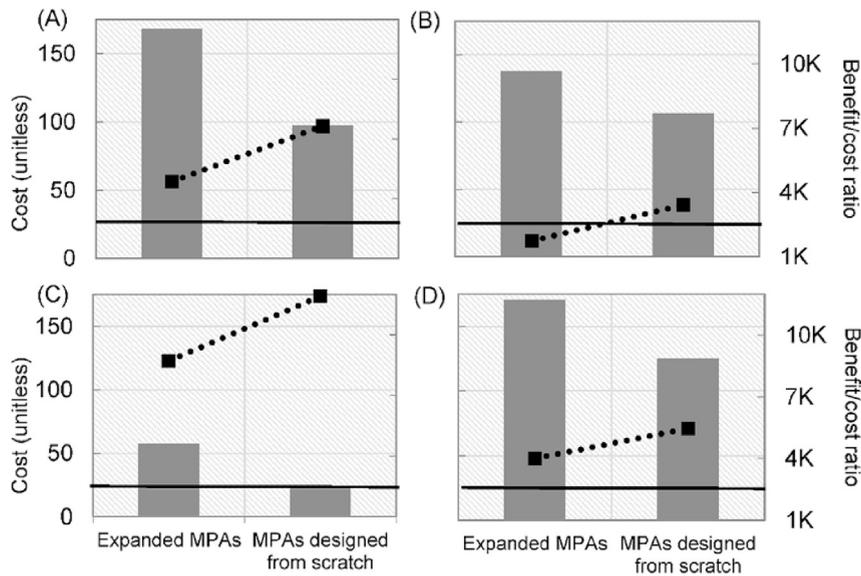
Managing the existing system of MPAs protecting coral reefs was estimated to cost around 3.9 million US\$ per year (black horizontal lines in Fig. 3A–D). The protection of larger coral reef areas in the expanded scenarios resulted in a slight increase in total configuration-specific management costs for individual sets of objectives and a greater increase when all sets of objectives were achieved together (an increase of US\$ 0.76 million per year; Fig. 3D). In contrast, expanded scenarios resulted in a strong increase in total cell-specific costs when compared to the costs of existing MPAs for all sets of objectives (increases of up to seven-fold in costs when all objectives were achieved; Fig. 4A–D).

Although MPAs designed from scratch for connectivity and global warming objectives separately were much cheaper in terms of configuration-specific management costs than the respective expanded scenarios (roughly 0.7 and 2.7 million US\$ per year, respectively; Fig. 3B–C), the total configuration-specific management cost of MPAs designed from scratch was more than that of the expanded scenario when planning for biodiversity pattern (Fig. 3A). The reason for this increase was the larger number of small MPAs, with higher per-unit-area management costs. This also influenced the result for planning to achieve all objectives together: MPAs designed from scratch reduced configuration-specific management costs by only US\$ 0.3 million per year relative to the expanded scenario (Fig. 3D). For total cell-specific costs, MPAs designed from scratch always reduced costs when compared to expanded MPA systems, regardless of the objectives targeted (Fig. 4A–D).

With regards to incidental achievement of objectives, expanding the existing MPA system for biodiversity pattern yielded a significantly greater incidental achievement of objectives for connectivity and global warming ( $p < 0.05$ ), relative to existing MPAs (Fig. 5A). Similarly, directing new MPAs from scratch toward biodiversity yielded significantly greater levels of



**Fig. 3.** Configuration-specific management costs and benefit-cost ratios for expanded MPAs and MPAs designed from scratch. Total costs are shown by gray bars. Benefit-cost ratios are shown by black markers linked by dotted lines. A: biodiversity pattern; B: connectivity; C: global warming; and D: all conservation objectives. Black horizontal lines denote the estimated total cost of the existing MPA system. Estimates are in annual US\$ and are based on regression analysis described in Appendix A.



**Fig. 4.** Total cell-specific costs and benefit–cost ratios for expanded MPAs and MPAs designed from scratch. Total costs are shown by gray bars. Benefit–cost ratios are shown by black markers linked by dotted lines. A: biodiversity pattern; B: connectivity; C: global warming; and D: all conservation objectives. Black horizontal lines denote the estimated opportunity cost of the existing MPA system.

achievement for other sets of objectives in comparison to the existing level of achievement (Fig. 5A). Expanding the MPA system for either connectivity (Fig. 5B) or global warming (Fig. 5C) significantly improved achievement of objectives, relative to existing MPAs, only for biodiversity pattern ( $p < 0.05$ ). Likewise, designing MPAs from scratch for these same sets of objectives enhanced incidental achievement of biodiversity objectives only, relative to existing MPAs ( $p < 0.05$ ).

Some reef cells contributed similarly to achieving all objectives, regardless of their current protection status (e.g. cells in light green within subregions “c” and “d” in Fig. 6A–B). However, we found that considering existing MPAs changed substantially the patterns of conservation importance. Overall solutions were more similar between expanded and MPAs designed from scratch for multiple-use zones (Fig. 6B) than between their counterparts for no-take zones (Fig. 6A).

To achieve all objectives, an increase in the coral reef area within no-take zones and conversion of parts of multiple-use zones to no-take zones were required in all expanded scenarios (Fig. 7). For biodiversity pattern, refinements mainly included additional protection of 20% of coral reefs by no-take zones, mostly by upgrading existing multiple-use zones. Achieving the connectivity objectives required an increase in the area protected by additional no-take zones (about 13%) and the conversion of a large coral reef area from multiple-use to no-take (about 30%). Among the three sets of objectives, global warming required the smallest extent of additional MPAs (additional 6% of the total coral reef area to be protected, consisting of increasing no-take zones by 2.4% and increasing multiple-use zones by 3.6%). Because existing MPAs contributed so little to the achievement of objectives, an additional 27% of the total coral reef area needed protection by some type of MPA to achieve all objectives together.

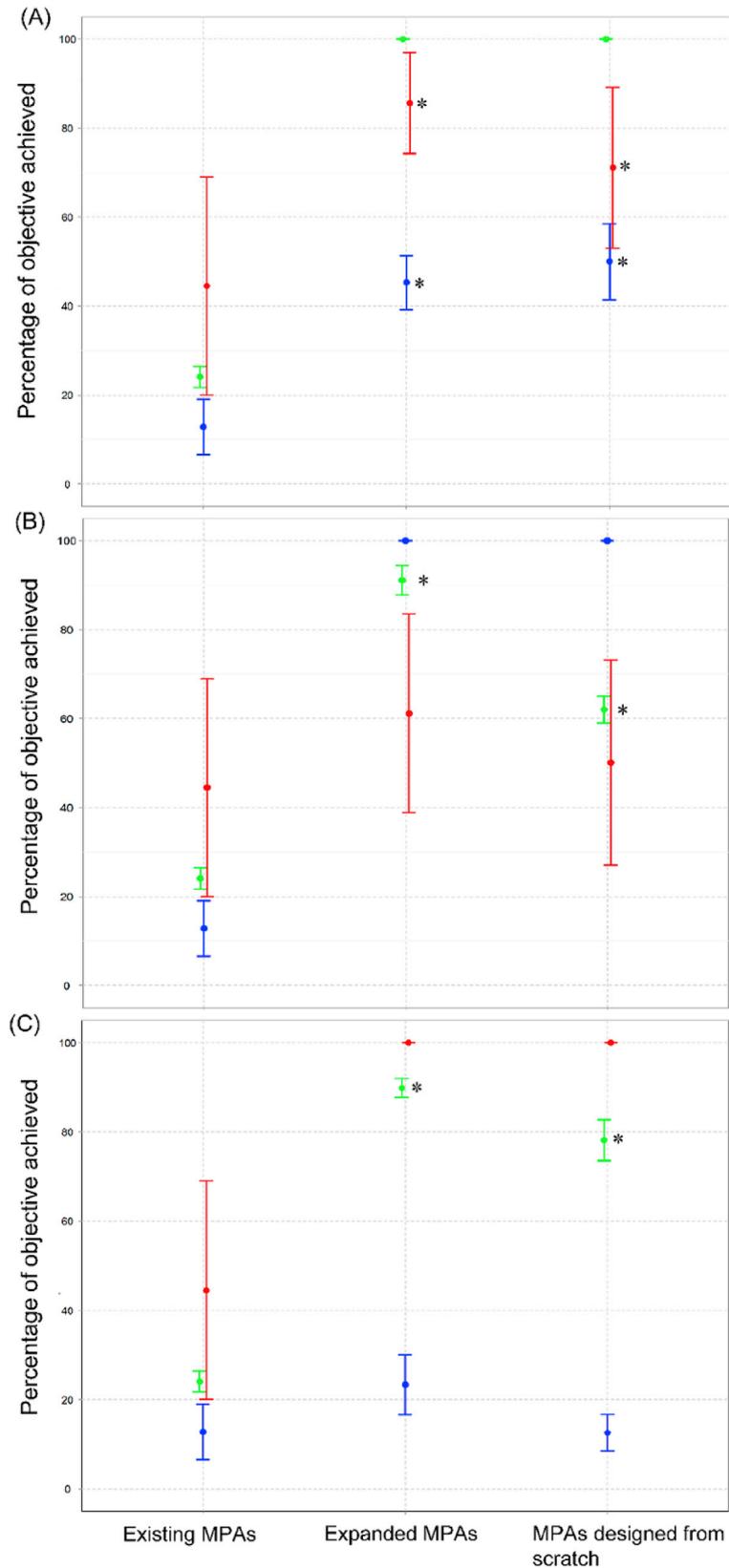
### 3.3. The value of integrated approaches from the outset of planning

As expected, designing new MPAs from scratch was always more cost-effective than expanded scenarios for all objectives when using total cell-specific costs to calculate benefit–cost ratios (Fig. 4). Indeed, MPAs designed from scratch outperformed expanded MPA scenarios by requiring smaller coral reef areas and smaller total cell-specific costs to achieve all objectives separately and simultaneously (Table 3). In contrast, based on configuration-specific management costs, expanded scenarios proved to be slightly more cost-effective than systems designed from scratch in achieving objectives for biodiversity pattern (Fig. 3A), and only slightly less cost-effective in achieving all sets of objectives together (Fig. 3D).

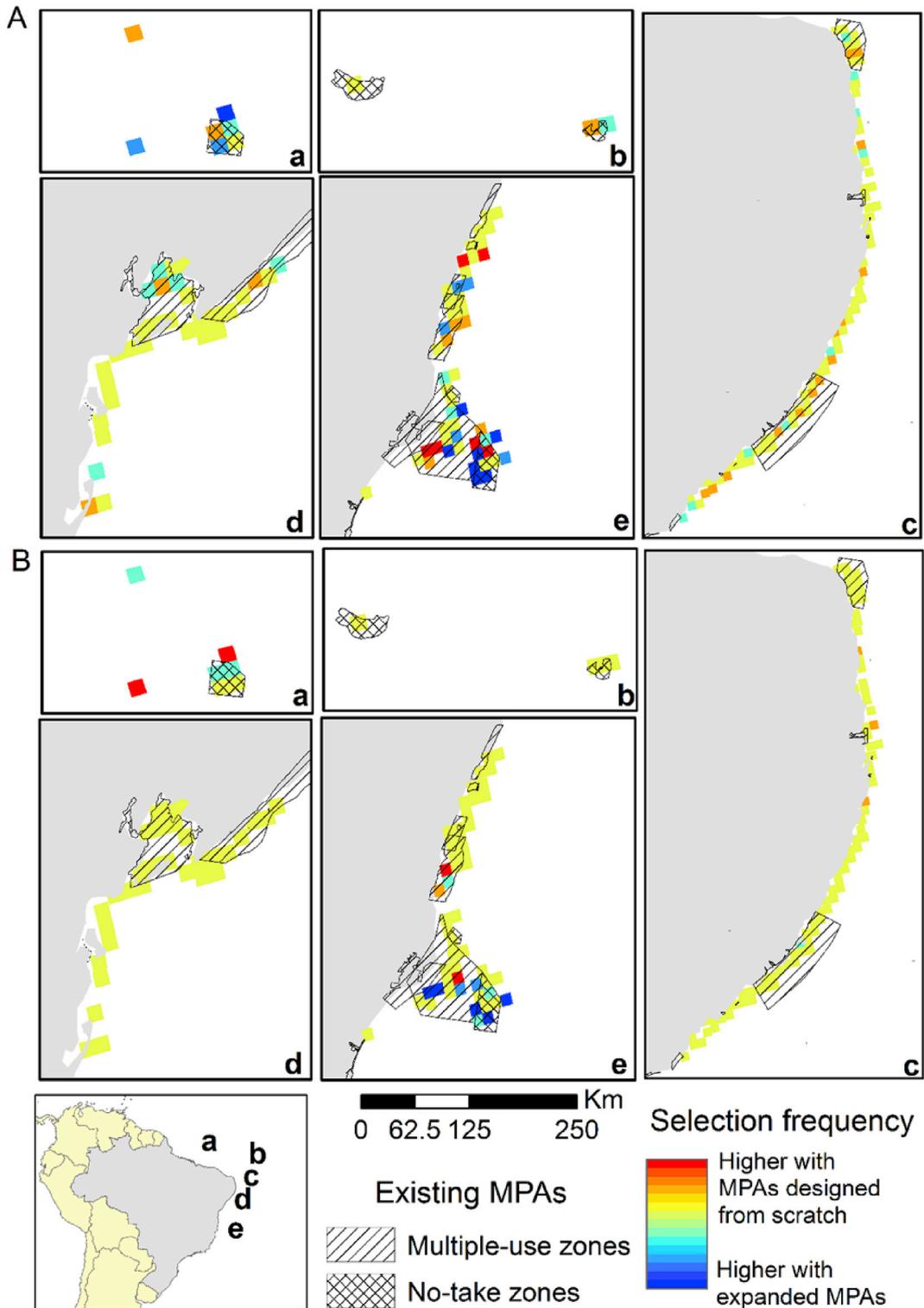
Finally, we compared the savings potential from integrated planning by assessing scenarios that combined all objectives and the combined best solutions, not counting overlapping areas, for scenarios focusing on individual sets of objectives (Table 3). Integrated planning led to smaller total coral reef areas required and smaller total cell-specific costs, whether planning from scratch or expanding existing MPAs. However, integrated planning required slightly more total configuration-specific management resources than planning for separate sets of objectives, whether from scratch or building on existing MPAs.

## 4. Discussion

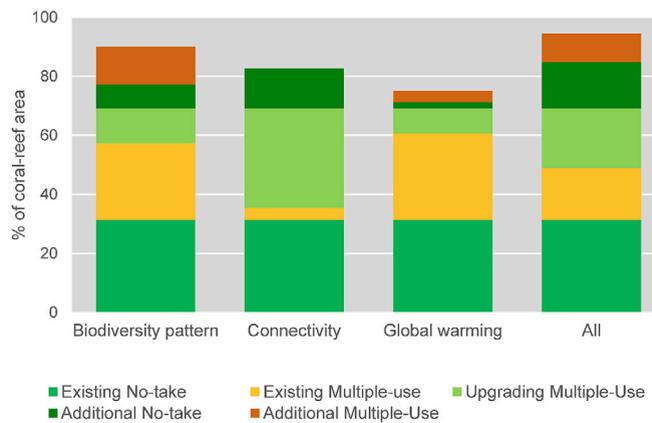
Marine protected areas (MPAs) are a commonly applied management tool aimed at achieving long-term biodiversity goals and managing extractive activities to minimise their impacts on biodiversity (Edgar et al., 2014). As MPA numbers and total



**Fig. 5.** Actual objective achievement by existing MPAs and incidental achievement of conservation objectives in expanded MPAs and MPAs designed from scratch. Mean objective achievements (and standard errors) are shown in each panel for each set of objectives (biodiversity pattern, connectivity, and global warming illustrated by green, blue, and red colours, respectively) when planning for biodiversity pattern (A), connectivity (B), and global warming (C). \*P < 0.05 for ANOVA comparisons against existing MPAs. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 6.** Differences in selection frequencies of reef cells between scenarios when existing MPAs were considered (expanded MPAs) or ignored (MPAs designed from scratch). The comparison is made for scenarios considering all objectives and results are shown for no-take zones (A) and multiple-use ones (B). Letters a-e denote approximate locations of reef cells along the Brazilian coast in the inset map.



**Fig. 7.** Spatial refinements required to expand the existing MPA system to achieve each set of objectives separately and all together (in terms of total coral reef area). Refinements include additional area allocated to new no-take and multiple-use zones and areas of existing multiple-use zones upgraded to no-take zones.

extent increase globally, there is a need for methods that enable an assessment of their protection levels against multiple objectives, particularly with respect to processes such as connectivity and global warming (Magris et al., 2014). We addressed this gap by presenting an MPA zoning approach for integrating biodiversity pattern, connectivity, and global warming into the refinement of an existing MPA system intended to protect coral reefs in Brazil. While current MPA design studies using different conservation zones have explored tradeoffs between conservation objectives and socioeconomic impacts in coral reef areas (e.g. Weeks et al., 2010; Makino et al., 2013), our study explores the consequences of any set of objectives not being directly addressed and relying on incidental achievement, and the additional implementation costs of prioritisations that address sets of objectives individually rather than in an integrated way. We found that a large expansion of MPAs is required for optimal zoning of the Brazilian coral reefs, but integration of multiple objectives did not necessarily result in a substantial increase in configuration-specific management costs. However, we also demonstrated the value of integrating multiple conservation objectives from the outset of MPA planning. Integrative approaches would avert an unbalanced achievement of objectives, thereby improving conservation outcomes, reducing the total area requiring protection, and reducing total implementation costs, resulting in a more cost-effective MPA system than progressive expansion of the established MPA system to achieve missing objectives.

Accounting for multiple objectives in conservation planning has recently emerged as an important theme. While Green et al. (2014) proposed general qualitative guidelines for the achievement of multiple objectives, Beger et al. (2015) first quantified the co-benefits of planning for multiple objectives in the Coral Triangle. Our study built on this previous work by focusing on defining objectives that provide adequate levels of protection to conservation features (Pressey et al., 2003), considering multiple management types in a multi-objective prioritisation, and estimating the relative configuration-specific management costs of alternative scenarios. We have also demonstrated that taking a more comprehensive view of all biodiversity components alters the inferences from gaps assessed only with biodiversity pattern and assuming uniform levels of protection.

We showed that, while the national system of MPAs in Brazil provides sufficient protection for some biodiversity features related to coral reefs, these MPAs failed substantially in meeting objectives for functional diversity, thermal refugia, and connectivity features. This problem might have arisen from contemporary conservation efforts in Brazil being primarily directed towards preventing species from becoming threatened or representing broad ecosystems (Amaral and Jablonski, 2005), with limited information on many important ecological and threatening processes of conservation interest. Also, this result can be attributed to the *ad hoc* manner in which MPAs have been historically added to the system, without taking into account emergent properties of the system as a whole, such as complementarity and connectivity between individual MPAs. The importance of incremental MPA refinement is recognised within adaptive management (McCook et al., 2010). Thus we emphasise the need for reconciling multiple objectives when systematically designing new MPAs as a strategy for increasing the likelihood that biodiversity patterns persist.

A limitation of our research and similar studies in the marine planning literature is that, to date, they have been largely focused on opportunity costs for fisheries (Ban and Klein, 2009). In reality, the potential costs of protected areas should be more comprehensive, considering other key stakeholder groups (Adams et al., 2010) and aiming for a more equitable distribution of costs (Gurney et al., 2015). This challenge is magnified when opportunity costs for more than one type of MPA zone are required (Makino et al., 2013; Metcalfe et al., 2015); thus, cost predictions in expanding the Brazilian MPA system should include the relative impacts of different zones on extractive activities as socio-economic information is gathered, to ensure that priority areas identified are as cost-effective as possible. Moreover, although our model of management costs is based on the reasonable assumption that proposed MPA size is a consistently good predictor of management cost per unit area (Ban et al., 2011), our statistical linear model did not capture any polynomial relationship between per-unit-area management cost and MPA size. Our research could then be extended to consider nonlinearities in this relationship.

**Table 3**

Total coral reef area and total costs required for scenarios. Total costs are shown in terms of cell-specific costs (opportunity and management) and configuration-specific management costs. Estimates are shown for planning that considered all conservation objectives separately (minus their overlapping areas) (A), and integrated planning that combined all objectives (B).

Separate scenarios	Coral reef area (% of total)	Cell-specific costs (unitless)	Configuration-specific management cost (US\$ millions year <sup>-1</sup> )
A) Sum of all separate conservation objectives			
MPAs designed from scratch	69.86	189.28	\$4,336,834.14
Expanded MPAs	97.68	320.9	\$4,141,625.05
B) Integrated conservation objectives			
MPAs designed from scratch	63.42	129.53	\$4,399,553.60
Expanded MPAs	94.43	170.74	\$4,697,914.90

Based on our results, a systematic expansion of existing MPAs should strive to incorporate competing planning objectives, rather than mirroring contemporary conservation efforts, often based on the opportunistic placement of MPAs. Our case study illustrated that the total areal extent and total cell-specific costs of new MPAs needed to attain all conservation objectives can be much larger than an optimal siting of MPAs designed from scratch. Other researchers have also reached this conclusion (Malcolm et al., 2011). However, the replacement of inefficient MPA systems based only on how they contribute to objectives is difficult in practice (Fuller et al., 2010), and could be used, not only to achieve benefits for biodiversity, but also to weaken protected areas and facilitate extraction of natural resources (Mascia and Pailler, 2011). In practice, MPA designers are better off adopting guidelines of adaptive spatial planning for improved resource-use zoning (Mills et al., 2015), optimal scheduling of conservation actions, and adjusted investments in ongoing MPA management in relation to budgetary constraints.

Our results also demonstrated that spatial overlap between sets of conservation objectives is variable and limited. This means that, as more objectives are added to MPA planning, the required areas and total resources required for protection will inevitably increase (and see Pressey et al., 2003). On the other side, the mission of protected areas has rapidly expanded from single-objective settings to new and increasingly diverse focal objectives added to the pre-existing ones (Watson et al., 2014). For instance, recent research efforts have recommended that, specifically for coral reefs, expansion of MPA coverage should go beyond the focus on protecting healthy ecosystems to also incorporate restoration of degraded areas (Abelson et al., 2016) or improve human welfare (Jupiter et al., 2014). Our work demonstrated some implications when operationalising the plurality of objectives: the integration of multiple objectives in the initial stages of MPA planning would serve as a cost-saving approach, compared with iterative refinements of selected MPAs required by additional objectives.

We recognise that MPA expansion and zoning are among several tools that might be used by managers to realise conservation objectives and reduce potential conflict. Further investigations of the synergies and trade-offs between different management tools (i.e. fishing restrictions, catchment-based management) are required. Moreover, the interactions among objectives might change over time, given the temporal dimension of MPA effectiveness when evaluated against multiple objectives. Additional guidance is needed to incorporate potential significant interactions of climate change on connectivity (e.g. Andrello et al., 2015) and biodiversity, and to tailor more informed conservation plans.

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.gecco.2017.05.002>.

## References

- Abelson, A., Nelson, P., Edgar, G., Shashar, N., Reed, D., Belmaker, J., Krause, G., Beck, M., Brokovich, E., France, R., 2016. Expanding marine protected areas to include degraded coral reefs. *Conserv. Biol.* 30, 1182–1191.
- Adams, V.M., Pressey, R.L., Naidoo, R., 2010. Opportunity costs: who really pays for conservation? *Biol. Conserv.* 143, 439–448.
- Amaral, A.C.Z., Jablonski, S., 2005. Conservation of marine and coastal biodiversity in Brazil. *Conserv. Biol.* 19, 625–631.
- Andrello, M., Mouillot, D., Somot, S., Thuiller, W., Manel, S., 2015. Additive effects of climate change on connectivity between marine protected areas and larval supply to fished areas. *Divers. Distrib.* 21, 139–150.
- Ban, N.C., Klein, C.J., 2009. Spatial socioeconomic data as a cost in systematic marine conservation planning. *Conserv. Lett.* 2, 206–215.
- Ban, N.C., Adams, V., Pressey, R.L., Hicks, J., 2011. Promise and problems for estimating management costs of marine protected areas. *Conserv. Lett.* 4, 241–252.

- Beger, M., Linke, S., Watts, M., Game, E., Treml, E., Ball, I., Possingham, H.P., 2010. Incorporating asymmetric connectivity into spatial decision making for conservation. *Conserv. Lett.* 3, 359–368.
- Beger, M., McGowan, J., Treml, E.A., Green, A.L., White, A.T., Wolff, N.H., Klein, C.J., Mumby, P.J., Possingham, H.P., 2015. Integrating regional conservation priorities for multiple objectives into national policy. *Nat. Commun.* 6 <http://dx.doi.org/10.1038/ncomms9208>.
- Bellwood, D., Hughes, T., Folke, C., Nyström, M., 2004. Confronting the coral reef crisis. *Nature* 429, 827–833.
- Chollett, I., Enriquez, S., Mumby, P.J., 2014. Redefining thermal regimes to design reserves for coral reefs in the face of climate change. *PLoS One* 9, e110634.
- Côté, I.M., Darling, E.S., 2010. Rethinking ecosystem resilience in the face of climate change. *PLoS Biol.* 8, e1000438.
- D'agata, S., Mouillot, D., Wantiez, L., Friedlander, A.M., Kulbicki, M., Vigliola, L., 2016. Marine reserves lag behind wilderness in the conservation of key functional roles. *Nat. Commun.* 7 <http://dx.doi.org/10.1038/ncomms12000>.
- Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T., Berkhout, J., 2014. Global conservation outcomes depend on marine protected areas with five key features. *Nature* 506, 216–220.
- Fuller, R.A., McDonald-Madden, E., Wilson, K.A., Carwardine, J., Grantham, H.S., Watson, J.E., Klein, C.J., Green, D.C., Possingham, H.P., 2010. Replacing underperforming protected areas achieves better conservation outcomes. *Nature* 466, 365–367.
- Game, E.T., Kareiva, P., Possingham, H.P., 2013. Six common mistakes in conservation priority setting. *Conserv. Biol.* 27, 480–485.
- Genner, M.J., Sims, D.W., Southward, A.J., Budd, G.C., Masterson, P., McHugh, M., Rendle, P., Southall, E.J., Wearmouth, V.J., Hawkins, S.J., 2010. Body size-dependent responses of a marine fish assemblage to climate change and fishing over a century-long scale. *Glob. Change Biol.* 16, 517–527.
- Gerhardinger, L.C., Godoy, E.A., Jones, P.J., Sales, G., Ferreira, B.P., 2011. Marine protected areas: the flaws of the Brazilian national system of marine protected areas. *Environ. Manage.* 47, 630–643.
- Gravestock, P., Roberts, C.M., Bailey, A., 2008. The income requirements of marine protected areas. *Ocean Coast. Manag.* 51, 272–283.
- Green, A., Smith, S.E., Lipsett-Moore, G., Groves, C., Peterson, N., Sheppard, S., Lokani, P., Hamilton, R., Almany, J., Aitsi, J., Bualia, L., 2009. Designing a resilient network of marine protected areas for Kimbe Bay, Papua New Guinea. *Oryx* 43, 488–498.
- Green, A.L., Fernandes, L., Almany, G., Abesamis, R., McLeod, E., Aliño, P.M., White, A.T., Salm, R., Tanzer, J., Pressey, R.L., 2014. Designing marine reserves for fisheries management, biodiversity conservation, and climate change adaptation. *Coast. Manag.* 42, 143–159.
- Guilhaumon, F., Albouy, C., Claudet, J., Velez, L., Ben Rais Lasram, F., Tomasini, J.A., Douzey, E.J., Meynard, C.N., Mouquet, N., Troussellier, M., 2014. Representing taxonomic, phylogenetic and functional diversity: new challenges for Mediterranean marine-protected areas. *Divers. Distrib.* 21 <http://dx.doi.org/10.1111/ddi.12280>.
- Gurney, G.G., Pressey, R.L., Ban, N.C., Álvarez-Romero, J.G., Jupiter, S., Adams, V.M., 2015. Efficient and equitable design of marine protected areas in Fiji through inclusion of stakeholder-specific objectives in conservation planning. *Conserv. Biol.* 29 <http://dx.doi.org/10.1111/cobi.12514>.
- Halpern, B.S., Warner, R.R., 2002. Marine reserves have rapid and lasting effects. *Ecol. Lett.* 5, 361–366.
- Halpern, B.S., Floeter, S.R., 2008. Functional diversity responses to changing species richness in reef fish communities. *Mar. Ecol. Prog. Ser.* 364, 147–156.
- Harnik, P.G., Simpson, C., Payne, J.L., 2012. Long-term differences in extinction risk among the seven forms of rarity. *Proc. R. Soc. Lond. B Biol. Sci.* 279, 4969–4976.
- Harrison, H.B., Williamson, D.H., Evans, R.D., Almany, G.R., Thorrold, S.R., Russ, G.R., Feldheim, K.A., Van Herwerden, L., Planes, S., Srinivasan, M., 2012. Larval export from marine reserves and the recruitment benefit for fish and fisheries. *Curr. Biol.* 22, 1023–1028.
- Jupiter, S.D., Cohen, P.J., Weeks, R., Tawake, A., Govan, H., 2014. Locally-managed marine areas: multiple objectives and diverse strategies. *Pac. Conserv. Biol.* 20, 165–179.
- Klein, C.J., Brown, C.J., Halpern, B.S., Segan, D.B., McGowan, J., Beger, M., Watson, J.E., 2015. Shortfalls in the global protected area network at representing marine biodiversity. *Sci. Rep.* 5, 17539.
- Klein, C.J., Jupiter, S.D., Selig, E.R., Watts, M.E., Halpern, B.S., Kamal, M., Roelfsema, C., Possingham, H.P., 2012. Forest conservation delivers highly variable coral reef conservation outcomes. *Ecol. Appl.* 22, 1246–1256.
- Magris, R., Heron, S.F., Pressey, R.L., 2015a. Conservation planning for coral reefs accounting for climate warming disturbances. *PLoS One* 10. <http://dx.doi.org/10.1371/journal.pone.0140828>.
- Magris, R., Mills, M., Fuentes, M., Pressey, R., 2013. Analysis of progress towards a comprehensive system of marine protected areas in Brazil. *Natureza Conservação* 11, 1–7.
- Magris, R.A., Pressey, R.L., Weeks, R., Ban, N.C., 2014. Integrating connectivity and climate change into marine conservation planning. *Biol. Conserv.* 170, 207–221.
- Magris, R.A., Treml, E.A., Pressey, R.L., Weeks, R., 2015b. Integrating multiple species connectivity and habitat quality into conservation planning for coral reefs. *Ecography* 39. <http://dx.doi.org/10.1111/ecog.01507>.
- Makino, A., Klein, C.J., Beger, M., Jupiter, S.D., Possingham, H.P., 2013. Incorporating conservation zone effectiveness for protecting biodiversity in marine planning. *PLoS One* 8, e78986.
- Makino, A., Yamano, H., Beger, M., Klein, C.J., Yara, Y., Possingham, H.P., 2014. Spatio-temporal marine conservation planning to support high-latitude coral range expansion under climate change. *Divers. Distrib.* 20, 1–13.
- Malcolm, H., Foulsham, E., Pressey, R., Jordan, A., Davies, P., Ingleton, T., Johnstone, N., Hessey, S., Smith, S., 2011. Selecting zones in a marine park: early systematic planning improves cost-efficiency; combining habitat and biotic data improves effectiveness. *Ocean Coast. Manag.* 59, 1–12.
- Mascia, M.B., Pailler, S., 2011. Protected area downgrading, downsizing, and degazettement (PADDD) and its conservation implications. *Conserv. Lett.* 4, 9–20.
- Mazor, T., Possingham, H.P., Edelist, D., Brokovich, E., Kark, S., 2014. The crowded sea: incorporating multiple marine activities in conservation plans can significantly alter spatial priorities. *PLoS One* 9, e104489.
- McCarthy, D.P., Donald, P.F., Scharlemann, J.P., Buchanan, G.M., Balmford, A., Green, J.M., Bennun, L.A., Burgess, N.D., Fishpool, L.D., Garnett, S.T., 2012. Financial costs of meeting global biodiversity conservation targets: current spending and unmet needs. *Science* 338, 946–949.
- McClanahan, T.R., Donner, S.D., Maynard, J.A., MacNeil, M.A., Graham, N.A., Maina, J., Baker, A.C., Beger, M., Campbell, S.J., Darling, E.S., 2012. Prioritizing key resilience indicators to support coral reef management in a changing climate. *PLoS One* 7, e42884.
- McCook, L., Almany, G., Berumen, M., Day, J., Green, A., Jones, G., Leis, J., Planes, S., Russ, G., Sale, P., 2009. Management under uncertainty: guide-lines for incorporating connectivity into the protection of coral reefs. *Coral Reefs* 28, 353–366.
- McCook, L.J., Ayling, T., Cappo, M., Choat, J.H., Evans, R.D., De Freitas, D.M., Heupel, M., Hughes, T.P., Jones, G.P., Mapstone, B., 2010. Adaptive management of the Great Barrier Reef: a globally significant demonstration of the benefits of networks of marine reserves. *Proc. Natl. Acad. Sci.* 107, 18278–18285.
- Metcalfe, K., Vaz, S., Engelhard, G.H., Villanueva, M.C., Smith, R.J., Mackinson, S., 2015. Evaluating conservation and fisheries management strategies by linking spatial prioritization software and ecosystem and fisheries modelling tools. *J. Appl. Ecol.* 52, 665–674.
- Mills, M., Weeks, R., Pressey, R.L., Gleason, M.G., Eisma-Osorio, R.-L., Lombard, A.T., Harris, J.M., Killmer, A.B., White, A., Morrison, T.H., 2015. Real-world progress in overcoming the challenges of adaptive spatial planning in marine protected areas. *Biol. Conserv.* 181, 54–63.
- Mouillot, D., Villéger, S., Parravicini, V., Kulbicki, M., Arias-González, J.E., Bender, M., Chabanet, P., Floeter, S.R., Friedlander, A., Vigliola, L., 2014. Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. *Proc. Natl. Acad. Sci.* 111, 13757–13762.
- Mumby, P.J., Steneck, R.S., 2008. Coral reef management and conservation in light of rapidly evolving ecological paradigms. *Trends Ecol. Evol.* 23, 555–563.
- Mumby, P.J., Harborne, A.R., 2010. Marine reserves enhance the recovery of corals on Caribbean reefs. *PLoS One* 5, e8657.
- Olds, A.D., Albert, S., Maxwell, P.S., Pitt, K.A., Connolly, R.M., 2013. Mangrove-reef connectivity promotes the effectiveness of marine reserves across the western Pacific. *Glob. Ecol. Biogeogr.* 22 <http://dx.doi.org/10.1111/geb.12072>.
- Pressey, R.L., Cowling, R.M., Rouget, M., 2003. Formulating conservation targets for biodiversity pattern and process in the Cape Floristic Region, South Africa. *Biol. Conserv.* 112, 99–127.

- Pressey, R.L., Visconti, P., Ferraro, P.J., 2015. Making parks make a difference: poor alignment of policy, planning and management with protected-area impact, and ways forward. *Philos. Trans. R. Soc. B* 370, 20140280.
- Pressey, R.L., Cabeza, M., Watts, M.E., Cowling, R.M., Wilson, K.A., 2007. Conservation planning in a changing world. *Trends Ecol. Evol.* 22, 583–592.
- Rowlands, G., Purkis, S., Riegl, B., Metsamaa, L., Bruckner, A., Renaud, P., 2012. Satellite imaging coral reef resilience at regional scale. A case-study from Saudi Arabia. *Mar. Pollut. Bull.* 64, 1222–1237.
- Selig, E.R., Casey, K.S., Bruno, J.F., 2012. Temperature-driven coral decline: the role of marine protected areas. *Glob. Change Biol.* 18, 1561–1570.
- Tulloch, V.J., Possingham, H.P., Jupiter, S.D., Roelfsema, C., Tulloch, A.I., Klein, C.J., 2013. Incorporating uncertainty associated with habitat data in marine reserve design. *Biol. Conserv.* 162, 41–51.
- van Hooidonk, R., Maynard, J., Liu, Y., Lee, S.K., 2015. Downscaled projections of Caribbean coral bleaching that can inform conservation planning. *Glob. Change Biol.* 21, 3389–3401.
- Venter, O., Fuller, R.A., Segan, D.B., Carwardine, J., Brooks, T., Butchart, S.H., Di Marco, M., Iwamura, T., Joseph, L., O'Grady, D., 2014. Targeting global protected area expansion for imperiled biodiversity, 12. <http://dx.doi.org/10.1371/journal.pbio.1001891>.
- Vila-Nova, D.A., Ferreira, C.E.L., Barbosa, F.G., Floeter, S.R., 2014. Reef fish hotspots as surrogates for marine conservation in the Brazilian coast. *Ocean Coast. Manag.* 102, 88–93.
- Watson, J.E., Dudley, N., Segan, D.B., Hockings, M., 2014. The performance and potential of protected areas. *Nature* 515, 67–73.
- Watts, M.E., Ball, I.R., Stewart, R.S., Klein, C.J., Wilson, K., Steinback, C., Lourival, R., Kircher, L., Possingham, H.P., 2009. Marxan with Zones: software for optimal conservation based land- and sea-use zoning. *Environ. Model. Softw.* 24, 1513–1521.
- Weeks, R., Russ, G.R., Bucol, A.A., Alcalá, A.C., 2010. Incorporating local tenure in the systematic design of marine protected area networks. *Conserv. Lett.* 3, 445–453.