

Biodiversity effects of the predation gauntlet

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Abstract The ubiquity of trophic downgrading has led to interest in the consequences of mesopredator release on prey communities and ecosystems. This issue is of particular concern for reef-fish communities, where predation is a key process driving ecological and evolutionary dynamics. Here, we synthesize existing experiments that have isolated the effects of mesopredators to quantify the role of predation in driving changes in the abundance and biodiversity of recently settled reef fishes. On average, predators reduced prey abundance through generalist foraging behavior, which, through a statistical sampling artifact, caused a reduction in alpha diversity and an increase in beta diversity. Thus, the synthesized experiments provide

evidence that predation reduces overall abundance within prey communities, but—after accounting for sampling effects—does not cause disproportionate effects on biodiversity.

Keywords Predator–prey · Rarefaction · Coral reef · Reef fish · Assembly · Invasive predators

Introduction

Declines in apex predator populations can cause irruptions in the abundance and shifts in the behavior of previously suppressed mesopredators (Prugh et al. 2009). This trophic ‘release’ of mesopredators is cause for conservation concern, because when abundant, they can cause extinctions and major shifts in ecosystem function (Crooks and Soulé 1999; Ritchie and Johnson 2009). The reduction of apex predators and subsequent mesopredator release is a widespread phenomenon across ecosystems (Estes et al. 2011) and is particularly prevalent in coral-reef ecosystems due to disproportionately high fishing rates at the top of the food chain (Stallings 2009; DeMartini and Smith 2015). Abundance of coral-reef mesopredators (e.g., small-bodied groupers and snappers) has also increased through the introduction of non-native predators. In some cases, these introduced predators have become extremely successful, for example, the intentionally introduced peacock grouper (*Cephalopholis argus*) in Hawaii (Meyer and Dierking 2011) and the accidentally introduced Pacific lionfishes (*Pterois volitans* and *Pterois miles*) in the Atlantic and Caribbean (Côté et al. 2013) have each become numerically dominant mesopredators in their respective invaded communities. Because predation is known to be a key driver of ecosystem and evolutionary dynamics (Hixon

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1991, 2015), these fishing- and invasion-associated shifts in the abundance and biomass of predators are considered cause for concern among coral-reef managers and conservation practitioners. Settling fishes experience extraordinarily high predation rates on coral reefs (Almany and Webster 2006), with an average of 50% mortality in their first 48 h on the reef (i.e., a ‘predation gauntlet’). This effect of predators declines rapidly with increases in prey body size (Sogard 1997; Goatley and Bellwood 2016). Thus, increases in mesopredator abundance have the capacity to drive major shifts in the abundance and biodiversity of coral-reef fish communities by amplifying the intensity of the predation gauntlet.

Mesopredator effects have historically been difficult to quantify on coral reefs, because these predators often positively covary in abundance and diversity with their prey due to shared reef habitat (Stier et al. 2014). Therefore, only a handful of field experiments have been able to isolate the role of mesopredators in altering prey community size and composition (Hixon 2015). Here, we conducted a meta-analysis of all (to our knowledge) published predation experiments to quantify the extent to which mesopredators affect prey abundance and biodiversity in coral-reef fishes. We focused on three distinct aspects of biodiversity including gamma diversity (species richness at the study scale), alpha diversity (species richness at the sample scale), and beta diversity (a measure of the spatial variability of community composition among samples across the study). We also used rarefaction methods to calculate corrected alpha and beta diversity measures by accounting for the effects of abundance on biodiversity. We then compared the effects of native mesopredators to those of invasives (peacock grouper and lionfish) and briefly identified two opportunities for future research on reef–fish predator–prey dynamics.

Methods

Focal experiments

We quantified the effects of reef-fish mesopredators on prey abundance and biodiversity in ten published studies 2002–2014 (Electronic supplementary material, ESM, Table S1). We identified these ten focal studies using extensive Google Scholar and ISI Web of Science literature searches from 1990 to 2016 in major ecological and marine journals using all combinations of the following keywords: *predation*, *coral reef fish*, *predation gauntlet*, *reef fish*, *community assembly*, and *depredation*. Each of these ten studies was conducted with similar methods, where isolated experimental reefs were constructed in sandy environments. Prey communities were manipulated prior to each study either through the removal of all prey or through the selective

removal of all recently recruited individuals. Predators were then manipulated on a subset of the patch reefs through selective additions and removals or cages; then, new prey communities were allowed to recruit to reefs with different predator treatments (control = predators absent, treatment = predators present). Predator manipulations were pressed in all studies (i.e., unwanted predators on control treatments were removed and predator-present treatments were maintained). Prey communities were visually surveyed by divers on a regular basis over a period of time that ranged from 42 to 120 d. Additional study details including predator species, duration, and additional manipulations of other variables such as adult damselfish abundance and habitat complexity (additional known drivers of reef-fish community assembly) can be found in ESM Table S1.

Measuring prey community response

We compared recruiting prey communities in experimental treatments with and without predators using five different response variables: (1) total abundance of all prey species; (2) gamma diversity measured as the species list on reefs with and without predators (i.e., the total number of prey species found in control or predator-present treatments); (3) alpha diversity measured as the number of species within a patch; (4) rarefied alpha diversity (the number of species within a patch, corrected for abundance); (5) beta diversity based on species incidence (the Jaccard index: a metric focused on the gain or loss of a species); and (6) rarefied beta diversity (Jaccard index corrected for differences in abundance). We quantified beta diversity in predator and no-predator treatments by estimating the median multivariate dispersion around the multivariate centroid of the community (Anderson et al. 2006).

Rarefaction

Communities with higher abundance tend to have higher alpha diversity and lower beta diversity (Gotelli and Colwell 2001; Cardoso et al. 2009; Stier et al. 2016). Because alpha diversity is often strongly correlated with abundance, predation can reduce observed alpha diversity and increase observed beta diversity simply because it causes a decline in the number of prey individuals (Fig. 1a, b). We used individual-based rarefaction to estimate rarefied alpha (Gotelli and Colwell 2001) and beta diversity (Stier et al. 2014) because control treatments tended to have a higher abundance than those with predators. Predator-induced reductions in rarefied diversity implicate biological process(es) rather than a statistical sampling artifact (Fig. 1c).

We define generalist predators as those that affect prey species in proportion to prey abundance. If predators eat prey in proportion to their abundance, rarefied alpha and

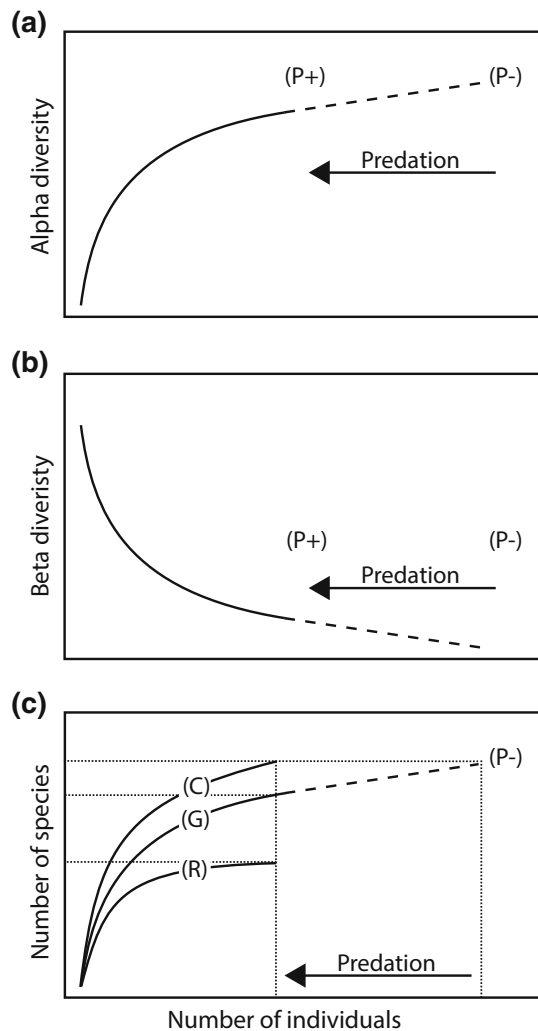


Fig. 1 When predators reduce abundance, alpha diversity should decrease and beta diversity should increase. This effect can provide insight into expected effects of predators on alpha and beta diversity through reductions in abundance (see *arrow*). Panels illustrate individual-based rarefaction curves (**a** alpha diversity, **b** beta diversity). Rarefaction of alpha diversity can be used to gain insights into whether predators disproportionately affect common or rare species. **c** Three different individual-based rarefaction curves that might emerge from different predator effects. A patch that has no predators will have a rarefaction curve labeled P^- . The manner in which reduced abundance by predators affects species richness depends on whether predators are generalists or whether they disproportionately affect common or rare species. If predators affect species in proportion to their abundance (i.e., generalists), they will have rarefaction curve G. If predators disproportionately affect common species, they will have a greater number of species per individual compared to generalist predators (curve C), and if predators disproportionately affect rare species, they will produce rarefaction curve R, decreasing diversity relative to generalist predators

beta diversity should remain the same across predator and control treatments. If predators disproportionately consume common or rare species or alter competitive dynamics, differences in alpha and beta diversity will emerge for

rarefied indices. The mesopredators involved in our meta-analysis are considered generalists though this has not been previously assessed quantitatively. For additional details on rarefaction, see ESM 2 and Stier et al. (2013b, 2014).

Effect sizes

We estimated the effect of predators ($P+$) relative to predator-free controls ($P-$) for each study using the log-response ratio (Osenberg et al. 1999):

$$\mu_i = \log\left(\frac{P_{i+}}{P_{i-}}\right), \quad (1)$$

where μ_i is the predation effect size, and P_{i+} and P_{i-} represent the abundance, alpha diversity, or beta diversity of prey in the presence and absence of predators, respectively, for the i th study.

Variance of the effect size was estimated using the delta method:

$$\text{var}(\mu_i) = \frac{\text{var}(P_{i-})}{(P_{i-})^2} + \frac{\text{var}(P_{i+})}{(P_{i+})^2}. \quad (2)$$

For abundance, alpha diversity, and beta diversity, we tested the hypothesis that the effect size differed from zero and estimated nonparametric bootstrapped confidence intervals using a random-effects model implemented in the metafor package in R (Viechtbauer 2010). We weighted studies by the inverse of the sampling variance of their effect sizes, as recommended by Hedges et al. (1999), to account for greater certainty in studies with less variation. However, there was no variance estimate for gamma diversity; therefore, we used a t test to compare the effect size to zero. We assumed that the response of each community was statistically independent. Experiments exhibited minor overlap in predator species; however, individual experiments had limited temporal overlap, suggesting prey recruitment events were largely independent. All analyses were made using the R statistical programming environment (R Development Core Team 2013).

Results and discussion

Mesopredators had substantial effects on prey abundance and biodiversity. Across the ten focal studies, prey communities on reefs with mesopredators had 60% lower abundance ($Q = 82.616$, $df = 10$, $P < 0.001$; Figs. 2, 3a) and an average of 35% lower gamma diversity ($t = 2.711$, $df = 10$, $P = 0.022$; ESM Fig. S1). This reduction in gamma diversity was primarily driven by the 36% average reduction in alpha diversity ($Q = 82.615$, $df = 10$, $P = 0.001$; Fig. 3b). However, there was no detectable effect of mesopredators on rarefied alpha diversity (0.1%

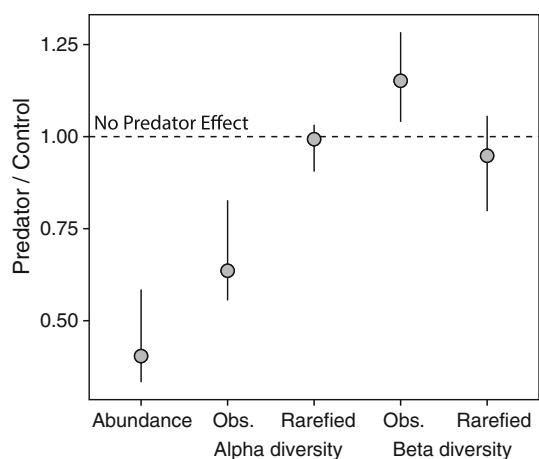


Fig. 2 Mean effects of predators on abundance and diversity (back transformed mean \pm bootstrapped 95% CI). Effects include abundance, alpha diversity (observed (obs.) and rarefied), and beta diversity measured based on species incidence—Jaccard index (obs. and rarefied). The *dashed horizontal line* represents no difference between predators and control treatment, values >1 represent positive effects of predators, and values <1 represent negative effects of predators

increase; $Q = 30.989$, $df = 10$, $P = 0.450$; Fig. 4a), suggesting that mesopredator-induced reductions in prey abundance caused the apparent decline in unrarefied alpha diversity. We found reefs with mesopredators had on average 15% higher beta diversity ($Q = 19.192$, $df = 10$, $P = 0.007$; Figs. 2, 3b), but that these effects similarly disappeared following rarefaction, with no detectible shift in rarefied beta diversity (5% decrease; $Q = 28.902$, $df = 10$, $P = 0.439$; Figs. 2, 4b). Thus, the reef mesopredators measured here were, on average, generalist predators that had strong negative effects on prey abundance and consequently altered patterns of alpha and beta diversity via a statistical sampling effect.

Our results suggest that mesopredators primarily affected prey diversity by reducing prey abundance (Fig. 3a). There were, however, two notable predator species that disproportionately affected rare prey species and significantly lowered rarefied diversity: the dottyback *Pseudochromis fuscus* (Almany et al. 2007) and peacock grouper *Cephalopholis argus* (Stier et al. 2014). From a conservation perspective, this disproportionate effect on rare species is particularly concerning in the case of the peacock grouper, because this non-native mesopredator, introduced to Hawaii in the mid-1950s, now constitutes more than 80% of the large piscivore biomass in some locations (Meyer and Dierking 2011). The unique effects of these two species suggest we need to further study the foraging behavior of mesopredators and in particular their functional responses (*sensu* Stier et al. 2013a; Stier and White 2014), because predators with a preference for rare species and a Type I or II functional response can

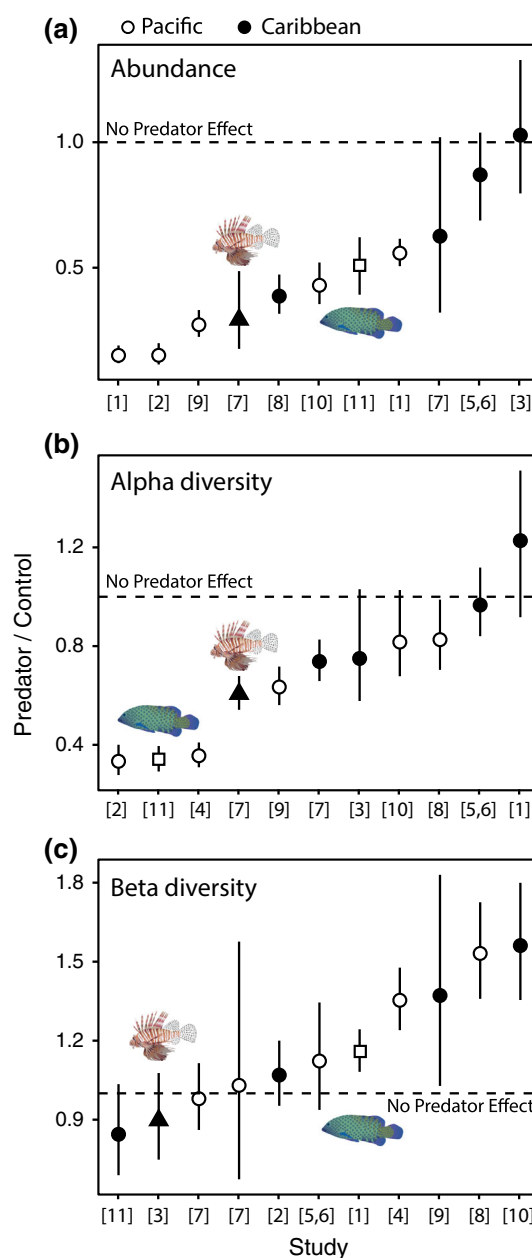


Fig. 3 Distribution of median predator effects ($\pm 95\%$ bootstrapped confidence limits) on abundance (a), alpha diversity (b), and beta diversity (c). *Dashed horizontal line* represents no-predator effect, and point color depicts Caribbean (black) and Pacific (white) studies. Lionfish silhouette (triangle) corresponds to effect measured from Albins (2013), and peacock grouper silhouette (square) corresponds to effect measured from Stier et al. (2014). Studies ranked by magnitude of effect, with strongest negative effects on left and strongest positive effects on right. Numbers correspond to reference numbers listed in ESM Table S1

destabilize prey population dynamics and catalyze reductions in reef biodiversity (White et al. 2010).

Our study also provides insight into the effects of lionfishes in the western Atlantic. The recent invasion and exponential growth of lionfishes in the Atlantic from the

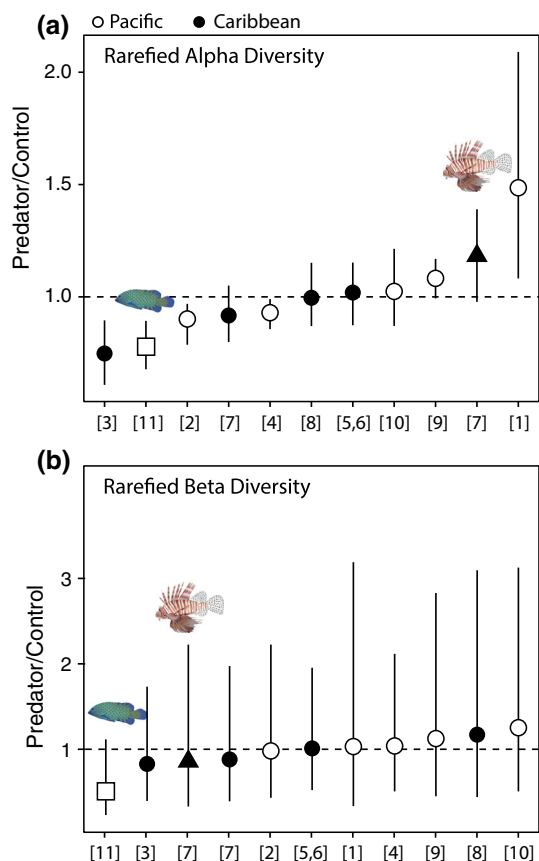


Fig. 4 Distribution of mean predator effects (95% bootstrapped confidence intervals) across studies ranked by strength of effect from left to right (strongest negative to positive effects). *Dashed horizontal line* represents no-predator effect on rarefied alpha diversity (species richness (a), and rarefied beta diversity (Jaccard index) (b). Lionfish silhouette and *triangle* correspond to effect measured from Albins (2013), and peacock grouper silhouette and *square* correspond to effect measured from Stier et al. (2014). Point color corresponds to ocean basin: Caribbean (*black*) and Pacific (*white*). Study number corresponds to reference numbers in ESM Table S1

central US to South America have generated widespread concern for their effects on the prey fish community. The effects of lionfish on abundance and diversity fell within the distribution of predator effects observed across all studies, but was the strongest effect measured in the region (Fig. 3). Rarefaction suggested that lionfish are generalists rather than disproportionately affecting common or rare species (Fig. 4). Therefore, in contrast to the peacock grouper, lionfish may be less likely to threaten prey biodiversity unless they drive prey to such low abundances that they are sensitive to extinction due to demographic stochasticity (*sensu* Rocha et al. 2015; Ingeman 2016). Such an outcome is likely in some locations based on the strong negative effects of lionfish on a wide variety of native prey species (Albins 2013). Of course, there are also additional biological and socio-economic concerns

associated with the lionfish invasion that extend beyond biodiversity effects.

Biodiversity can be associated with ecosystem functioning, productivity, and evolutionary dynamics in marine systems (Gamfeldt et al. 2015). The studies synthesized here offer key insights into how mesopredators affect prey fish abundance and biodiversity and, more broadly, the role mesopredators play in driving spatio-temporal variation in reef-fish biodiversity. However, a number of questions remain unanswered about the role of predation in driving reef-fish assembly, such as: (1) How do these small spatial scale and short temporal scale studies scale up to population and community dynamics on contiguous reefs over longer periods of time? (2) How do the effects of predators on prey community structure cascade to affect the benthic community (Casey et al. 2016)? (3) How do cooperative and antagonistic interactions within and among predator species modify the effect of predators on community structure? As humans continue to alter marine ecosystems through a variety of stressors, a deeper understanding of how invasive predators drive ecosystem structure and function will provide much needed detail to improve conservation and management.

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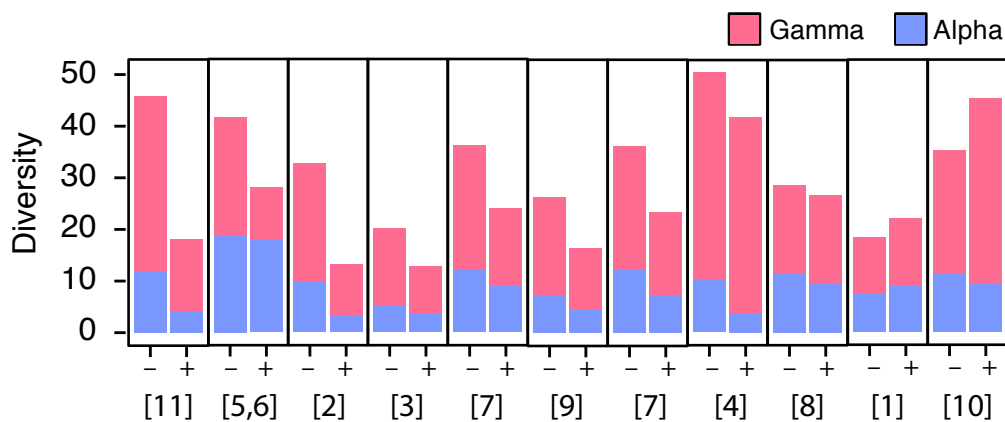
ESM 1

Table S1 Focal studies, species, and study durations. Note that Albins (2013) examined *Pterois volitans* and *Cephalopholis fulva* independently and each species is plotted separately in the main text. All other studies listed below examined either a single predator effect or the combined effect of multiple predator species

| Predator Species | Duration (days) | Reference | Reference No. |
|---|-----------------|------------------------------|---------------|
| <i>Cephalopholis boenak</i> ; <i>Pseudochromis fuscus</i> | 50 | (Webster and Almany 2002) | 1 |
| <i>Cephalopholis boenak</i> ; <i>Pseudochromis fuscus</i> | 42 | (Webster 2002) | 2 |
| <i>Cephalopholis cruentata</i> ; <i>Cephalopholis fulva</i> ; <i>Epinephelus striatus</i> ; <i>Gymnothorax moringa</i> ; <i>Gymnothorax vicinus</i> | 44 | (Almany 2003) | 3 |
| <i>Cephalopholis boenak</i> ; <i>Pseudochromis fuscus</i> | 50 | (Almany 2004a) | 4 |
| <i>Cephalopholis cruentata</i> ; <i>Epinephelus striatus</i> ; <i>Serranus tigrinus</i> ; <i>Rypticus bistrispinus</i> ; <i>Gymnothorax moringa</i> ; <i>Gymnothorax vicinus</i> | 60 | (Almany 2004b; Almany 2004c) | 5,6 |
| <i>Pterois volitans</i> ; <i>Cephalopholis fulva</i> | 70 | (Albins 2013) | 7 |
| <i>Cephalopholis fulva</i> ; <i>Cephalopholis cruentata</i> | 52 | (Stallings 2009) | 8 |
| <i>Balistapus undulatus</i> ; <i>Rhinecanthus aculeatus</i> ; <i>Bothus spp.</i> ; <i>Caranx melampygus</i> ; <i>Halichoeres hortulanus</i> ; <i>Halichoeres trimaculatus</i> ; <i>Lethrinus olivaceus</i> ; <i>Parapercis spp.</i> ; <i>Pterois radiata</i> ; <i>Epinephelus merra</i> ; <i>Synodus spp.</i> | 54 | (Heinlein et al. 2010) | 9 |
| <i>Paracirrhites arcatus</i> | 120 | (Stier et al. 2013) | 10 |
| <i>Cephalopholis argus</i> | 60 | (Stier et al. 2014) | 11 |

ESM 2: Rarefaction methods

Estimates of species richness and beta diversity can be sensitive to differences in overall abundance within and among patches (Gotelli and Colwell 2001; Cardoso et al. 2009). Because predators reduce prey abundance, we expected that they would also reduce species richness, either through frequency dependent foraging (in particular, the preferential consumption of rare species) or simply by reducing overall density (i.e., a sampling effect). If predators were primarily generalists, reducing overall density, then among-treatment differences in species richness would subside after rarefaction (Almany and Webster 2004). Individual-based rarefaction has classically been used to adjust species richness estimates for differences in abundance of organisms across sites by estimating the mean species richness in repeated subsamples from each site (Gotelli and Colwell 2001). Although the importance of bias in species richness estimates due to differential sample sizes across treatments has been previously recognized, its effect on estimates of beta diversity is less clear. Developing estimates of differences in beta diversity that account for differences in sample size is particularly important in empirical ecology, where manipulating a given ecological factor with a focus on changes in species diversity often leads to concurrent shifts in the number of individuals. For example, in this study, experimental reefs with predators tended to have approximately half as many fish as reefs without predators. Here, we conducted individual-based rarefaction to estimate rarefied alpha diversity and beta diversity that ensured that the number of individuals sampled was comparable across reefs and treatments. For additional details on the methodology see: (Stier et al. 2013; Stier et al. 2014; Stier et al. 2016).



ESM Fig. S1 Distribution of predator effects on gamma (*pink*) and alpha (*blue*) diversity across studies ranked by strength of predator effect on gamma diversity. Predator present treatments are marked as + and predator absent treatments are marked as -. Numbers correspond to reference number and species in Table S1

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