

## LETTER

# Marine protected areas enhance coral reef functioning by promoting fish biodiversity

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## Abstract

Preserving biodiversity and ecosystem function in the Anthropocene is one of humanity's greatest challenges. Ecosystem-based management and area closures are considered an effective way to maintain ecological processes, especially in marine systems. Although there is strong evidence that such measures positively affect community structure, their impact on the rate of key ecological processes remains unclear. Here, we provide evidence that marine protected areas enhance herbivory rates on coral reefs via direct and indirect pathways. Using meta-analysis and a path-analytical framework, we demonstrate that, on average, protected areas increase the species richness of herbivorous fishes, which, in turn, enhances browsing rates on macroalgae. However, in all three regions studied (the Atlantic, Indian, and Pacific Ocean), a small subset of the herbivore assemblage accounted for the majority of browsing. Our results therefore indicate that ecosystem functioning on coral reefs may respond positively to both area closures and the protection of key species.

## KEYWORDS

biodiversity ecosystem functioning (BEF), browsing, coral reef conservation, ecosystem-based management (EBM), herbivory, macroalgae, marine reserve, phase shift, resilience

## 1 | INTRODUCTION

Fluxes of energy and nutrients, quantified as rates of consumption, production, and decomposition of biomass, are integral to all ecosystems. These rates are often termed “ecosystem functioning” and in turn, govern the goods and services that ecosystems provide (Isbell et al., 2017). Sustaining ecosystem functioning in the Anthropocene is therefore of fundamental human interest. To date, ecosystem-based management (EBM) approaches, such as protected areas, are the gold standard for humanity's stewardship of nature (Leslie & McLeod, 2007). Yet, implementing EBM and evaluating its performance remains challenging (Link & Browman, 2014), not least because reliable indicators of, and criteria

for, success are unclear or lack integration with management practices across systems (Bruno, Côté, & Toth, 2019; Link & Browman, 2014).

The past two decades have revealed biodiversity as a major driver of ecosystem functioning (the biodiversity–ecosystem functioning relationship [BEF]). Specifically, experimental manipulations of species richness across ecosystems have demonstrated that more diverse assemblages often produce, consume, and decompose biomass at higher rates than less diverse assemblages (O'Connor et al., 2017), which can increase the provision of ecosystem services to humanity. This has brought biodiversity conservation into focus within management and policy circles (Isbell et al., 2017). However, scaling up experimental results to the real world is difficult,

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as is the development of management approaches that protect biodiversity at large (Balvanera et al., 2014). Such challenges have led to a wide chasm between scientific evidence for biodiversity-mediated effects and implementation of management actions centered on this paradigm (Cavanagh et al., 2016; Dee, De Lara, Costello, & Gaines, 2017).

Although coral reefs are among Earth's best studied marine ecosystems, remarkably few studies have described the effect of their remarkable biodiversity on ecosystem functioning. Now, as temperature-induced coral bleaching and local stressors (e.g., overfishing) are pushing the world's reefs to a tipping point, calls for new management approaches that preserve coral reef functioning are mounting (Hughes et al., 2017). Rapid advances in understanding and addressing social drivers of reef decline show promise for mediating the response of reef assemblages to human impacts and conservation measures (Cinner et al., 2016). However, the degree to which local conservation increases reef resilience remains variable: while local management can benefit fish biomass (e.g., MacNeil et al., 2015), other variables such as adult coral cover seem to derive little benefit from current local conservation measures (Bruno et al., 2019). This equivocality may, in part, stem from a focus on static variables that are the end product of dynamic, multifaceted processes rather than rates of ecological processes. Although the latter are more labor intensive to monitor, detailed documentation of ecological processes may improve our understanding of the effects of management on coral reefs (Partelow, Schlüter, von Wehrden, Jänig, & Senff, 2018).

Herbivory on coral reefs is considered a key function because it often mediates coral–algal interactions in favor of reef-building corals (Bellwood, Hughes, Folke, & Nyström, 2004; Burkepile & Hay, 2010). Coral reef herbivory is, however, a multifaceted process, often divided into several subcategories such as grazing, cropping, sediment removal, or macroalgal browsing (Brandl & Bellwood, 2016; Nash et al., 2016). Throughout the paper, we use the term herbivory in the context of macroalgal browsing, unless otherwise specified. Because macroalgae can proliferate on reefs following disturbance (but see Bruno, Sweatman, Precht, Selig, & Schutte, 2009), the removal of macroalgae (i.e., browsing) is considered essential to reef recovery (Bellwood et al., 2004). Many studies have determined browsing rates using feeding assays in which strands of macroalgae are transplanted to coral reefs (reviewed in Puk, Ferse, & Wild, 2016). Such browsing assays offer a standardized, rate-based metric of a key process that can be used to examine links between herbivore assemblages, ecosystem functioning, and their response to conservation actions (Bonaldo, Pires, Guimarães, Hoey, & Hay, 2017; Gilby et al., 2017). However, to date, there has been no large-scale analysis of how herbivore browsing rates respond to management practices on coral reefs.

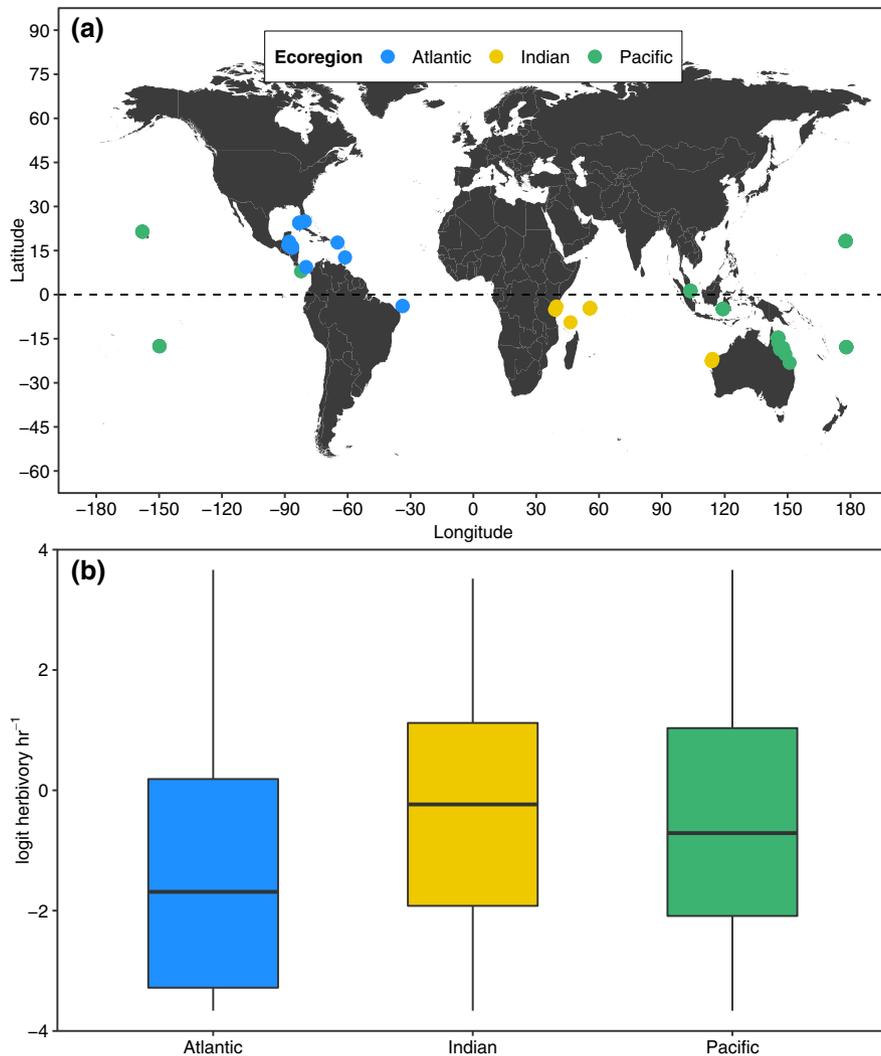
Here, we synthesize published experimental data on rates of macroalgal removal by herbivores on coral reefs worldwide and link them to hypothesized drivers in a causal, path-analytical framework. We hypothesize, as proposed by BEF theory and empirical evidence (Rasher, Hoey, & Hay, 2013), that (a) locations with higher local richness and biomass of browsing herbivores will exhibit higher browsing rates and (b) both of these attributes of herbivore community structure will respond positively to protection via marine reserves, ultimately enhancing algal removal rates where protection is in place.

## 2 | MATERIALS AND METHODS

### 2.1 | Data extraction

To explore drivers of macroalgal browsing by herbivores on tropical coral reefs, we gathered peer-reviewed articles using the *Web of Science* search engine. We defined our search terms a priori to mitigate bias (see Electronic Supplemental Material [ESM] for details). Our final search took place in May of 2017 and yielded 262 studies, 53 of which were included in our analyses.

For each study, we recorded location and experimental design details including whether assays were deployed in Marine Protected Areas (MPAs) or unprotected areas; for all papers that did not explicitly specify the management zone, we assumed that fishing was allowed. The exception was the Great Barrier Reef in Australia, where most research is performed in MPAs (e.g., Lizard and Orpheus Island) and recreational and commercial fishing pressure on herbivores is weak even where fishing is permitted. We determined the duration of each algal assay, and standardized reported browsing rates to the peak period of diurnal fish herbivory (6 hr, between 10:00 a.m. and 04:00 p.m.), resulting in the transformation of 24- and 48-hr deployments to 6 and 12 hr, respectively (Hoey & Bellwood, 2011). We then extracted browsing rates at the finest spatial and temporal resolution available from the text, tables, or graphs using the web-based software WebPlotDigitizer. For all experimental studies that tested for additional effects (e.g., nutrient input), we used values from “control” assays to obtain unbiased estimates of local herbivory. To permit comparison of browsing rates among studies, we included only results presented or derivable as percent loss of algae over time (percent per hour). For each study, we also calculated or extracted the regional and local richness of herbivorous fishes, as well as their local biomass (see ESM). Finally, to determine whether some fishes contributed disproportionately to the removal of macroalgae, we extracted ranked contributions of the top three species contributing to browsing, when reported (both qualitative and quantitative).



**FIGURE 1** Geographic spread of study locations and geographic variation in browsing rate. (a) Study locations from papers included in the meta-analysis and their respective defined ecoregion. (b) Boxplot of the logit transformed browsing rates for each ecoregion

## 2.2 | Statistical analysis

We used two nested datasets to assess the drivers of herbivory at different scales. First, we performed a large-scale, regional comparison of browsing rates that incorporated all estimates obtained from the literature ( $N = 740$ ). Second, we used a pruned dataset ( $N = 219$ ) that included only studies with local herbivore biomass and diversity estimates to test the importance of local drivers. For both models, we logit transformed browsing estimates (as percent consumed per hour) to achieve normality in the residual error distributions and homogeneity of variance. The regional-scale effects were tested by running two separate linear mixed effects models to predict browsing (due to collinearity), with Ocean basin and  $\gamma$ -diversity as respective predictors and study identity as a random effect. Conformance to model assumptions was confirmed visually.

To test for direct and indirect relationships in our data at the local scale (i.e., using the pruned dataset), we used a piecewise structural equation model (SEM) based on d-separation tests (Lefcheck, 2016). Ocean basin was excluded from this analysis, as representation beyond the Pacific was poor (Atlantic:  $n = 0$ ; Indian Ocean:  $n = 31$ ; Pacific:  $n = 188$ ) in the pruned dataset. We validated assumptions and performance for each component model visually (through plots of residuals and predicted vs. raw values) and assessed the adequacy of our specified global model using a series of d-separation tests (Lefcheck, 2016). We then extracted the range-transformed coefficients for each predictor in the Gaussian models (as normalization of coefficients cannot yet be implemented in generalized models). Finally, we extracted and plotted the partial effects of each predictor found to have a significant effect and determined model fits via pseudo  $R^2$  values. All statistical

**TABLE 1** Summary of model formulations and fits for component models of the structural equation model

Model	Class	Family	R <sup>2M</sup>	R <sup>2C</sup>
I. $\gamma$ -diversity ~ latitude + (1 study/site)	glmer	Poisson	0.03	0.84
II. $\alpha$ -diversity ~ $\gamma$ -diversity + MPA + (1 study/site)	glmer	Poisson	0.27	0.88
III. log(Biomass) ~ $\alpha$ -diversity + MPA + (1 study/site)	lmer	Gaussian	0.35	0.86
IV. logit(Herbivory) ~ $\alpha$ -diversity + biomass + $\gamma$ -diversity + latitude + algal type + MPA	lmer	Gaussian	0.45	0.80

analyses and data visualization were performed in R v3.4.1 (R Core Team, 2017).

### 3 | RESULTS

#### 3.1 | Regional and local drivers of herbivory

Despite broad representation of different ecoregions (Figure 1), neither ecoregion (marginal  $r^2 = 0.0153$ ) nor  $\gamma$ -diversity (marginal  $r^2 = 0.0418$ ) predicted standardized herbivore browsing rates. In contrast, the SEM for local drivers of browsing revealed several significant effects (Table 2) and provided a good fit to the data (Fisher's

$C = 2.034$ ;  $df = 12$ ;  $P = 0.999$ ). Regional ( $\gamma$ -) diversity (Model I) had poor predictive power in the pruned dataset but models II, III, and IV had excellent fits (Table 1), demonstrating that (a) both local herbivore richness ( $\alpha$ -diversity) and biomass were significantly enhanced by local protection, and (b) herbivore  $\alpha$ -diversity and protection status (but not herbivore biomass) significantly predicted browsing rate (Table 2, Figure 2). Moreover,  $\alpha$ -diversity was positively linked to herbivore biomass, latitude had a negative effect on herbivory rates, and brown algae showed higher rates of loss than other algal taxa.

#### 3.2 | Consumer species

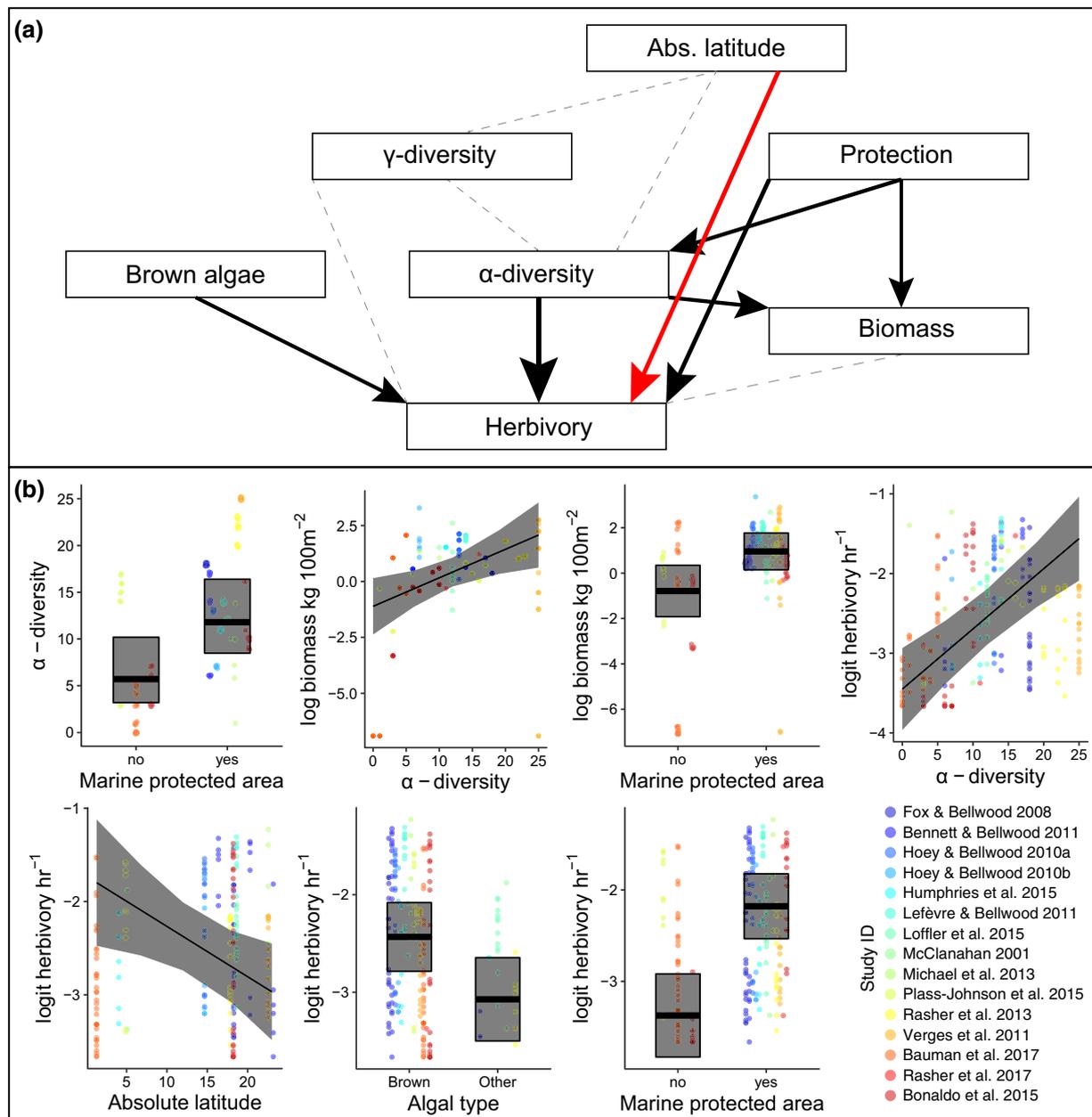
Of the six herbivorous fish species recorded for the Atlantic, the parrotfish *Sparisoma aurofrenatum* was the most important macroalgal browser, ranking first each time it was reported as a contributor (Figure 3a). The surgeonfish *Acanthurus chirurgus* also ranked highly but only when *Spar. aurofrenatum* was not present. *Acanthurus coeruleus* never ranked higher than second. In the Indian Ocean, no single species repeatedly dominated browsing (Figure 3b), with six species fluctuating as the top three consumers. In the Pacific, the chub *Kyphosus vaigiensis* and rabbitfish *Siganus doliatus* were important browsers (Figure 3c), but whenever present, the surgeonfish *Naso unicornis* was ranked first in contribution. Of the eleven herbivore species recorded in Pacific studies, four (*K. vaigiensis*, *Sig. doliatus*, *N. unicornis*, and *Sig. canaliculatus*) were mentioned in the top-three six or more times.

### 4 | DISCUSSION

Sustaining ecosystem functioning is one of the greatest challenges of our time (Isbell et al., 2017; Partelow et al.,

**TABLE 2** Component results of structural equation model. Bolded  $P$ -values denote significant results ( $P < 0.05$ ). Model fits are listed in Table 1

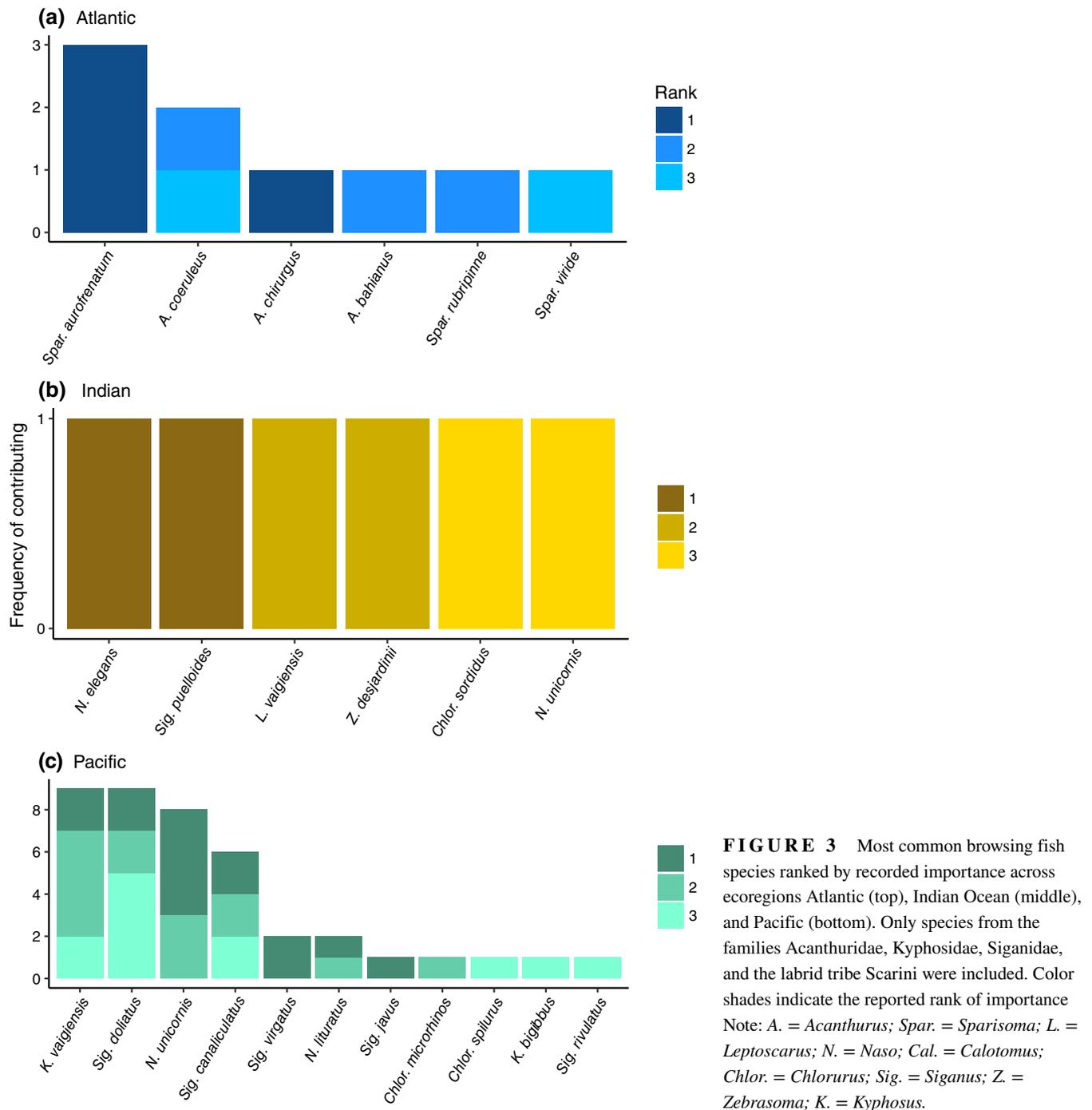
Response	Predictor	Estimate	SE	df	Crit. value	P-value	Std. estimate
$\gamma$ -diversity	Latitude	-0.0079	0.0073	219	-1.0788	0.2807	NA
$\alpha$ -diversity	$\gamma$ -diversity	-0.0024	0.0091	219	-0.2574	0.7969	NA
$\alpha$ -diversity	Latitude	0.0176	0.0235	219	0.747	0.4551	NA
$\alpha$ -diversity	Protection	0.7253	0.3322	219	2.183	<b>0.0290</b>	NA
Biomass	$\alpha$ -diversity	0.1275	0.0485	181	23.6302	<b>0.0093</b>	0.3126
Biomass	Protection	1.7449	0.723	21	2.4135	<b>0.0250</b>	0.712
Herbivory	$\alpha$ -diversity	0.0755	0.0157	198	4.8115	<b>0.0000</b>	0.7759
Herbivory	Biomass	0.0153	0.196	198	0.7827	0.4348	0.0641
Herbivory	$\gamma$ -diversity	0.0446	0.0099	198	1.1704	0.2433	0.2282
Herbivory	Latitude	-0.0539	0.0225	198	-2.6965	<b>0.0175</b>	-0.4847
Herbivory	Brown algae	0.6392	0.1476	198	4.3292	<b>0.0000</b>	0.2626
Herbivory	Protection	1.946	0.7855	198	6.4411	<b>0.0000</b>	0.4908



**FIGURE 2** Topology and partial effects of the structural equation model employed to test drivers of herbivory on coral reefs. (a) Path diagram displaying the pathways specified in the model. Solid arrows indicate significant positive (black) or negative (red) effects. The size of the arrow denotes the standardized magnitude of the effect, with the path from the Poisson component-model (MPA to  $\alpha$ -diversity) scaled to a constant of 1. Specified but non-significant paths ( $P > 0.05$ ) are provided as gray, dashed lines. (b) Partial effect plots showing the independent effect of each significant predictor on the response. Shaded lines and ribbons (continuous predictors) and crossbars and boxes (categorical predictors) mark the predicted model fits ( $\pm 95\%$  confidence intervals) obtained from the component models, while colored dots represent the raw data at the study level

2018). By decomposing drivers of herbivore browsing on coral reefs, we demonstrate that MPAs both directly and indirectly enhance an important ecosystem function on coral reefs via increases in species richness of browsing herbivores. Specifically, MPAs increase local herbivore richness ( $\alpha$ -diversity) and biomass; however,  $\alpha$ -diversity directly affected the removal of macroalgae from the reef, whereas biomass had no discernable effect after  $\alpha$ -diversity was accounted for. This is important, given that biomass is

regularly used as a proxy for herbivory, reef resilience, and management success. Although a range of species contributed to macroalgal removal in each region (further supporting the observed effect of  $\alpha$ -diversity), the most dominant browsers represent only a small fraction of total herbivore species richness. Our results therefore indicate that local management centered on promoting biodiversity, including the presence of key browsers, can predictably help to safeguard or enhance the process of removing algae from tropical coral reefs.



#### 4.1 | Positive effects of herbivore diversity on browsing

Positive effects of biodiversity on ecosystem functioning have been reported widely (O'Connor et al., 2017), but stem largely from temperate ecosystems with relatively low diversity (Clarke, York, Rasheed, & Northfield, 2017). Our results suggest that, in line with recent findings on reef fish productivity, coral calcification, and herbivore grazing (Duffy, Lefcheck, Stuart-Smith, Navarrete, & Edgar, 2016; Lefcheck et al., 2019; McWilliam, Chase, & Hoogenboom,

2018), biodiversity-mediated effects also operate on tropical coral reefs.

Herbivore diversity may enhance ecosystem functioning (browsing) on coral reefs through two, not mutually exclusive, mechanisms. First, a more diverse herbivore assemblage may increase browsing rates through niche partitioning (functional complementarity), whereby species target different algal resources (Loreau & Hector, 2001), leading to a more efficient utilization of resources in communities with higher species richness. Functional complementarity has been demonstrated in both grazing (Brandl & Bellwood, 2014;

Burkepile & Hay, 2010) and browsing herbivorous coral reef fishes (Rasher et al., 2013; Streit, Hoey, & Bellwood, 2015) and has an intuitive basis: as browsers have differing tolerances for the varied chemical and structural defenses displayed by macroalgal species (Rasher et al., 2013), a broad suite of browsers with complementary niches might be more effective at consuming the diverse suite of macroalgae found in the ecosystem. In fact, removal of some algae (or their parts) by an herbivore may even enhance consumption of other algal species (or parts) by a different herbivore (Streit et al., 2015) via a break down of associational refuges. This may further boost net herbivory via biological facilitation in more diverse herbivore assemblages (Bruno, Stachowicz, & Bertness, 2003).

The second means by which diversity can increase ecosystem functioning is through the sampling (identity) effect, where increasing herbivore diversity results in a higher probability of including species with dominant effects on the process. Although the presence of a relatively small suite of high-performing species in each region provides some evidence for this mechanism, the emergence of the sampling effect is, of course, contingent on the number of macroalgal species present in the environment (or in a feeding assay) and the spatial scale at which herbivory is considered. If only one or a few species of macroalgae are present (as is true for most studies in our meta-analysis), herbivore identity effects may emerge given the species-specific feeding preferences described above. Yet, as more species of algal prey (and more localities) are considered, complementarity effects are likely to prevail. Thus, the nature of the analyzed studies may bias our results toward finding a sampling effect.

Although herbivory has a strong impact on benthic structure (Burkepile & Hay 2010) and has been linked to coral reef resilience for decades (Bellwood et al., 2004), macroalgae are also an integral feature of coral reef ecosystems (Ceccarelli et al., 2018). Further, the global prevalence of reef phase shifts to macroalgae continues to be debated (Bruno et al., 2009; Jouffray et al., 2015; Smith et al., 2016), in part because some regions are more prone to macroalgal blooms than others (Roff & Mumby 2012), and multiple states (e.g., turf-algal mats) are possible following reef disturbance (Donovan et al., 2018). Importantly, studies in our synthesis that assessed other types of herbivory, such as grazing and scraping, also recorded higher herbivory on turf algae at sites with high herbivore diversity (Bonaldo et al., 2017; Rasher et al. 2017), suggesting that the mechanisms underpinning our results may apply to other aspects of herbivory and reef functioning (Lefcheck et al., 2019).

## 4.2 | Management implications

Documented examples in which biodiversity conservation has enhanced ecosystem functioning are rare, and the feasibility

of protecting biodiversity to preserve ecosystem functioning has been rightly questioned (Cavanagh et al., 2016; Dee et al., 2017). Yet our synthesis confirms that protection of biodiversity is indeed feasible via area closures, and shows, for the first time, that the increased diversity resulting from protection can enhance ecosystem functioning on coral reefs (i.e., macroalgal removal). Although a similar positive relationship between protection status and herbivory rate has been shown for grazing (Nash, Abesamis, Graham, McClure, & Moland, 2016), browsing (Rasher et al., 2013), or both (Bonaldo et al., 2017) at local scales, our study suggests that these effects do not depend on higher fish biomass but higher diversity in protected areas, and that these biodiversity effects are generalizable across the wide range of biotic and abiotic conditions found on Indo-Pacific coral reefs. Although the strong representation of the GBR in the dataset may have a considerable influence on the obtained results, the consistent effect of protection on diversity and herbivory in other regions such as Fiji (Bonaldo et al., 2017; Rasher et al., 2013) suggests that our results are not merely driven by studies from the GBR.

Our synthesis also shows that, at least under experimental conditions with a limited set of macroalgal species, a substantial proportion of browsing is often performed by a subset of herbivores at any given locale (Bennett & Bellwood, 2011). Many of the most important contributors (a) are large-bodied species of high fisheries and/or cultural value (Bejarano, Golbuu, Sapolu, & Mumby, 2013), (b) display life-history traits that make them vulnerable to exploitation (Taylor, Houk, Russ, & Choat, 2014), and (c) are among the first to disappear in response to fishing (Edwards et al., 2014). Thus, beyond localized conservation tools such as MPAs to increase herbivore richness, broader scale conservation efforts for high-performing browser species appear warranted (and may be necessary). The recovery time for targeted species after a closure is established varies (MacNeil et al., 2015), but protection can lead to quick (<5 years) increases in abundance (Babcock et al., 2010). Thus, our results suggest that macroalgal removal will be promoted by both managing local herbivore richness through MPAs, and potentially supplemental protection of the highest contributing species where possible (e.g., parrotfishes in the Caribbean), which gives managers and stakeholders the flexibility to promote herbivory through various avenues, depending on local cultural and economic constraints (Cinner et al., 2016).

Notably, a lack of empirical evidence that herbivore protection leads to higher coral cover, a key metric for coral reef conservation, has recently been identified (Bruno et al., 2019). It is well known that herbivores suppress algae (Burkepile & Hay, 2010) and that algae—when abundant—suppress coral survival and reproduction (McCook, Jompa, & Diaz-Pulido, 2001). However, consistent linear correlations between herbivore protection and recovery of coral cover following mass disturbance are indeed prone to be

rare, as coral recovery hinges on a plethora of other factors (e.g., propagule supply, abiotic conditions, and additional disturbances; Graham, Nash, & Kool, 2011). Nevertheless, the likelihood of coral recovery is demonstrably lower on reefs where macroalgae or turf algae dominate (Kuffner et al., 2006). Given this, management for high rates of herbivory as a precautionary approach to prevent algal blooms may increase the potential for coral recovery, but only if external conditions are conducive to coral re-establishment (Graham, Jennings, MacNeil, Mouillot, & Wilson, 2015). Our results suggest that area closures effectively promote herbivory via herbivore diversity, thus potentially satisfying one of the many conditions that ought to prevail if coral cover is to rebound in the wake of disturbance.

## 5 | CONCLUSION

Given the overarching effects of rising sea surface temperatures, global action on climate change is critical for conserving coral reefs (Bruno et al., 2019; Hughes et al., 2017). Yet, local actions may help to maintain ecological processes at the core of coral reef functioning, such as herbivory on macroalgae that may otherwise prevent coral recovery after disturbance (Graham et al., 2015). Indeed, our findings indicate that MPAs indirectly enhance herbivory by promoting local fish biodiversity. Such local management efforts may be particularly important in regions where macroalgal phase shifts are common (Roff & Mumby, 2012). Further research is needed to reveal whether our results extend to other key ecological processes; if so, conserving biodiversity could represent an important, and achievable, component of our efforts to bolster coral reef resilience in the Anthropocene.

## ACKNOWLEDGMENTS

This is contribution 33 from the Smithsonian's Tennenbaum Marine Observatories Network. S.J.B. was supported by a MarineGEO postdoctoral fellowship; Z.M.T. was supported by a MarineGEO internship. Data are available in the supplemental material of the paper.

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## REFERENCES

- Babcock, R., Shears, N. T., Alcala, A. C., Barrett, N. S., Edgar, G. J., Lafferty, K. D., ... Russ, G. R. (2010). Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 18256–18261.
- Balvanera, P., Siddique, I., Dee, L., Paquette, A., Isbell, F., Gonzalez, A., ... Griffin, J. N. (2014). Linking biodiversity and ecosystem services: Current uncertainties and the necessary next steps. *BioScience*, *64*, 49–57.
- Bejarano, S., Golbuu, Y., Sapolu, T., & Mumby, P. J. (2013). Ecological risk and the exploitation of herbivorous reef fish across Micronesia. *Marine Ecology Progress Series*, *482*, 197–215.
- Bellwood, D. R., Hughes, T. P., Folke, C., & Nyström, M. (2004). Confronting the coral reef crisis. *Nature*, *429*, 827–833.
- Bennett, S., & Bellwood, D. (2011). Latitudinal variation in macroalgal consumption by fishes on the Great Barrier Reef. *Marine Ecology Progress Series*, *426*, 241–252.
- Bonaldo, R. M., Pires, M. M., Guimarães, P. R., Hoey, A. S., & Hay, M. E. (2017). Small marine protected areas in Fiji provide refuge for reef fish assemblages, feeding groups, and corals. *PLoS ONE*, *12*, e0170638.
- Brandl, S. J., & Bellwood, D. R. (2014). Individual-based analyses reveal limited functional overlap in a coral reef fish community. *Journal of Animal Ecology*, *83*, 661–670.
- Brandl, S. J., & Bellwood, D. R. (2016). Microtopographic refuges shape consumer-producer dynamics by mediating consumer functional diversity. *Oecologia*, *182*, 203–217.
- Bruno, J. F., Côté, I. M., & Toth, L. T. (2019). Climate change, coral loss, and the curious case of the parrotfish paradigm: Why don't marine protected areas improve reef resilience? *Annual Review of Marine Science*, *11*, 307–334.
- Bruno, J. F., Stachowicz, J. J., & Bertness, M. D. (2003). Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution*, *18*, 119–125.
- Bruno, J. F., Sweatman, H., Precht, W. F., Selig, E. R., & Schutte, V. G. (2009). Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. *Ecology*, *90*, 1478–1484.
- Burkpile, D. E., & Hay, M. E. (2010). Impact of herbivore identity on algal succession and coral growth on a Caribbean reef. *PLoS ONE*, *5*, e8963.
- Cavanagh, R. D., Broszeit, S., Pilling, G. M., Grant, S. M., Murphy, E. J., & Austen, M. C. (2016). Valuing biodiversity and ecosystem services: A useful way to manage and conserve marine resources? *Proceedings of the Royal Society B: Biological Sciences*, *283*, 20161635.
- Ceccarelli, D. M., Löffler, Z., Bourne, D. G., Al Moajil-Cole, G. S., Boström-Einarsson, L., Evans-Illidge, E., ... McLeod, I. (2018). Rehabilitation of coral reefs through removal of macroalgae: State of knowledge and considerations for management and implementation. *Restoration Ecology*, *26*, 827–838.
- Cinner, J. E., Huchery, C., MacNeil, M. A., Graham, N. A., McClanahan, T. R., Maina, J., ... Mora, C. (2016). Bright spots among the world's coral reefs. *Nature*, *535*, 416–419.
- Clarke, D. A., York, P. H., Rasheed, M. A., & Northfield, T. D. (2017). Does biodiversity–ecosystem function literature neglect tropical ecosystems? *Trends in Ecology & Evolution*, *32*, 320–323.
- Dee, L. E., De Lara, M., Costello, C., & Gaines, S. D. (2017). To what extent can ecosystem services motivate protecting biodiversity? *Ecology Letters*, *20*, 935–946.
- Donovan, M. K., Friedlander, A. M., Lecky, J., Jouffray, J.-B., Williams, G. J., Wedding, L. M., ... Selkoe, K. A. (2018). Combining fish and benthic communities into multiple regimes reveals complex reef dynamics. *Scientific Reports*, *8*, 16943.

- Duffy, J. E., Lefcheck, J. S., Stuart-Smith, R. D., Navarrete, S. A., & Edgar, G. J. (2016). Biodiversity enhances reef fish biomass and resistance to climate change. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 6230–6235.
- Edwards, C. B., Friedlander, A., Green, A., Hardt, M., Sala, E., Sweatman, H., ... Smith, J. (2014). Global assessment of the status of coral reef herbivorous fishes: Evidence for fishing effects. *Proceedings of the Royal Society of London B: Biological Sciences*, *281*, 20131835.
- Gilby, B. L., Tibbetts, I. R., & Stevens, T. (2017). Low functional redundancy and high variability in Sargassum browsing fish populations in a subtropical reef system. *Marine and Freshwater Research*, *68*, 331–341.
- Graham, N., Nash, K., & Kool, J. (2011). Coral reef recovery dynamics in a changing world. *Coral Reefs*, *30*, 283–294.
- Graham, N. A., Jennings, S., MacNeil, M. A., Mouillot, D., & Wilson, S. K. (2015). Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature*, *518*, 94–97.
- Hoey, A. S., & Bellwood, D. R. (2011). Suppression of herbivory by macroalgal density: A critical feedback on coral reefs? Macroalgal density suppresses herbivory. *Ecology Letters*, *14*, 267–273.
- Hughes, T. P., Barnes, M. L., Bellwood, D. R., Cinner, J. E., Cumming, G. S., Jackson, J. B., ... Morrison, T. H. (2017). Coral reefs in the Anthropocene. *Nature*, *546*, 82–90.
- Isbell, F., Gonzalez, A., Loreau, M., Cowles, J., Díaz, S., Hector, A., ... Duffy, J. E. (2017). Linking the influence and dependence of people on biodiversity across scales. *Nature*, *546*, 65–72.
- Jouffray, J.-B., Nyström, M., Norström, A. V., Williams, I. D., Wedding, L. M., Kittinger, J. N., & Williams, G. J. (2015). Identifying multiple coral reef regimes and their drivers across the Hawaiian archipelago. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*, 20130268.
- Kuffner, I. B., Walters, L. J., Becerro, M. A., Paul, V. J., Ritson-Williams, R., & Beach, K. S. (2006). Inhibition of coral recruitment by macroalgae and cyanobacteria. *Marine Ecology Progress Series*, *323*, 107–117.
- Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*, 573–579.
- Lefcheck, J. S., Innes-Gold, A. A., Brandl, S. J., Steneck, R. S., Torres, R. E., & Rasher, D. B. (2019). Tropical fish diversity enhances coral reef functioning across multiple scales. *Science Advances*, *113*, 6230–6235.
- Leslie, H. M., & McLeod, K. L. (2007). Confronting the challenges of implementing marine ecosystem-based management. *Frontiers in Ecology and the Environment*, *5*, 540–548.
- Link, J. S., & Browman, H. I. (2014). Integrating what? Levels of marine ecosystem-based assessment and management. *ICES Journal of Marine Science*, *71*, 1170–1173.
- Loreau, M., & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, *412*, 72–76.
- MacNeil, M. A., Graham, N. A. J., Cinner, J. E., Wilson, S. K., Williams, I. D., Maina, J., ... McClanahan, T. R. (2015). Recovery potential of the world's coral reef fishes. *Nature*, *520*, 341–344.
- McCook, L., Jompa, J., & Diaz-Pulido, G. (2001). Competition between corals and algae on coral reefs: A review of evidence and mechanisms. *Coral Reefs*, *19*, 400–417.
- McWilliam, M., Chase, T. J., & Hoogenboom, M. O. (2018). Neighbor diversity regulates the productivity of coral assemblages. *Current Biology*, *28*, 3634–3639.
- Nash, K., Abesamis, R., Graham, N., McClure, E., & Moland, E. (2016). Drivers of herbivory on coral reefs: Species, habitat and management effects. *Marine Ecology Progress Series*, *554*, 129–140.
- O'Connor, M. I., Gonzalez, A., Byrnes, J. E., Cardinale, B. J., Duffy, J. E., Gamfeldt, L., ... Paquette, A. (2017). A general biodiversity–function relationship is mediated by trophic level. *Oikos*, *126*, 18–31.
- Partelow, S., Schlüter, A., von Wehrden, H., Jänig, M., & Senff, P. (2018). A sustainability agenda for tropical marine science. *Conservation Letters*, *11*, e12351.
- Puk, L. D., Ferse, S. C., & Wild, C. (2016). Patterns and trends in coral reef macroalgae browsing: A review of browsing herbivorous fishes of the Indo-Pacific. *Reviews in Fish Biology and Fisheries*, *26*, 53–70.
- Rasher, D. B., Hoey, A. S., & Hay, M. E. (2013). Consumer diversity interacts with prey defenses to drive ecosystem function. *Ecology*, *94*, 1347–1358.
- Rasher, D. B., Hoey, A. S., & Hay, M. E. (2017). Cascading predator effects in a Fijian coral reef ecosystem. *Scientific Reports*, *7*, 15684.
- R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Roff, G., & Mumby, P. J. (2012). Global disparity in the resilience of coral reefs. *Trends in Ecology & Evolution*, *27*, 404–413.
- Smith, J. E., Brainard, R., Carter, A., Grillo, S., Edwards, C., Harris, J., ... Sala, E. (2016). Re-evaluating the health of coral reef communities: Baselines and evidence for human impacts across the central Pacific. *Proceedings of the Royal Society B: Biological Sciences*, *283*, 20151985.
- Streit, R. P., Hoey, A. S., & Bellwood, D. R. (2015). Feeding characteristics reveal functional distinctions among browsing herbivorous fishes on coral reefs. *Coral Reefs*, *34*, 1037–1047.
- Taylor, B. M., Houk, P., Russ, G. R., & Choat, J. H. (2014). Life histories predict vulnerability to overexploitation in parrotfishes. *Coral Reefs*, *33*, 869–878.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**How to cite this article:** Topor ZM, Rasher DB, Duffy JE, Brandl SJ. Marine protected areas enhance coral reef functioning by promoting fish biodiversity. *Conservation Letters*. 2019;12:e12638. <https://doi.org/10.1111/conl.12638>