

ECOLOGY

Participation, not penalties: Community involvement and equitable governance contribute to more effective multiuse protected areas

Robert Y. Fidler^{1*}, Gabby N. Ahmadi², Amkieltiela^{3,4,5}, Awaludinnoer⁶, Courtney Cox⁷, Estradivari^{3,8,9}, Louise Glew¹⁰, Christian Handayani³, Shauna L. Mahajan¹⁰, Michael B. Mascia¹¹, Fitryanti Pakiding¹², Dominic A. Andradi-Brown², Stuart J. Campbell¹³, Kelly Claborn^{10,14}, Matheus De Nardo¹⁰, Helen E. Fox¹⁵, David Gill¹⁶, Nur I. Hidayat¹⁷, Raymond Jakub¹³, Duong T. Le^{16,18}, Purwanto^{12,19}, Abel Valdivia⁷, Alastair R. Harborne¹

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Accelerating ecosystem degradation has spurred proposals to vastly expand the extent of protected areas (PAs), potentially affecting the livelihoods and well-being of indigenous peoples and local communities (IPLCs) worldwide. The benefits of multiuse PAs that elevate the role of IPLCs in management have long been recognized. However, quantitative examinations of how resource governance and the distribution of management rights affect conservation outcomes are vital for long-term sustainability. Here, we use a long-term, quasi-experimental monitoring dataset from four Indonesian marine PAs that demonstrates that multiuse PAs can increase fish biomass, but incorporating multiple governance principles into management regimes and enforcing rules equitably are critical to achieve ecological benefits. Furthermore, we show that PAs predicated primarily on enforcing penalties can be less effective than those where IPLCs have the capacity to engage in management. Our results suggest that well-governed multiuse PAs can achieve conservation objectives without undermining the rights of IPLCs.

INTRODUCTION

Sustaining human well-being without exacerbating ecosystem degradation is a critical challenge in the Anthropocene (1), requiring conservation initiatives that empower diverse actors to effectively manage natural resources, including governments, local stakeholders, and conservation organizations. Global agreements, such as the Convention on Biological Diversity (CBD), have a critical role in creating the policy imperatives for this empowerment to occur. As negotiations for the post-2020 CBD targets framework progress, there have been multiple calls for the substantive expansion of protected areas (PAs), including a growing movement to cover 50% of the Earth's surface with PAs (2, 3). To achieve this target without

causing considerable social impacts, a global PA network will need to incorporate a range of strategies, from PAs that prohibit all extractive activities to multiuse PAs that allow for nonindustrial resource extraction (3, 4). While nonextractive PAs are an effective means to achieve conservation targets in isolated systems (5), in populated areas, they often result in social conflict and economic stressors that disproportionately affect communities that are most reliant on natural resources (6–8). Of particular importance, therefore, is the development of multiuse PAs that can preserve biodiversity and ecosystem services without undermining the autonomy and livelihoods of the indigenous peoples and local communities (IPLCs) that manage nearly 25% (38 million km²) of the world's lands and 37% of remaining intact natural areas (9).

Previous research has indicated that in multiuse PAs, governance—the formal and informal institutions through which authority and power are conceived and exercised (10)—interacts with local context to shape social-ecological dynamics and conservation outcomes (11–14). A multitude of frameworks and recommendations for effective resource governance exist [e.g., (15–17)], with many drawing extensively from common-pool resource governance theory developed by Ostrom and colleagues (11), which prescribes eight principles for sustainable governance (Table 1). Studies across regions and biomes have highlighted the effectiveness of applying Ostrom's governance principles for achieving sustainable outcomes (13), particularly inclusive collective choice arrangements (18). These investigations have contributed to a rich body of literature and yielded invaluable insights into the attributes of effective resource governance but are frequently restricted to individual case studies (19), often do not include quantitative measures of governance (20) or ecological trends (21), or do not have the study design required for causal inference (22). These limitations have prompted calls for quantitative approaches that more clearly discern causality and allow for integration of findings across studies (23).

¹Institute of Environment and Department of Biological Sciences, Florida International University, 3000 NE 151st St., North Miami, FL 33181, USA. ²Ocean Conservation, World Wildlife Fund US, 1250 24th St NW, Washington, DC 20037, USA. ³World Wildlife Fund Indonesia, Gedung Graha Simatupang Tower 2C Lantai 7, Jl. Letjen TB Simatupang kav.38, South Jakarta, Indonesia. ⁴Department of Earth and Environmental Science, Katholieke Universiteit Leuven, Celestijnenlaan 200E, Leuven, Belgium. ⁵Yayasan PADMI Mandiri, Graha Mampang Lantai 3 Suite 305, Jl. Mampang Prapatan Raya Kav 100, South Jakarta, Indonesia. ⁶The Nature Conservancy Indonesia, Graha Iskandarsyah 3rd Floor Jl. Iskandarsyah Raya No. 66C Kebayoran Baru, Jakarta, Indonesia. ⁷Rare US, 1030 N Courthouse Rd., Suite 110, Arlington, VA 22201, USA. ⁸Leibniz Center for Tropical Marine Research (ZMT), Fahrenheitstraße 6, 28359 Bremen, Germany. ⁹Marine Ecology Department, Faculty of Biology and Chemistry (FB2), University of Bremen, Bibliothekstraße 1, 28359 Bremen, Germany. ¹⁰Global Science, World Wildlife Fund US, 1250 24th St. NW, Washington, DC 20037, USA. ¹¹Conservation International, 2011 Crystal Dr., Suite 600, Arlington, VA 22202, USA. ¹²University of Papua, Jl. Gunung Salju, Amban, Manokwari 98314, West Papua, Indonesia. ¹³Rare Indonesia, Jl. Gunung Gede I No. 6, Bogor 16153, West Java, Indonesia. ¹⁴School of Human Evolution and Social Change, Arizona State University, 900 S. Cady Mall, Tempe, AZ 94612, USA. ¹⁵Coral Reef Alliance, 1330 Broadway, Suite 600, Oakland, CA 94612, USA. ¹⁶Duke University Marine Laboratory, 135 Duke Marine Lab Rd., Beaufort, NC 28516, USA. ¹⁷Conservation International Indonesia, Jl. Pejaten Barat No. 16 A, Kemang, Jakarta, Indonesia. ¹⁸The World Bank, 1818 H Street, Washington, DC 20433, USA. ¹⁹Coral Triangle Center, Jl. Betngandang II No. 88-89, Sanur 80228, Bali, Indonesia.

*Corresponding author. Email: rfidleri@fiu.edu

Table 1. Ostrom's design principles for common-pool resource governance. "O" numbers will be used in the main text to reference indicators that align with each design principle.

	Design principle	Brief definition
O1	Clearly defined boundaries	Boundaries are clearly defined both for the resource itself and who is permitted to use the resource.
O2	Congruence between appropriation and provision rules and local conditions	Harvest rules are tailored to local conditions, and benefits and costs to resource users are proportional.
O3	Collective choice arrangements	Resource users can participate in modifying rules that affect them.
O4	Monitoring	Monitoring and enforcement are accountable to both resources and users.
O5	Graduated sanctions	Graduated sanctions are enforced on rule breakers, with punishments being proportional to the severity of offenses.
O6	Conflict resolution mechanisms	Low-cost conflict resolution mechanisms are readily available.
O7	Minimal recognition of rights to organize	Management rights of resource users are not challenged by external authorities.
O8	Nested enterprises	Governance is organized into multiple and reinforcing nested enterprises.

Here, we use a long-term, quasi-experimental monitoring dataset to quantitatively examine the relationships between social context, resource governance, and the ability of IPLCs to exercise resource management rights on biomass changes of coral reef fishes in multiuse marine PAs (MPAs). We do so using methodologies that allow for causal inference of the effects of MPA establishment on fish biomass changes (24–26) by limiting environmental sources of variation in the relationships between MPA governance and ecological outcomes. Our dataset encompassed four multiuse MPAs with varying governance regimes, sizes, and compositions of no-take and regulated fishing zones (Fig. 1 and Table 2). Although these MPAs are controlled by national or provincial governments, various site-specific agreements have incorporated customary management into zoning and governance arrangements, allowing us to assess the importance of site-level “comanagement” through indicators of community-level marine property rights. Study sites were located in the Bird’s Head Seascape of eastern Indonesia, a region containing the world’s greatest diversity of corals and reef fishes (27), heavy reliance on marine fisheries (28), and a long history of stewardship by IPLCs under customary management (29–31).

We calculated temporal changes in fish biomass (kilograms per hectare) at 59 treatment and 28 control (non-MPA) sites from

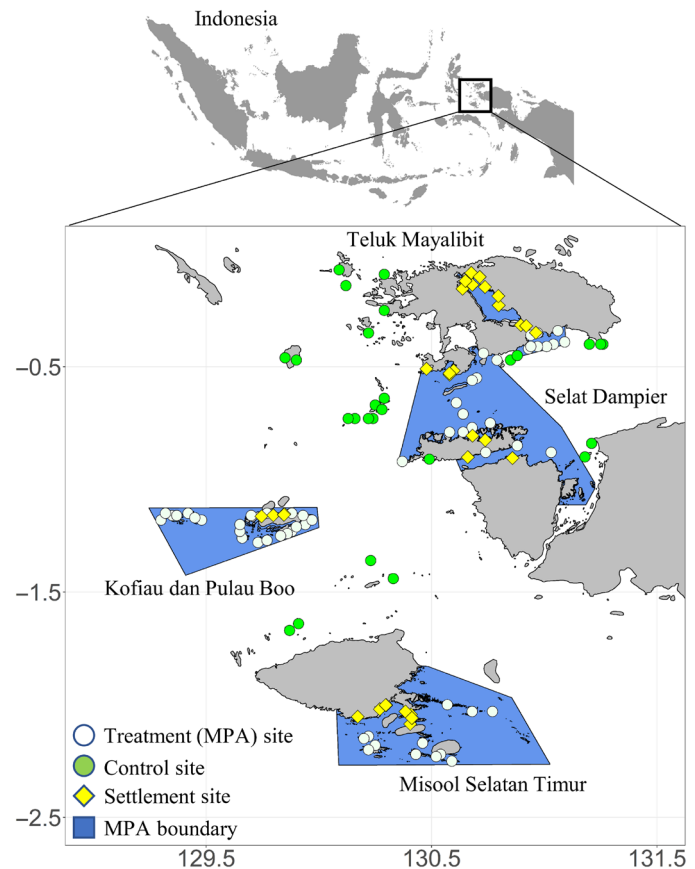


Fig. 1. Location of ecological sites and settlements across the Bird's Head Seascape. Ecological treatment sites ($n = 59$) are represented by white circles, ecological control sites ($n = 28$) are represented by green circles, and settlement sites ($n = 32$) are represented by yellow diamonds. MPAs are bounded in blue.

two underwater visual surveys conducted at each site between 2010 and 2016 (mean replicate gap: 3.48 years). Biomass was aggregated across seven fish families, representing the majority of reef-associated fishable biomass in the region, and changes between surveys were converted to logged response ratios (lnRRs). Treatment sites consisted of 20 no-take zones and 39 multiple-use zones, and initial surveys were conducted within ± 2 years of MPA establishment. We then statistically matched each treatment site to two controls based on 11 ecological variables and site-level characteristics. Hereafter referred to as MPA_{Effect} , we calculated the relative impact of MPAs at each treatment site (compared to controls) on fish biomass change by taking the average difference in lnRR values between that site and both matched controls. Using household surveys, key informant interviews, and focus group discussions with community members in 32 settlements, we operationalized 25 social, governance, and property rights indicators at each settlement. We then assigned unique values of these indicators to each treatment site by weighting values from associated settlements by their distance to the treatment site and total number of fishers. Last, we used a conditional random forest to test the impact of these indicators on MPA_{Effect} and examine the relative importance of MPA characteristics, social context, property rights distributions, and governance principles to ecological outcomes.

Table 2. Number of settlements and ecological treatment sites analyzed at each MPA. Ecological treatment sites are further broken down by management status, with “NTZ” representing the number of surveyed ecological sites that had “no-take” regulations and “Use” representing the number of sites that are not fully no-take but use alternative regulations such as gear restrictions or temporal closures. The “Settlements” column represents the number of individual settlements included in social and governance surveys. Total MPA area and no-take area (NTZ area) are also presented.

MPA name	Ecological sites	NTZ	Use	Settlements	MPA area (ha)	NTZ area (ha)
Kofiau dan Pulau Boo	22	9	13	4	149,208	15,955
Misool Selatan Timur	13	5	8	9	346,189	81,394
Selat Dampier	14	4	10	8	353,531	53,615
Teluk Mayalibit	10	2	8	11	49,451	14,684
Sum	59	20	39	32	898,379	165,648

Table 3. Summary of observed changes in fish biomass and MPA_{Effect}. Changes in fish biomass between replicate surveys at no-take (NTZ) and multiple-use (Use) zones inside MPAs and control sites, as well as MPA_{Effect} (the difference in biomass changes between matched MPA and control sites) values for each MPA.

MPA	Zone type (n)	Biomass change		MPA _{Effect} (mean)	MPA _{Effect} (SD)
		Mean (kg ha ⁻¹)	SD (kg ha ⁻¹)		
Kofiau dan Pulau Boo	NTZ (9)	94.28	256.85	-0.28	0.60
	Use (13)	-28.53	97.52	-0.85	0.55
	Controls (9)	58.10	135.71	-	-
Misool Selatan Timur	NTZ (5)	-48.59	19.18	-0.78	0.34
	Use (8)	-19.00	101.37	-0.76	0.80
	Controls (4)	-30.80	20.69	-	-
Selat Dampier	NTZ (4)	612.51	379.60	1.25	0.21
	Use (10)	82.53	263.43	0.23	0.87
	Controls (13)	-0.10	256.40	-	-
Teluk Mayalibit	NTZ (2)	-144.32	202.77	-2.06	0.64
	Use (8)	-121.46	158.26	-0.82	0.30
	Controls (10)	154.10	315.50	-	-

RESULTS

Fish biomass changes and MPA_{Effect}

Changes in total fish biomass (aggregated across all seven families) within MPAs between survey periods ranged between -379.9 and 1162.4 kg ha⁻¹ and were slightly positive overall but highly variable across sites (means ± SD: 35.55 ± 254.20 kg ha⁻¹; Table 3). Control sites exhibited similarly high variability, with biomass changes between periods ranging from -534.5 to 984.5 kg ha⁻¹ (41.0 ± 205.0 kg ha⁻¹). Changes in no-take areas were not only generally more positive than in multiple-use zones but were also more variable (no-take: 138.35 ± 344.43 kg ha⁻¹; multiple-use: -17.16 ± 175.77 kg ha⁻¹). There was considerable variation in outcomes across MPAs, with much greater inter-MPA variation than intra-MPA variation (fig. S1). Selat Dampier performed the best in terms of percentage of sites that exhibited increased raw biomass [four no-take sites (100% of sites) and six multiple-use sites (75%)], followed by Kofiau dan

Pulau Boo [five no-take (56%) and four multiple-use (31%)], Misool Selatan Timur [zero no-take and two multiple-use (25%)], and Teluk Mayalibit [zero no-take and two multiple-use (25%)].

MPA impacts were highly variable, with positive impacts distributed almost equally between no-take and multiple-use zones. Although the mean MPA_{Effect} (the difference in biomass changes between matched MPA and control sites) across all sites was slightly negative, many sites within multiuse MPAs demonstrated positive impacts on fish biomass. MPA_{Effect} ranged from -2.5 to 1.9 (means ± SD: -0.46 ± 0.89). No-take zones (-0.27 ± 1.05) performed better than multiple-use zones (-0.55 ± 0.79) when averaged across all MPAs; however, this trend was not true within Misool Selatan Timur and Teluk Mayalibit (Table 3). Selat Dampier again had the greatest percentage of positive impacts across sites [four no-take sites (100% of sites) and seven multiple-use sites (88%)], followed by Kofiau dan Pulau Boo [two no-take (22%) and one multiple-use (8%)], Misool Selatan Timur [zero no-take and one multiple-use (13%)], and Teluk Mayalibit (zero no-take and zero multiple-use). Similarly to raw biomass changes, variation between sites was much greater between MPAs than within individual MPAs (fig. S2).

Model inputs and variable importance measures

We used a conditional random forest model to examine the relative explanatory power of 4 site-level characteristics, as well as 14 governance, 9 social, and 2 property rights indicators on MPA_{Effect}. Although we collected data on all eight of Ostrom’s governance principles, there was insufficient data (e.g., a high frequency of “not applicable” or “I don’t know” responses) for indicators relating to principles O6 (the availability of low-cost conflict resolution mechanisms) and O8 (the organization of governance into multiple nested enterprises). To cross-validate variable importance, we used two importance calculations: conditional permutation importance and drop-column importance (for a full explanation of each measurement, see the “Statistical analysis” section).

Impacts of governance, management rights, and social factors on MPA_{Effect}

Variable importance between permutation and drop-column analyses was in general agreement, suggesting strong and consistent relationships between the indicators identified as important by both measurements and MPA_{Effect}. Governance indicators were consistently among the variables with the strongest associations with observed outcomes, comprising three of the top five most important

indicators in both analyses (Figs. 2 and 3). The governance indicators strongly associated with increased fish biomass across both variable importance measurements included the presence of user-specific rules (O2), user participation in decision-making regarding MPA establishment and management (O3), penalties that are congruent with the nature of offenses (O5), the presence of graduated sanctions for repeated offenses (O5), and support from the national government for local autonomy over resource management (O7). The only highly important governance indicator that was related to negative outcomes was increased frequency of penalty enforcement (O4).

Substantial increases in fish biomass were also observed when a large proportion of community members exercised “management rights” defined as the three collective choice rights described by Schlager and Ostrom (12): rights to (i) manage by regulating internal use patterns and transforming the resource by making improvements, (ii) exclude by determining who will have access to marine resources and how those rights may be transferred, and (iii) alienate by selling or leasing either management or exclusion rights. These rights served as our primary indicator of comanagement, as they represented the level to which local resource users had autonomy over resource management.

Increased participation in nonmarine community organizations (local group membership) had the strongest association with positive outcomes in permutation tests but decreased overall model accuracy in drop-column analyses. This metric was correlated with several other important variables (fig. S3), specifically management rights (Spearman’s ρ : 0.91), decision-making participation (0.74), penalty frequency (-0.70), graduated sanctions (0.62), and the presence of sanctions that were equitable to the nature of offenses (0.57). However, the latter indicators were confirmed to be highly important across both calculations, which provides stronger support for their influence on MPA_{Effect}. It is therefore possible that the high permutation importance value for local group membership is primarily a consequence of correlations with metrics that are more likely to directly affect ecological outcomes. Thus, while local group membership may play a role in observed outcomes, the relationship may be indirect and should be interpreted with caution.

Indicators related to reliance on marine resources generally resulted in more negative outcomes, although these metrics were less important than governance and property rights indicators across both importance calculations. An increased percentage of respondents identifying fishing as their primary occupation [primary fishers (%)], as well as higher rates of reliance on fish for income and as a

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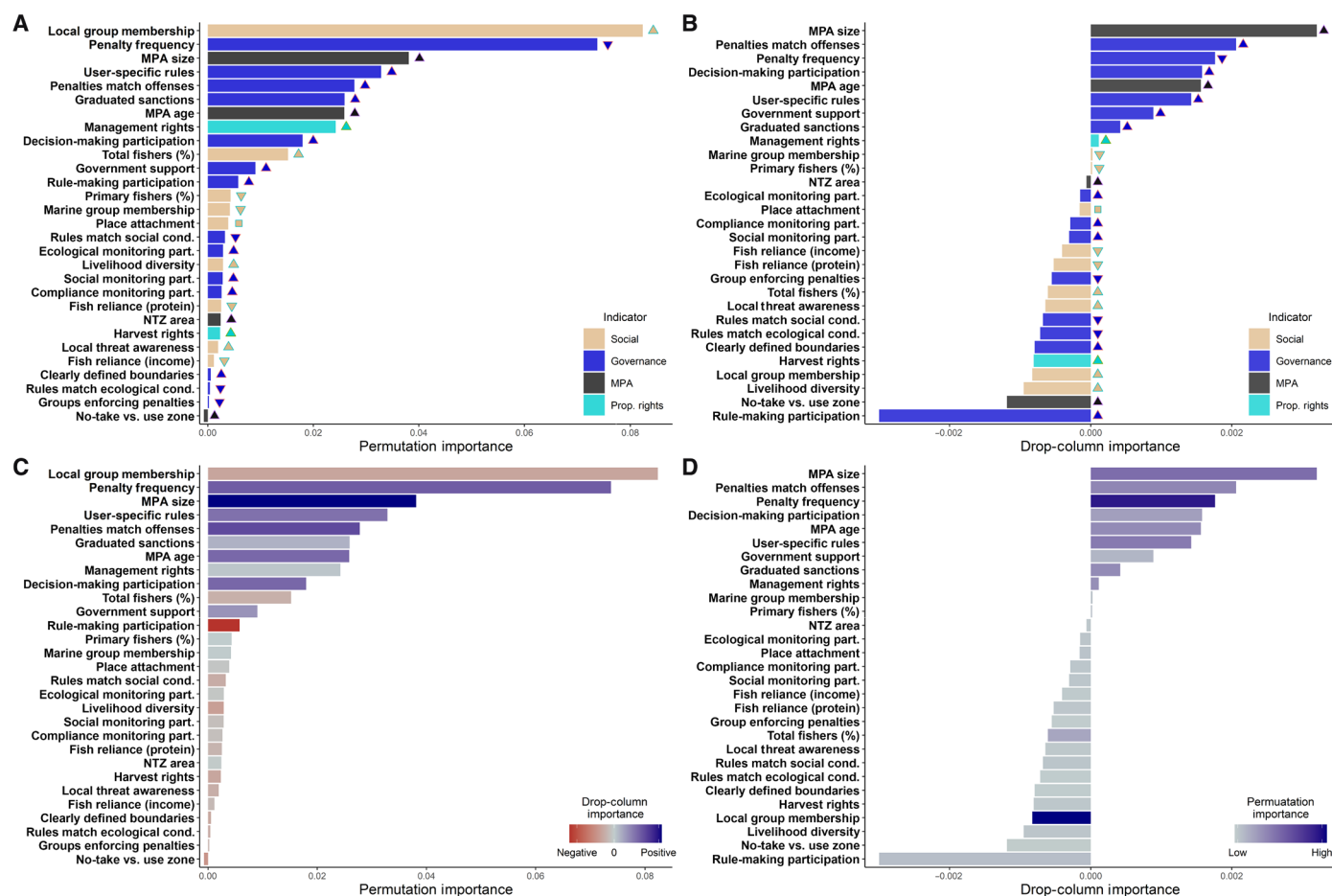


Fig. 2. Relative importance of social, governance, and MPA indicators. Variable importance by permutation importance (A and C) and drop-column importance (B and D). The colors of bars in (A) and (B) represent the category of each indicator, while the directionality of impacts of indicators on MPA_{Effect} is represented by shapes to the right of each bar (positive: upward triangle; negative: downward triangle; variable: square). Color ramps in (C) and (D) represent the relative importance of each metric by drop-column importance and permutation importance, respectively.

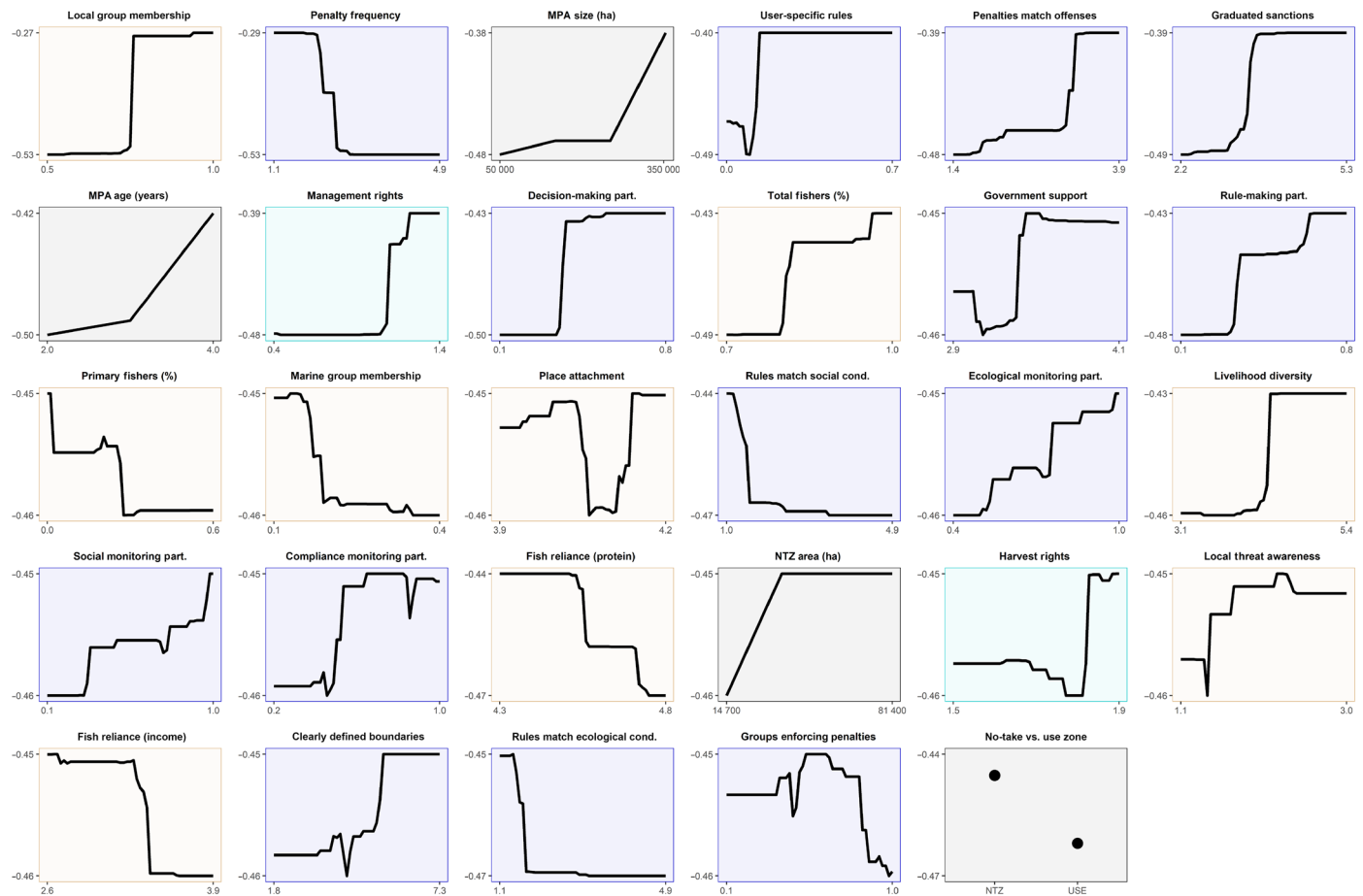


Fig. 3. Directionality of indicator impacts on MPA_{Effect} . Partial dependence plots of all indicators demonstrating their directional impacts on MPA performance in order of permutation importance. Y axes of partial dependence plots indicate the expected change in MPA_{Effect} given a particular value of a predictor marginalized over values of all other predictors rather than the predicted MPA_{Effect} for that predictor value. Plot colors indicate the category of each indicator: governance (blue), social (yellow), tenure (light blue), and MPA characteristics (gray).

primary source of protein, reduced MPA_{Effect} across sites. In addition, higher proportions of respondents indicating that they were members of marine-centric local organizations were also associated with more negative ecological outcomes. Conversely, increases in the proportion of respondents indicating that fishing was among their top three income sources [total fishers (%)] were associated with improved outcomes, as was increased rates of exercising “harvest rights” (rights to access MPAs and harvest resources from them, potentially translating into higher fishing pressure).

Both MPA size (hectares) and age (years after formalization of MPA zonation at the time of repeat surveys) were among the most important indicators that exhibited positive effects on MPA_{Effect} across both importance calculations. However, increased total no-take area (hectares) and stronger fishing regulations at individual sites (i.e., no-take compared to multiple-use zones) did not have strong predictive power in the random forest model, despite no-take zones performing better on average in terms of both site-level biomass change and MPA_{Effect} . Both metrics were associated with more positive outcomes, but their overall impacts on fish biomass changes were among the weakest of all predictors, as trends in MPA_{Effect} within each type of zone tended to change in similar ways along gradients of governance characteristics (figs. S4 and S5).

DISCUSSION

Governance characteristics were strongly associated with patterns of ecological outcomes across MPAs in the Bird’s Head Seascape. The governance indicators related to positive outcomes for fish biomass primarily involved establishing and enforcing equitable rules, both in terms of tailoring marine management to local conditions [user-specific rules (O2)] and responding to variable levels of non-compliance with proportionate penalties [graduated sanctions and penalties that match offenses (O5)], highlighting the roles of social-ecological fit and adaptive management in effective resource governance (11, 15). The benefits of rule congruency to local conditions (O2) and the use of sanctions that both match the nature of offenses and gradually increase with repeated noncompliance (O5) are consistent with previous investigations indicating that these principles are critically important across systems and geographies (13, 32, 33). The remaining important governance indicators included the percentage of respondents indicating participation in decision-making (O3) regarding MPA establishment, setting MPA boundaries, or administration of MPAs, as well as the degree to which the national government supported local user rights to manage resources (O7). Both of these indicators relate to the devolution of decision-making authority to local resource users, which

can improve the efficacy of marine conservation initiatives through a variety of mechanisms—for example, through the integration of traditional knowledge, increased trust and equity between local users and governmental authorities, and the development of management regimes that are perceived as more legitimate and accountable to communities (34).

Across both importance measures, penalty frequency—how often penalties were enforced on rule breakers (O4)—was consistently one of the top three most predictive indicators for model outcomes. Contrary to expectations, however, increased penalty frequency was associated with declines in MPA_{Effect} . Common-pool resource theory would predict that increased penalty frequency is indicative of strong accountable monitoring structures and therefore improved governance. However, at our study sites, increased penalty frequency is more likely representative of (or a response to) similarly high levels of conflict and noncompliance, which can significantly reduce the efficacy of conservation initiatives (35). There are numerous drivers of noncompliance with marine resource management regulations, but note that increased penalty frequency was negatively correlated with both management rights and decision-making participation (fig. S3). It is therefore possible that communities with little or no ability to participate in the design of governance structures and management were more prone to noncompliance due to a lack of legitimacy of local rules (36).

In the Bird's Head Seascape, in particular, greater efficacy when communities actively manage resources themselves is likely a consequence of customary governance structures nested within formalized MPA management regimes. This effect is highlighted by the positive impact of marine management rights, which represent the most direct pathway by which local users actively participate in resource governance (37). At our study sites, the comanagement of MPAs is primarily “consultative” or “instrumental” (38, 39), wherein authorities may consult with local user groups during and after MPA implementation, but management authority ultimately lies solely with the government. Nevertheless, traditional fishing and other activities are permitted within MPA zoning regulations, and customary (*adat*) laws have been recognized by some national-level fisheries legislation (31, 40). Hence, community-level management rights may provide an indicator of local-scale decision-making despite a lack of formal management authority. Increased exercise of management rights promoted increases in fish biomass regardless of the underlying social-ecological context, providing strong quantitative support for previous investigations in Indonesia and elsewhere, which have suggested that incorporating customary management rights into conservation initiatives can significantly improve social-ecological outcomes (32, 41, 42). However, note that the presence of long-standing customary management in the region likely enhanced the ecological benefits of management rights at our study sites and that conservation initiatives need to carefully consider underlying social contexts to determine how to most effectively integrate traditional management into larger initiatives (42).

Local group membership was the most important indicator identified by permutation importance but reduced the overall predictive accuracy of the drop-column model, suggesting impacts that may be indirect and potentially weaker than indicated by permutation analysis. This indicator specifically refers to involvement in nonmarine organizations and is thus more representative of general civic engagement than direct involvement in marine resource management. Given the high correlation between local group membership

and other important participatory governance indicators (e.g., management rights and decision-making participation; fig. S3), it is possible that local organizations provide a mechanism for individuals to become more formally involved in management through increased connections within the community (43). In addition, an increase in the percentage of community members participating in general civic and political engagement may also foster higher levels of trust and accountability, which is critical for collective action in common-pool resource systems (44), as well as providing experience in collective action and decision-making. Last, civic participation may promote greater equity, as community engagement may help prevent “elite capture” of resource benefits under certain conditions (45).

In general, indicators relating to social context tended to exhibit little to no impact on MPA_{Effect} , especially in comparison to governance indicators and MPA characteristics. Only two social indicators were confirmed to be important drivers across both variable importance calculations, and both were associated with negative outcomes: the percentage of individuals reporting fishing as their primary occupation and the percentage of individuals identifying as belonging to a local marine-centric organization. In the case of primary fishers, conventional theory would suggest that the absence of alternative sources of income increases strain on fish populations, as communities have more fishers overall and are more prone to noncompliance to rules (46). Negative impacts from marine group involvement are more puzzling, as they would seem to contrast with other indicators that suggest that community involvement in marine resource management improves ecological outcomes. However, it is possible that marine-oriented groups are more prevalent where ecological degradation is more pronounced, thereby leading to the perceived need to organize (47). The minimal importance of these two metrics—along with the even smaller impact of the remaining social indicators—suggests that while social context will likely play a role in MPA performance, governance that is tailored to these contexts can mitigate social-ecological conditions that may otherwise produce negative outcomes.

A large body of literature has demonstrated the importance of MPA attributes for efficacy, including the size, age, and fishing restrictions of spatial management regimes (5, 48, 49). Our results not only reinforce many of these findings but also reveal that governance has impacts similar in magnitude on the success of conservation initiatives. This effect is most clearly demonstrated by impacts in the well-governed Selat Dampier, which exhibited the most consistently positive trends in fish biomass changes and MPA_{Effect} and did so across both multiple-use and no-take zones. The greatest disparities in outcomes were between Selat Dampier and the neighboring Teluk Mayalibit, which was the only MPA with no positive MPA_{Effect} values at any site. Although Selat Dampier contains more than three times the no-take area of Teluk Mayalibit, total no-take area and whether sites were designated as no-take or multiple-use zones did not strongly influence observed outcomes in our model. Selat Dampier also exhibited better outcomes than Kofiau dan Pulau Boo, despite both MPAs being the same age during secondary surveys. Last, while Selat Dampier was the largest of the four MPAs, it was only slightly larger than Misool Selatan Timur, which did not perform nearly as well despite having considerably more no-take area. This is consistent with previous studies that have demonstrated that no-take management does not always confer additional benefits to fish biomass in the region, potentially due to limited enforcement capabilities in large MPAs, especially in remote areas (49). This result suggests that while some MPA design

attributes are likely to be critical to success, how areas are governed may be as or more important to outcomes than MPA size and the specific fishing regulations that are in place.

Sites in Selat Dampier tended to present the lowest penalty frequency, the most user-specific rules, the greatest use of graduated sanctions and penalties that matched the nature of offenses, and the highest levels of decision-making participation across all study sites (figs. S1 and S2). Furthermore, when sites in other MPAs had similar values for any individual governance indicator, ecological benefits were generally less than those observed in Selat Dampier. This likely represents the synergistic effects of numerous governance structures working in concert, many of which may covary with underlying attributes of management regimes (e.g., collective choice arrangements). Thus, the positive impacts observed in Selat Dampier reinforce that the establishment of strong, sustainable governance is likely the result of complex interactions between multiple factors rather than the implementation of any single principle (33). This indicates that while achieving desired conservation outcomes is possible in large, multiuse MPAs, no individual factor is likely to drive success or failure and that establishing a variety of good governance structures is critically important for long-term efficacy.

Given the inherent difficulty in isolating causal effects in coupled social-ecological systems (50), our approach is not without limitations. We used multiple mechanisms to ensure the selection of appropriate counterfactuals for reef sites within MPAs and account for additional variation in biomass driven by matching covariates. However, we were unable to control for variation in relative fishing pressure across sites zoned for multiple use, impacts of reef tourism, or shifts in human behavior after MPA establishment (e.g., fishing displacement, livelihood shifts, or changes in market pressures) that may have affected fish biomass trends. In addition, while social and governance survey protocols attempted to encompass a full spectrum of perspectives and conditions within diverse communities, we did not explicitly examine how heterogeneity within communities, including differences in gender (51), socioeconomic status (52), or political influence (53), affected individual participation in resource management and subsequently ecological outcomes. Although community demographics are likely to influence governance structures, zoning plans for MPAs in the region were developed using socioeconomic criteria and in collaboration with local communities to maximize equity, management rights, and access to resources among multiple user groups (54), which may have mitigated these effects. Last, care must be taken when extrapolating our results to other contexts, as institutional frameworks and sociocultural norms may cause formal management regimes and preexisting customary management practices to interact in ways that produce significantly different outcomes than those seen here. Future investigations that use similar quantitative methods in varying geographies and biomes will be critical to develop best-practice recommendations that are effective across multiple contexts.

Despite these limitations, our results suggest that multiuse MPAs with strong local involvement may represent an inclusive and just approach to achieving joint biological conservation and development goals in the Anthropocene (7). Here, we have provided quantitative evidence that it is possible for multiuse MPAs to increase fish biomass, but that the implementation of effective governance structures is critical for their success; MPAs that use a combination of good governance principles within management regimes are more likely to achieve their stated goals; incorporating customary management,

procedural equity and recognition, and management that is tailored to specific user groups into the design of formalized conservation initiatives can improve ecological outcomes; and conservation initiatives predicated on enforcing penalties on rule breakers can be less effective than those in which resource users have the capacity to engage in local resource management. In addition, strong benefits of local engagement in management add to growing evidence that IPLC-managed areas are better maintained than those where resource users are excluded from governance structures (55).

Where appropriate, therefore, present and future conservation efforts need to reinforce—not undermine—the ability of IPLCs to sustainably manage resources (56). This can be achieved through developing and strengthening inclusive and participatory governance systems, more purposefully integrating customary or *de jure* and/or *de facto* management into conservation initiatives, and supporting strong and secure local tenure rights (57, 58). The processes by which this goal can be accomplished will vary across regions, systems, and social-ecological contexts. Successful implementation of comanagement will require inclusive participatory processes that prevent governance arrangements from leveraging existing power dynamics to further marginalize vulnerable groups (59) and ensure that management strategies match socioeconomic and cultural conditions (42). Long-term sustainability will also require adaptive and evidence-informed conservation decision-making, necessitating an expansion of monitoring and research programs aimed at complementing qualitative investigations with quantitative links between resource governance and outcomes in social-ecological systems.

MATERIALS AND METHODS

Ecological survey data

We calculated benthic characteristics and fish biomass from survey data collected from 84 sites within four MPAs and 41 control sites in the Bird's Head Seascape across two replicate survey periods (Fig. 1) between 2010 and 2016 using standardized protocols (60). Treatment sites (those within MPAs) were included in the analysis only if initial ecological surveys were available within 1 year of social and governance survey periods at associated settlement sites and were within ± 2 years of MPA establishment (here, the year in which zonation of fishing regulations went into effect). Benthic data were collected along three replicate 50-m point intercept transects at each site, with substrates categorized at 0.5-m intervals. Benthic data were aggregated into four categories: live hard coral, live soft coral, algae, and other substrates. Fish assemblages were quantified using underwater visual census (UVC). Two divers conducted UVCs on five replicate transects, with one diver recording all individuals < 35 cm in 5 m-by-50 m transects and the other recording all individuals ≥ 35 cm on 20 m-by-50 m transects. Fish biomass represents the combined biomass of recorded individuals from seven reef fish families (table S1), which were selected on the basis of (i) high economic and/or ecological importance, (ii) families that are known to contain primarily reef-resident species, and (iii) those that were surveyed at all ecological sites. We therefore restricted data to fishes from the families Acanthuridae (surgeonfish), Haemulidae (grunts), Lethrinidae (emperors), Lutjanidae (snappers), subfamily Scarinae (parrotfish), Serranidae (groupers), and Siganidae (rabbitfish). While there was variation in the magnitude of raw biomass changes between families across MPAs and zone types (fig. S6), these disparities were effectively normalized across families (fig. S7) through statistical

matching protocols (described below). Consequently, as these families represent the majority of reef-resident fishes that are targeted by local fishermen and therefore serve as suitable indicators of total “fishable biomass” in the region, we model all families together in statistical analyses. To account for differences in transect sizes, we standardized all fish data to individuals per hectare before analysis. We converted the length estimate of each individual fish to body mass (kilograms) using allometric length-weight constants from FishBase (<http://fishbase.org>) (61) and aggregated fish assemblage data to the site level by averaging across transects.

Determining causal effects of MPAs on fish biomass

Assessing the impact of MPAs on fish biomass requires isolating MPA protection from other confounding factors. We determined MPA causal effects by comparing lnRRs (the natural logarithm of the ratio of biomass at repeated and baseline surveys) of fish biomass in sites within MPAs to those of controls (sites outside of MPAs) through statistical matching (described below). By matching sites on a suite of confounding factors that may affect MPA placement or drive changes in fish biomass independent of MPA implementation, we can establish control sites as functional counterfactuals to MPA sites. By minimizing the effects of confounding factors on fish biomass changes, we can effectively treat control and treatment sites as belonging to the same population (62). We can then attribute most of the remaining observed variation in fish biomass changes between sites to MPA protection, allowing us to examine associations between ecological outcomes and the social, governance, and management conditions within each MPA.

Selection of environmental matching covariates

To identify the environmental factors that most strongly influenced changes in fish biomass during our study period, we used a regression tree random forest with the Boruta extension to test the relative importance of a suite of 22 environmental characteristics on observed outcomes (lnRR values of fish biomass change between replicate surveys) in all 41 potential control sites (table S2). Random forest models are decision tree-based algorithms, which produce multiple independent trees in parallel with random subsets of variables on each tree to test the importance of each predictor variable to changes in the response variable. Random forests were conducted using the randomForest function in package randomForest v4.6.14 (63) for R statistical software v3.6.0 (64).

Many procedures exist to conduct feature selection through random forest models, but the Boruta algorithm has recently been demonstrated to outperform other feature selection methods in terms of final predictive accuracy (65). Therefore, following the random forest, variable significance to MPA_{Effect} was tested with the Boruta algorithm using the Boruta function in the R package Boruta v6.0.0 (66). The Boruta algorithm assigns values of “confirmed,” “rejected,” or “tentative” to each variable by assessing whether the original variable serves as a better predictor of changes in the response than random permutations of itself. Random forest and Boruta models were conducted 999 times, with each iteration using a random subset of 16 (73%) of the possible 22 environmental covariates available. Covariates that were identified as either confirmed or tentative by the Boruta algorithm at least 15% of the time that they were included in model iterations were selected as final matching covariates. Data sources (67–70) for all potential matching covariates and results of covariate selection models can be found in table S2.

Ecological site matching and MPA_{Effect}

We performed genetic matching of treatment (MPA) and control sites based on covariates determined to be important to ecological outcomes in control sites and site-level characteristics necessary to ensure the selection of proper counterfactual sites using the GenMatch function of the R package Matching v4.9.6 (71). Because there were fewer control than treatment sites, we matched with replacement and conducted 2:1 control-to-treatment matching to (i) allow the matching algorithm to match each treatment site to the most appropriate controls and (ii) reduce the influence of any single control site on model outcomes. Genetic matching aims to give equal weight to all matching covariates; however, we also applied “calipers” restricting the allowable difference between five covariates—MPA location, initial fish biomass, reef slope, survey year 1, and survey gap—to ensure that initial conditions and survey periods were equivalent between treatment and control sites (table S2). Although calipers increased the similarity of initial conditions at matched sites, they reduced the number of possible matches, resulting in 25 treatment sites (29.7%) being dropped from the model, as appropriate control sites were not available. The number and protection status of final treatment sites across MPAs can be found in Table 2.

Match balance and bias adjustments

The suitability of control sites to serve as adequate counterfactuals to treatment sites was assessed both pre- and post-matching using tests of covariate balance. Covariate match balance describes the remaining difference in covariates between matched sites and was assessed for each covariate using standardized mean differences and for overall model balance using the xBalance function of the R package RItools v.0.1-17 (72, 73). Although covariate balance was improved compared to pre-matching (table S3), MPA and control sites retained significant overall covariate imbalance post-matching ($\chi^2 = 43.59$, $df = 11$, $P < 0.001$). To account for this imbalance and remove the remaining covariate-driven differences in changes in fish biomass between MPA and control sites, we implemented a post hoc bias adjustment (74). To establish the local relationship between biomass change and the covariates (in the absence of management), we built a random forest model based on the 28 control sites selected in the matching protocol, with lnRR values of fish biomass change at each site as the response variable, and the final matching covariates as predictors. We then used this model to predict lnRR values for both the 28 control and 59 treatment sites and used the predicted values to remove the differences between the observed \lnRR_{MPA} and $\lnRR_{Control}$ that was explained by the covariates. MPA_{Effect} values were then calculated as

$$MPA_{Effect} = (\lnRR_{MPA[Observed]} - \lnRR_{Control[Observed]}) - (\lnRR_{MPA[Predicted]} - \lnRR_{Control[Predicted]}) \quad (1)$$

with the mean of the two values calculated from each matched control site taken as the final MPA_{Effect} for that treatment site.

Settlement survey protocols and indicators

Governance, social, and property rights indicators were operationalized from data collected from household surveys ($n = 767$), key informant interviews ($n = 53$), and focus group discussions ($n = 32$) in settlements ($n = 32$) associated with MPAs between 2010 and 2014 using standardized instruments (28). Household surveys were

conducted with individuals from settlements associated with PAs on a randomized basis to ensure adequate representation of social and geographic subgroups within each settlement (28). Settlement sizes and associations with MPAs were defined by the most recent available census data and PA boundaries before sampling. Sample sizes for surveys at each settlement were determined by a power analysis to ensure that monitoring could detect substantive changes ($\pm 10\%$) from baseline values (28). Random selection was conducted by either stratified random or cluster sampling, dependent on population sizes, PA size, and logistical constraints. Household survey instruments contained a series of constrained choice and open-ended questions aimed at obtaining information regarding household well-being and activities. Household surveys were conducted with the head of the household, defined as the individual that provided the household's main source of income and was responsible for making decisions regarding the household.

Key informant interviews and focus group discussions were conducted with community members and government officials with roles in MPA management to obtain information on both the formal and informal rules that govern local resources. Key informant interviews and focus group discussions were designed to obtain information that could operationalize indicators from common-pool resource theory (11) and capture fine-scale variation in governance between settlements. Focus group discussions generally involved between 6 and 12 participants and aimed to represent the full range of stakeholder groups that used PAs (including nonfishers and people of all socioeconomic backgrounds). Participants were selected for focus group discussions based on having considerable knowledge about the status, use, and management of local marine resources. Focus group discussions were supplemented by key informant interviews, which were conducted with individuals that had specific, detailed knowledge of how local marine resources are used and managed. Key informants were identified through multiple, iterative sampling methods that included consultations with local officials, identifying “standout” participants from focus group discussions and obtaining referrals from other key informants. Where possible, indicators derived from social and governance survey instruments were converted to continuous scales by calculating means or percentages of respondents in each settlement reporting a given answer. Indicator calculations for all instruments, descriptive statistics for each indicator, and question framing for specific indicators can be found in tables S4 and S5.

Data imputation

Indicators were not always relevant to all respondents or settlements, resulting in occasional high proportions of responses of I don't know or not applicable to specific survey questions. When settlements did not have representative values for a given indicator, data were imputed when $<15\%$ of data points were missing across all settlements. Data imputation was conducted using the `missForest` function in the R package `missForest` v1.4 (75), which performs iterative imputations on each predictor containing missing values based on a random forest. Information regarding the identity and quantity of imputed values can be found in table S6.

Fishing gravity weighting

We used survey and interview data from multiple neighboring settlements to calculate unique values for governance, social, and property rights indicators for each reef site. To account for the likelihood that

settlements closer to ecological sites and those with greater numbers of fishers exerted greater influence on ecological outcomes, we calculated site-level indicators using a weighted average of values from each associated settlement site. Indicators were weighted by relative “fishing gravity,” a metric derived from previous investigations indicating higher anthropogenic impacts on reefs that are more accessible to humans and those with greater nearby human populations (76). Fishing gravity was calculated as the number of fishers in a settlement divided by the squared straight line distance between an ecological treatment site and that settlement. The number of fishers in a settlement was calculated by multiplying the population within a 5-km radius of the settlement by the percentage of respondents from that settlement self-identifying as fishers in household surveys. Fishing gravity was calculated three times, using the percentage of individuals that identified fishing as their (i) primary occupation; (ii) primary or secondary occupation; or (iii) primary, secondary, or tertiary occupation. The mean of these values was taken as the final metric of fishing gravity. This allowed settlements that were closer to an ecological site, more populous, and with a higher proportion of fishers to have a greater influence on the final indicator value. We derived population sizes at settlements from the Marine Socio-Environmental Covariates database of the National Socio-Environmental Synthesis Center (70).

Statistical analysis

We used a regression tree conditional random forest to test the relative importance of MPA characteristics and social, property rights, and governance indicators on MPA_{Effect} . Random forest models were ideal for our analysis, as they do not require many of the strict assumptions of parametric models and are able to account for higher-order interactions and nonlinear relationships between variables (66), which are inherent in complex social-ecological systems. We included all governance, social, and property rights indicators as predictors within the model, as well as site-level characteristics (e.g., MPA identity, size, no-take area, and zone type; table S4). Including these variables as predictors allowed us to determine the relative impact of all potentially important factors while also accounting for any interactions between them. Conditional random forest models were conducted using the `cforest` function in the R package `party` v1.3-7 (77–79). To ensure stability in model outcomes, we produced 10,000 trees in each forest. We selected “mtry”—the number of input variables randomly sampled as candidates at each tree node—by examining models with mtry values ranging from 2 to 28 using three different “seed” values to account for the influence of random number generation. An mtry of six produced the lowest root mean square error (RMSE) and was therefore used for the overall model, although values of five and seven performed similarly well.

Predictors with high variance inflation factors (VIFs)—those with high levels of multicollinearity with other predictors—have been demonstrated to have inflated relative importance values in random forest models (78–80). We calculated the VIFs of all predictors before analysis by placing them into a linear model and assessing VIFs using the `vif` function in the R package `car` v3.0.3 (81) and found high levels of multicollinearity (fig. S3). To ensure that the importance of correlated variables was not artificially high, we used two separate measures of variable importance that can account for multicollinearity: conditional permutation importance and drop-column importance. Both methods calculate variable importance by determining the amount of predictive information in each variable that is already

contained within other correlated variables but do so in slightly different ways.

Permutation importance tests the importance of a variable to model prediction performance by randomly permuting a predictor within the random forest model and recalculating the model's predictive performance. The importance of that variable is then calculated as the change in the predictive accuracy between models with the original variable and the permuted copy of that variable. Permutation importance was calculated using the `varimp` function in the R package `party` v1.3-7, using a conditional importance calculation (69). Drop-column importance is a more direct calculation of the importance of each variable on predicted outcomes and can be used to "ground-truth" permutation importance. However, drop-column importance is not often used in decision tree-based algorithms because it requires iteratively retraining the random forest, which can be computationally expensive. Drop-column importance tests variable importance by completely removing a variable from the model, retraining the random forest, and testing the predictive power of the drop-column model against the original model containing all predictors. Drop-column variable importance is then calculated as the decrease or increase in predictive accuracy when that variable is removed. Drop-column importance was calculated for each variable with the same three seed values as used previously and seven values of `mtry` (3 to 9) to account for differences in random number generation and tree building between model runs. The average change in predictive accuracy (in this case, RMSE) across all model runs was used to calculate the final drop-column importance of each variable. Last, the directionality of indicator impacts on MPA_{Effect} was visualized using partial dependence plots using the `partial` function in the R package `pdp` v0.7.0 (82).

SUPPLEMENTARY MATERIALS

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Robert Y. Fidler, Gabby N. Ahmadi, Amkieltiela, Awaludinnoer, Courtney Cox, Estradivari, Louise Glew, Christian Handayani, Shauna L. Mahajan, Michael B. Mascia, Fitriyanti Pakiding, Dominic A. Andradi-Brown, Stuart J. Campbell, Kelly Claborn, Matheus De Nardo, Helen E. Fox, David Gill, Nur I. Hidayat, Raymond Jakub, Duong T. Le, Purwanto, Abel Valdivia, and Alastair R. Harborne

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