

Biodiversity enhances reef fish biomass and resistance to climate change

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Fishes are the most diverse group of vertebrates, play key functional roles in aquatic ecosystems, and provide protein for a billion people, especially in the developing world. Those functions are compromised by mounting pressures on marine biodiversity and ecosystems. Because of its economic and food value, fish biomass production provides an unusually direct link from biodiversity to critical ecosystem services. We used the Reef Life Survey's global database of 4,556 standardized fish surveys to test the importance of biodiversity to fish production relative to 25 environmental drivers. Temperature, biodiversity, and human influence together explained 47% of the global variation in reef fish biomass among sites. Fish species richness and functional diversity were among the strongest predictors of fish biomass, particularly for the large-bodied species and carnivores preferred by fishers, and these biodiversity effects were robust to potentially confounding influences of sample abundance, scale, and environmental correlations. Warmer temperatures increased biomass directly, presumably by raising metabolism, and indirectly by increasing diversity, whereas temperature variability reduced biomass. Importantly, diversity and climate interact, with biomass of diverse communities less affected by rising and variable temperatures than species-poor communities. Biodiversity thus buffers global fish biomass from climate change, and conservation of marine biodiversity can stabilize fish production in a changing ocean.

global change | fisheries | functional diversity | macroecology | structural equation model

Understanding the controls on marine fish biomass production is central to both sustaining ecosystems and human development goals. Ultimately, the quantity and distribution of biomass in ecosystems is determined by availability of resources and the physical conditions that make life possible. Temperature is a fundamental control on rates of cellular metabolism and biological processes at all levels (1) and, together with the solar energy and mineral nutrients that support plant growth, sets the template for global patterns of biomass production and other biological activities. Superimposed on this bottom-up control are interactions among organisms that mediate biomass production. Top-down control by consumers commonly limits biomass of lower trophic levels below what resources could support (2), with often far-reaching direct and indirect effects on ecosystems (3). Human harvesting is increasingly the dominant top-down control in many ecosystems (4) and, in the ocean, industrialized *Homo sapiens* has emerged as both a dominant and a keystone predator, strongly reducing fish biomass and transforming marine ecosystems worldwide (5, 6).

Fundamental to the interactions of organisms with one another and with the environment is evolutionary adaptation, which molds populations toward more efficient resource use and, consequently, greater biomass production. In natural, environmentally heterogeneous ecosystems, theory predicts that this adaptation results in communities of many species using a larger fraction of available resources than species-poor communities, and thus that diversity of both traits and species promotes higher total biomass production (7). Meta-analysis of hundreds of experiments supports the

positive effect of biodiversity on productivity (8), and suggests that such biodiversity effects are comparable in magnitude to those of other global-change drivers (9). Because resource use efficiency is mediated by functional traits of organisms, functional diversity may be a more direct measure of a community's capacity for production than species richness (10). As such, theory predicts (11) and experiments confirm (12) that functional differences among species result in diverse communities having more stable community-level production in the face of perturbations. Most of these inferences, however, come from highly controlled, often trophically simplified, and artificial experiments (10), and the influence of biodiversity on productivity in wild ecosystems remains controversial, reflecting a long-running debate over both the importance of biodiversity relative to other global-change drivers, and the difficulty of disentangling their influences using observational data (13, 14).

Resolving the controversy over the contributions of biodiversity to productivity and stability has important implications for conservation and fishery management because the major drivers of biomass production—temperature, resources, fishing, and biodiversity—are changing rapidly alongside growing human population and resource consumption. Biodiversity is declining on average at marine sites impacted by human activity (15), and is decreasing globally at rates orders-of-magnitude above historical background levels (6, 16), with some suggesting that biodiversity loss is already approaching a planetary tipping point beyond which ecosystems may be irreparably compromised (17). This information raises a practical question: how does declining biodiversity affect the resilience of ecosystems to other stressors, specifically climate change and human harvesting?

Quantifying the influence of declining biodiversity on ecosystem services remains a major challenge (18) because interactions

Significance

Marine fisheries provide a major global source of protein, feeding billions of people, but they face destabilization in many regions from overexploitation and climate change. Using the most comprehensive dataset of fish diversity and abundance, encompassing over 4,500 surveys from nearshore habitats around the world, we show that biodiversity is among the strongest predictors of reef fish community biomass, comparable in importance to global temperature gradients and human impacts. Importantly, diverse fish communities were more resistant to rising and variable temperature, suggesting that high biodiversity also buffers against changing climate. Maintaining taxonomically and functionally diverse fish communities can thus stabilize fisheries' yields in a changing ocean.

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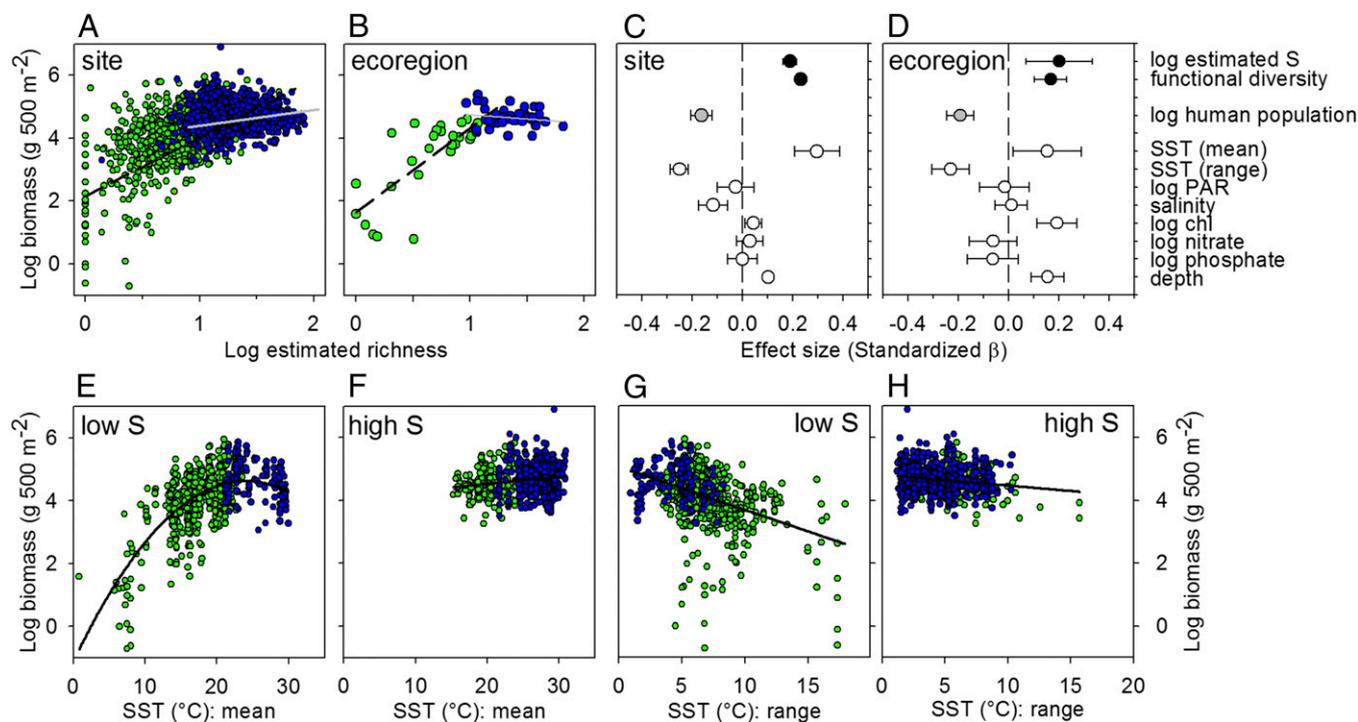


Fig. 2. Global estimates of the effects of biodiversity and environmental drivers on reef fish community biomass. (A) Log biomass as a function of log estimated richness (corrected for sample coverage) (52). (B) Same as A, but using ecoregion means. (C and D) Effect sizes (standardized partial regression coefficients) of 11 predictors of (log) reef fish biomass from the global hierarchical model among (C) sites and (D) ecoregions. (E and F) Log biomass as a function of mean annual temperature at low- and high-richness sites (relative to median richness), respectively. (G and H) Log biomass as a function of annual temperature range at low- and high-richness sites, respectively. S, estimated richness. Blue and green symbols represent tropical and temperate sites, respectively.

that is, the result of a shifting baseline. This finding is supported by the high and relatively invariant (log) human population index among temperate (mean \pm SD = 4.71 ± 0.90) compared with tropical sites (2.61 ± 2.23 , respectively), and by the unstandardized (i.e., raw) effects of human population, which are comparable between temperate ($\beta = -0.072 \pm 0.031$) and tropical sites ($\beta = -0.058 \pm 0.015$). Thus, the smaller relative impact of humans at temperate sites (Fig. 3 E and F) probably reflects the rarity of sparsely populated sites, and accordingly smaller gradient in human population outside the tropics. Our results may therefore reflect both strong historical impacts of human activities on temperate fishes, as well as emerging impacts in less-populated tropical sites.

Human influence also appeared to shift ecosystem control from bottom-up to top-down: considering only tropical sites (because all temperate sites had nearby human population), sites far from human influence showed a dominant signal of bottom-up forcing by dissolved phosphate, a key limiting nutrient in oligotrophic waters. In contrast, sites close to human population showed no phosphate effect and instead a modest but highly significant increase in fish biomass with depth (SI Appendix, Fig. S4), a pattern often associated with intensive fishing in shallow waters (30). This apparently human-mediated shift from bottom-up to top-down forcing supports previous analyses (31) and may explain the otherwise surprising weakness of nutrient effects on fish production in the global analysis (Fig. 1), which seems at odds with some regional analyses supporting bottom-up control of fish biomass in pelagic and sediment-bottom habitats (32, 33). The strong impact of humans on global reef fish biomass and trophic control illustrates clearly that human activity has become a pervasive force of marine nature.

All fishes do not contribute equally to the ecosystem service of fish production for human consumption. Thus, evaluating the role of biodiversity in providing this service requires focusing more specifically on preferred targets of fishers. Although many types of fishes are harvested as availability declines, fishers generally and

preferentially target large individuals, which also include top carnivores (28). Our data corroborate this behavior, showing that human impacts are strongest on large fishes (>35 cm) (SI Appendix, Fig. S3) and on top and benthic carnivores (Fig. 3). Importantly, biodiversity remains among the strongest predictor of biomass for the largest fishes (SI Appendix, Fig. S3) and for top carnivores (Fig. 3), rivaling or surpassing the effect of temperature at the global scale. In the tropics, biodiversity and human impacts were in fact the only significant predictors of large fish biomass (SI Appendix, Fig. S3D). These effect sizes (partial regression coefficients) account statistically for other predictors in the model, and therefore quantify the effect of biodiversity at a given level of human impact (e.g., harvest). Thus, our global analysis provides strong evidence that maintaining biological diversity enhances the ecosystem service of high-value harvestable fish production.

A frontier in global-change research is understanding how different stressors interact. The link between biodiversity and biomass raises the question of how biodiversity affects responses of fish biomass to ongoing climate change and human impacts. Because biodiversity is strongly controlled by temperature, changing climate is expected to reorganize marine communities, as is already happening (34–36). Our results show that this reorganization has important consequences for fish biomass production because higher diversity buffers fish biomass against expected direct effects of climate. First, although climate variability (temperature range) reduced fish biomass on average, this effect was halved in the richest communities (Fig. 2 G and H and SI Appendix, Table S2), possibly because species-rich communities harbor fishes with a range in thermal niches. The stronger decline in low-richness fish communities is not explained by lower coral cover at those sites (SI Appendix), and remained significant after excluding sites with sea-surface temperature (SST) range >9 °C, beyond the range of most high-richness sites. Second, diverse assemblages had higher mean biomass at higher temperatures (Fig. 2 E and F). Specifically, in low-richness communities, biomass had a hump-shaped relationship to temperature

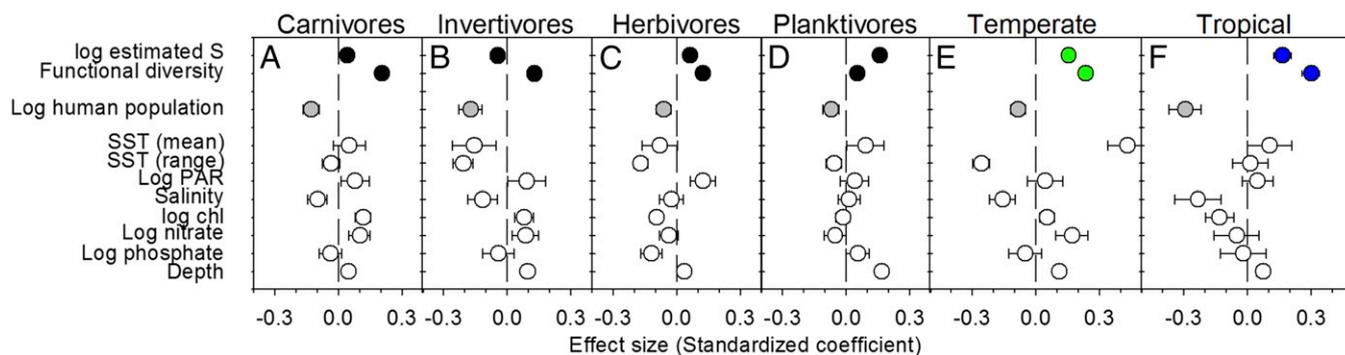


Fig. 3. Relative influence of biodiversity and environmental factors on log biomass of reef fishes by trophic level (A–D) and latitudinal zone (E and F). Effect sizes are standardized partial regression coefficients (β) from hierarchical linear models estimated separately for each case. Carnivores, top carnivores; invertivores, benthic carnivores; PAR, photosynthetically active radiation.

(Akaike Information Criterion confirmed that the quadratic fit was better than linear), increasing over the low range and declining again at the highest temperatures, whereas in high-richness communities fish biomass showed a weaker, linear increase with temperature (Fig. 2 E and F). In short, diversity tends to stabilize fish biomass production against rising and more variable temperatures. This finding suggests that the buffering capacity of biodiversity against climate variability may be a general phenomenon because it has also been documented in grassland plants (37).

Tropical ecosystems were especially sensitive to human impacts (Fig. 3F) and are considered highly vulnerable to warming-induced reduction in species richness because of strongest warming in tropical (and polar) regions and because many tropical species are near their upper thermal tolerance limits (19, 38). Our analysis suggests, however, that vulnerability of fish biomass to warming should be buffered in tropical communities as a result of their high diversity, which provides resilience to both increasing mean temperatures and increasing climate variability (Fig. 2 E–H and *SI Appendix, Table S2*). To explore more broadly the sensitivity of marine ecosystems to biodiversity loss, we obtained separate estimates of the dependence of biomass on richness for each of the 68 ecoregions for which estimates could be reliably obtained (39). Fish biomass was most sensitive to changing fish diversity at cooler, nutrient-rich sites also characterized by low richness and abundance (Fig. 4). The relative importance of these influences is difficult to disentangle because they tend to occur together. However, the explanation suggested by theory and prior empirical results is that the naturally low species richness at cooler sites results in low functional redundancy. Thus, at cooler, less diverse sites species fill more unique roles on average (40) and loss of a single species reduces biomass production more than it does at richer sites, where the remaining ecologically similar species can compensate for that loss (41). This finding implies that high-latitude marine ecosystems are especially ecologically vulnerable to climate change, due not only to higher projected invasion rates (19), but also to stronger impacts of species loss on production (Fig. 4) and stronger trophic cascades (31), compared with lower latitudes.

Although high diversity thus appears to buffer reef fish communities against climate change, diversity provides no such benefit to other impacts of human population. A previous analysis reported a negative interaction between (trophic) diversity and human population density for tropical reef fish biomass (23). In our more geographically comprehensive analysis, we found no interaction between human density and either species richness or multivariate functional diversity (*SI Appendix, Table S2*). However, fishing pressure and high temperatures act synergistically to increase vulnerability of coral reef fishes (42), potentially explaining our finding of greater sensitivity of reef fish biomass to human impacts in the tropics (Fig. 3). Moreover, many tropical fishes and reef corals appear to be living near the upper limits of their thermal ranges (38, 43). Most forecasts predict widespread loss of coral habitat with warming ocean temperature over the coming century, which will

likely have serious negative consequences for associated reef fishes (44). These considerations illustrate that biodiversity can interact differently with different stressors and underscore the importance of reducing overfishing and conserving habitat, including coral reefs, to maintain marine biodiversity and ecosystem services.

In summary, our analysis of global, fishery-independent data provides a uniquely powerful test of the long-debated questions of whether biodiversity promotes greater production and stability in nature, how important those biodiversity effects are relative to other drivers, and how they interact. We find that biodiversity is equally and often more important than water quality, nutrient supply, and human influence in controlling the global distribution of reef fish biomass, and that more diverse fish communities are more resilient to impacts of changing climate. Moreover, both species richness and functional trait diversity contributed roughly equally to fish biomass globally, generalizing local inferences that reef fish trophic interactions (45, 46) and functional diversity (47–49) are key mediators of the community structure and resilience of coral reef ecosystems. Because reef fish biomass provides an important protein source for many people, particularly in the developing world, our results suggest that management to sustain reef fish diversity, of both species and functional types, will also promote higher productivity of fish biomass and higher resilience of that ecosystem service in the face of rising and more variable temperatures.

Materials and Methods

Reef Life Survey. Standardized quantitative censuses of reef fishes were undertaken by trained recreational SCUBA divers on shallow hard substrate habitats worldwide through the Reef Life Survey program. Data came from 4,556 transects at 1,844 sites, from 55°S to 78°N latitude, and 74 ecoregions and 11 realms (39). Details of fish census methods, data quality, and diver training are in refs. 21, 40, and 50, and an online methods manual (reeflifesurvey.com). Fish counts per 500-m² transect (2 × 250-m² blocks) and size estimates were converted to biomass estimates using species-specific length–weight relationships from Fishbase (www.fishbase.org). Where length–weight relationships were described in Fishbase in terms of standard or fork length, equations in Fishbase allowed conversion to total length. Bias in divers' perception of fish size underwater was corrected using empirical calibrations (51). Length–weight coefficients from similar-shaped close relatives were used for species whose length–weight relationships were not available in Fishbase.

Selection of Variables Used in Models. As the primary response variable in all of our analyses, we focused on fish biomass rather than productivity because productivity is estimated from biomass and temperature, and is thus a more derived variable. The inclusion of temperature in the equation to estimate productivity also precludes a rigorous test of the effect of temperature on productivity. Biomass is a logical metric of many ecosystem functions performed by fishes because it is tightly linked to many components of metabolism and productivity (23).

From the diver surveys we computed two estimates of fish diversity per transect: species density (richness) and functional trait diversity. An inherent

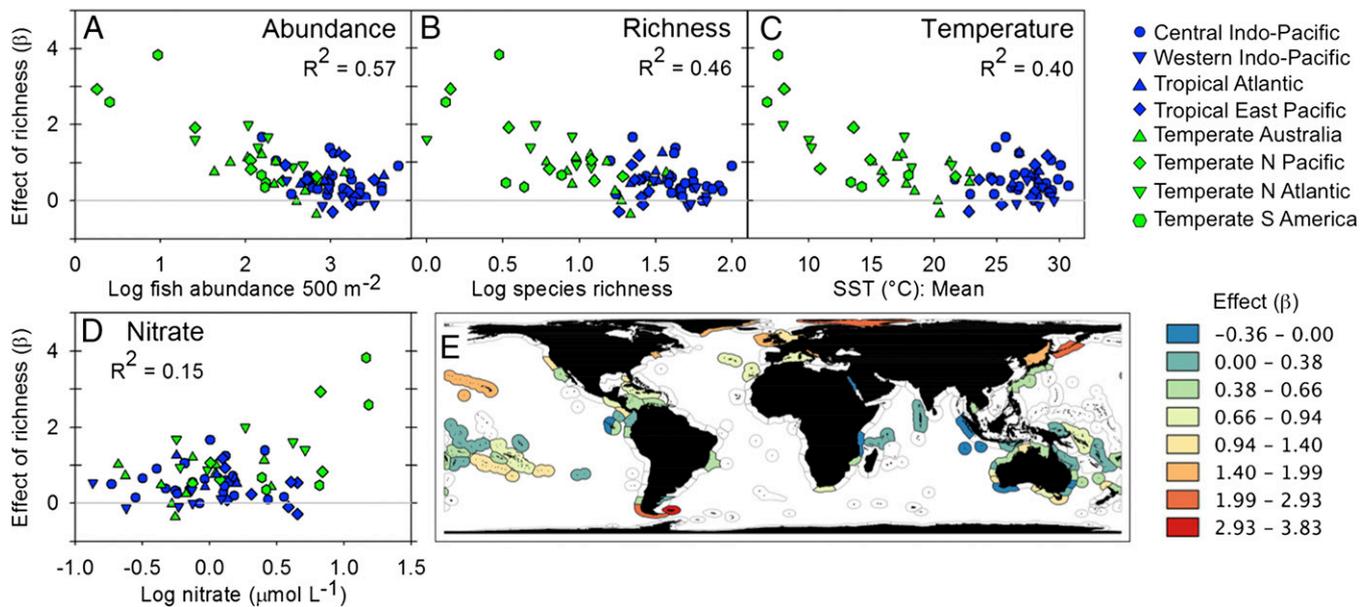


Fig. 4. Variation in the effect of species richness on biomass as a function of (A–D) environmental drivers and (E) geography. Shown are standardized partial regression coefficients (β) from the hierarchical model, with coefficients estimated separately by ecoregion. $P < 0.001$ for all relationships.

challenge to estimating biodiversity effects on biomass from observational data is the inherent positive correlation between estimated species richness and the number of individuals sampled, obscuring the direction of causality between abundance (or biomass) and richness. We derived estimates of species richness that account for this dependency using fixed-coverage subsampling (52). This approach first computes a rarefaction curve for a given survey by randomly sampling individuals from the survey and calculating for each such subsample the probability that adding a new individual will add a new species; this then allows, by rarefaction (of high-richness samples) or extrapolation (of low-richness samples) a measure of sample completeness: that is, the proportion of the total number of individuals in the community that belong to species represented in the survey (52). Once this process is completed, survey richness is compared at a common (fixed) value of coverage that can be estimated reliably from all samples in the dataset. We used a value of 99% coverage (completeness), meaning that for any survey a new individual fish added to a survey would have a 99% probability of belonging to a species already represented on the survey. This criterion was met by 97% of the surveys in our dataset; the remaining surveys were discarded from the analysis either because they sampled too few individuals or too many individuals of the same species (e.g., a large school of one species) to construct a reliable rarefaction curve. By accounting for the dependence of richness on sample size, the fixed-coverage estimate of richness minimizes the possibility that observed correlations between richness and biomass result simply from larger samples (higher fish densities) capturing more species. This coverage-based estimate of richness yields conservative estimates of the importance of diversity to biomass; fitting the same models with raw number of species recorded per transect produced substantially higher partial coefficients for effect of richness on biomass (SI Appendix, Table S1).

Second, we estimated functional diversity based on data on eight traits and using Rao's quadratic entropy (Q). Rao's Q is not constrained to increase with increasing richness (53), and thus can be treated as an independent predictor of diversity in our analyses. Functional diversity was further transformed by $1/(1 - Q)$ to express it in comparable units to species richness: that is, the effective number of functionally unique species in the sample (54). The eight traits used to calculate functional diversity (SI Appendix, Table S3) came from the database used by Stuart-Smith et al. (40); details of trait assignment and values are provided in that report. Traits were chosen to encompass attributes known to influence functional roles in a fish assemblage, including life history, trophic position, behavior, and habitat associations (SI Appendix, Fig. S5B).

We assembled data on 25 environmental and human-impact variables taken from the Bio-ORACLE dataset (55), a comprehensive, uniform, high-resolution global dataset of geophysical, biotic, and climate rasters. Bio-ORACLE data on SST, photosynthetically active radiation, and surface chlorophyll ($\text{chl } a$) were remotely sensed, taken from monthly level 3 preprocessed data from the Aqua-MODIS and SeaWiFS satellites at a $\sim 9.2\text{-km}$ spatial resolution. Other

water-quality parameters, including dissolved nutrients, were spatially interpolated based on data from in situ surface measurements in the World Ocean Database 2009 (56). An index of human population was calculated by fitting a smoothly tapered surface to each settlement point on a glp00g world population density grid using the quadratic kernel function described by Silverman (57). Populations were screened for a density greater than 1,000 people per 0.04° cell and the search radius was set at 3.959° .

To reduce the list of predictor variables to a more manageable set, we first conducted a random forest analysis to identify those with the most explanatory power (SI Appendix, Fig. S2). Random forest analysis is a machine-learning technique that is insensitive to underlying distributions, collinearity, or interactions among variables, and thus is ideal for ranking closely related or interacting variables (58). Because random forests can be sensitive to overfitting, we pruned the forest to 100 trees based on visual assessment of change in mean-square error with increasing number of trees. We then selected 12 of the top variables to use as the starting point for linear modeling, choosing in decreasing order of explanatory power (percent change in mean-square error of the model based on random permutations of that variable), with the exception that we excluded variables describing local conditions, like algal cover and pollution because these had relatively few measured observations and were largely interpolated. We then subjected the chosen predictor variables to variance inflation factor analysis to assess collinearity. After removing the predictor with the highest value (minimum SST, variance inflation factor = 52.3), the remaining 11 variables had variance inflation factor values < 4 and were retained in the global model. The centering and scaling of predictors used to generate the final linear models and corresponding path coefficients should also alleviate the influence of collinear variables. The final list of predictors retained for model building included: log-estimated species richness, functional diversity, log human population index, mean annual SST, salinity, survey depth, log phosphate concentration, range in annual SST, log chlorophyll concentration, log photosynthetically active radiation, and log nitrate concentration.

Modeling Approach. We used two general approaches to analyze controls on global reef fish biomass. First, we evaluated controls on fish biomass using hierarchical linear models, including the 11 predictor variables that emerged from our variable selection process described above. Fish biomass was modeled at the site level, with the response variable being mean total biomass of fish per survey at a site; the random effect of site was nested within ecoregion and realm, and the intercept of estimated richness was allowed to vary among ecoregions. This model structure was used in separate analyses of fish biomass at the global level, in temperate versus tropical regions, by trophic level, and for large fish ($> 35\text{ cm}$) specifically.

Second, to obtain a more integrated picture of the direct and indirect influences on global fish biomass, we conducted confirmatory path analysis

based on piecewise fitting of component hierarchical linear mixed-effects models (59, 60). The global-path model was nearly saturated in the sense that the component model for each endogenous variable included paths from all exogenous variables plus remaining endogenous variables, with the proviso that the model was nonrecursive (i.e., with no reciprocal paths between the same variables). Thus, nitrate and phosphate were modeled as a function of all other abiotic variables plus human population; richness and functional diversity were modeled as a function of all abiotic variables plus human population, and biomass was modeled as a function of all 11 variables (Fig. 1 and *SI Appendix, Fig. S1*). The overall path model was evaluated using Shipley's test of directed separation (59), which yields a Fisher's C statistic that can be compared with a χ^2 -distribution. If the resulting P value is >0.05 , then the model can be said to adequately reproduce the hypothesized causal network.

To examine how the richness–biomass relationship varied geographically, we fit the richness–biomass relationship separately for each of the world's 68 marine ecoregions (39) for which we have sufficient survey data, using a hierarchical model and allowing the slope of the richness effect to vary by

ecoregion. We then extracted the slope estimates representing the richness–biomass relationships among ecoregions and plotted them as a function of sampling effort (number of surveys per ecoregion), ecoregion mean richness, and ecoregion environmental characteristics.

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1 **Supporting information: Appendix**

2 **Tests for robustness of the richness-biomass relationship.** Because our results are based on
3 observational data, establishing causality of the diversity-biomass relationship faces the
4 challenge that richness estimates depend inherently on sample size (number of individuals). We
5 took several measures to evaluate the importance of this effect and minimize it. Most
6 importantly, our estimates of species richness based on sample coverage (1) rigorously account
7 for this dependence, allowing comparisons among samples with different numbers of
8 individuals. To test whether any residual correlation between abundance and richness estimate
9 remained after this correction we conducted three additional analyses. First, we asked whether
10 the richness-biomass relationship was unduly influenced by small samples (surveys with few
11 fish). We created a new data subset by removing all surveys with fewer than 100 individual fish
12 observed, and reran the global analysis on this subset. Fitting the global hierarchical model to
13 this subset (3873 surveys of 4556 in the complete data set) produced slightly smaller estimates of
14 the effects of species richness (standardized $\beta = 0.172 \pm 0.034$) and functional diversity ($0.178 \pm$
15 0.023) on fish biomass, but these diversity components remained among the strongest predictors.
16 Removal of surveys with fewer than 500 individuals (leaving 2466 surveys) produced a slightly
17 larger estimate of the effect of species richness (0.200 ± 0.042) and a smaller estimate of
18 functional diversity (0.165 ± 0.030). For all of these estimates, $P < 0.001$.

19 A second analysis similarly supported the robustness of the richness effect on biomass.
20 Comparison of the slope of the richness-biomass relationship estimated separately for each
21 ecoregion showed a stronger relationship in ecoregions with fewer individuals but the effect of
22 estimated richness on biomass nevertheless remained positive even where mean abundance per
23 survey approached 10,000 individuals (Fig. 4a).

24 Third, we partially decoupled the influence of survey-level abundance on richness
25 estimates by using regional species pool size as the estimate of richness in predicting biomass.
26 As an estimate of species pool size we used the observed richness within the surrounding
27 ecoregion. Because the validity of this approach depends on a robust estimate of regional
28 richness, we restricted the analysis to a subset of ecoregions with at least 20 surveys each and
29 included only surveys with >50 individual fish. These criteria ensured that the estimated species
30 pool for each ecoregion in the analysis was based on a minimum of 1000 individuals (i.e.,
31 minima of 20 surveys x 50 individuals per survey). Applying these criteria produced a data
32 subset of 1374 surveys (of 4556 total) from 26 ecoregions (of 75 total). Fitting the global model
33 to this data subset produced a standardized estimate of the partial effect of log ecoregion richness
34 on log survey biomass of $\beta = 0.404 \pm 0.130$ ($P = 0.012$). Thus, the estimated effect of ecoregion-
35 level richness on biomass was even stronger than that based on survey-level richness, although
36 the P-value was larger due in part to the 70% reduction in sample size compared with the full
37 data set.

38 Finally, there is some evidence that the relationship between species richness and
39 biomass production differs among scales, with stronger relationships at the regional than local
40 scales (2, 3). To explore this possibility we fit parallel models (same set of predictor variables)
41 using survey data aggregated at site and ecoregion scales. Results were generally quite similar
42 among scales, qualitatively and quantitatively (Fig. 2a-d): fish biomass was affected similarly at
43 both scales by diversity, human population, temperature, and depth.

44 A different challenge in testing the diversity-biomass relationships with observational
45 data stems from the possibility that the relationship reflects a shared correlation with some
46 unmeasured variable. We tested for such spurious correlations in two ways. First, we tested

47 whether the diversity effect on biomass was robust to shared correlations by conducting a
48 random forest analysis with species richness, functional diversity, and 25 other predictors, and
49 found that (coverage-corrected) species richness and functional diversity were the top two
50 predictors (SI Appendix, Fig. S2). Second, our use of hierarchical mixed models accounted for
51 shared correlations by measuring environmental and human-impact variables as well as
52 unexplained spatial variation in biomass by including random terms for marine realm, province,
53 and ecoregion. For example, if a bivariate correlation between richness and biomass was actually
54 driven by effects of temperature on both, then including all three variables in a model should
55 return a strong partial effect of temperature on biomass with no partial effect of richness. As a
56 final check on the robustness of our model we tested whether our final selection of variables
57 influenced the estimated richness effect on biomass by refitting the global model with 0-8
58 environmental predictors (functional diversity was left out to simplify the model interpretation),
59 and each time calculated the partial effect of estimated richness. The number of other predictors
60 had almost no effect on the estimated effect of richness (SI Appendix, Fig. S5a). In summary,
61 one or both components of biodiversity were consistently strong predictors of fish community
62 biomass across latitudes, regions, and trophic levels in all our analyses.

63 Finally, diversity can be modeled as a predictor only for sites where fish are present. All
64 surveys used in our analyses recorded fish, but not all trophic groups and size classes were
65 present on all surveys. Therefore, analyses of specific trophic levels and of large fishes used only
66 subsets of the data. To check whether use of such subsets changed our estimates of the effects of
67 predictors, we fit a second set of models for each trophic level, and for large fishes, that excluded
68 diversity as predictors. This ensured that all surveys were included (even those with no
69 individuals of the group in question); the regression coefficients produced by these models (SI

70 Appendix, Figs. S3b, S6) can be interpreted as quantifying the importance of human population
71 and environmental drivers in influencing both presence/absence and abundance of the focal
72 group. The results show that exclusion of diversity in this way generally had little influence on
73 estimates of human and environmental drivers (compare SI Appendix, Figs. S3a,b, S6). The
74 exceptions were top carnivores and planktivores, which showed stronger forcing by temperature
75 when diversity was excluded (compare Figs. 3a,d; SI Appendix, S6a,d); this can be interpreted to
76 mean that top carnivores and planktivores were present primarily at warmer sites.

77

78 **Interactions of diversity with stressors.** We tested whether species richness stabilized reef fish
79 biomass against stressors by fitting separate models that included interactions of species richness
80 with rising temperature, temperature variability, or human impact (population index) (SI
81 Appendix, Table S2). To explore visually the findings (see Results) that high species richness
82 stabilized biomass against rising and variable temperatures, we divided the dataset into sites
83 below (low-richness) and above (high-richness) the median richness value, and fit separate
84 regressions of biomass against mean annual temperature (Fig. 2e,f) and annual temperature range
85 (Fig. 2g,h).

86 A possible alternative hypothesis for the steeper decline in biomass with temperature
87 range in low-richness communities is that sites with higher temperature variability have lower
88 coral cover, and therefore lower fish biomass. To explore this hypothesis we first fit the global
89 model described above with addition of log coral cover, using only tropical sites since coral is
90 absent or low at temperate sites. Log coral cover had no significant partial effect on fish biomass
91 ($\beta = 0. -0.041 \pm 0.039$, $P = 0.291$) when the other predictors were included in the model. We then
92 fit the same model with an interaction between log coral cover and temperature range, to test

93 whether higher temperature range and low coral cover might explain the difference in biomass
94 between low- and high-richness tropical sites. There was no significant interaction between log
95 coral cover and temperature range ($P = 0.660$). Nor was coral cover lower in more thermally
96 variable tropical environments ($P = 0.232$).

97

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106

107 **Table S1:** SEM coefficients, standard errors, and P-values for the hierarchical model fit
 108 separately for the global data set, temperate and tropical data sets, individual trophic levels, for
 109 large (> 35 cm) fishes, and using observed rather than estimated richness.

110

111 **Table S1a:** Standardized coefficients (scaled by mean and variance) from the global structural
 112 equation model including all fishes. Coefficients correspond to arrow widths in Figure 1a and
 113 Extended Data Figure 1.

Response	Predictor	Estimate	Standard error	P-value
Biomass	Functional diversity	0.230	0.019	0.000
Biomass	log ₁₀ (Estimated richness)	0.189	0.027	0.000
Biomass	Temperature (range)	-0.252	0.037	0.000
Biomass	Depth	0.101	0.015	0.000
Biomass	log ₁₀ (Population index)	-0.164	0.042	0.000
Biomass	Temperature (mean)	0.296	0.090	0.001
Biomass	Salinity	-0.117	0.057	0.041
Biomass	log ₁₀ (Chlorophyll)	0.043	0.033	0.198
Biomass	log ₁₀ (Nitrate)	0.028	0.053	0.589
Biomass	log ₁₀ (PAR)	-0.027	0.073	0.708
Biomass	log ₁₀ (Phosphate)	-0.001	0.058	0.985
Functional diversity	log ₁₀ (Estimated richness)	0.221	0.034	0.000
Functional diversity	Temperature (range)	0.263	0.047	0.000
Functional diversity	Temperature (mean)	0.494	0.133	0.000
Functional diversity	log ₁₀ (Nitrate)	-0.169	0.069	0.014
Functional diversity	log ₁₀ (Phosphate)	0.162	0.074	0.028
Functional diversity	Salinity	0.132	0.076	0.080
Functional diversity	log ₁₀ (Chlorophyll)	0.022	0.043	0.603
Functional diversity	log ₁₀ (Population index)	0.021	0.055	0.704

Functional diversity	Depth	0.005	0.019	0.779
Functional diversity	log ₁₀ (PAR)	0.021	0.094	0.823
log ₁₀ (Estimated richness)	Temperature (mean)	0.489	0.089	0.000
log ₁₀ (Estimated richness)	Temperature (range)	-0.143	0.033	0.000
log ₁₀ (Estimated richness)	log ₁₀ (Chlorophyll)	-0.092	0.030	0.002
log ₁₀ (Estimated richness)	log ₁₀ (Population index)	0.081	0.038	0.036
log ₁₀ (Estimated richness)	log ₁₀ (PAR)	-0.130	0.064	0.043
log ₁₀ (Estimated richness)	Depth	-0.020	0.014	0.159
log ₁₀ (Estimated richness)	Salinity	0.053	0.051	0.301
log ₁₀ (Estimated richness)	log ₁₀ (Phosphate)	-0.023	0.052	0.658
log ₁₀ (Estimated richness)	log ₁₀ (Nitrate)	-0.006	0.047	0.905
log ₁₀ (Chlorophyll)	Temperature (range)	0.348	0.026	0.000
log ₁₀ (Chlorophyll)	log ₁₀ (Population index)	0.198	0.036	0.000
log ₁₀ (Chlorophyll)	Salinity	-0.292	0.060	0.000
log ₁₀ (Chlorophyll)	Temperature (mean)	-0.367	0.085	0.000
log ₁₀ (Chlorophyll)	Depth	-0.036	0.010	0.001
log ₁₀ (Chlorophyll)	log ₁₀ (PAR)	0.185	0.059	0.002
log ₁₀ (Chlorophyll)	log ₁₀ (Phosphate)	0.141	0.046	0.002
log ₁₀ (Chlorophyll)	log ₁₀ (Nitrate)	0.089	0.041	0.031
log ₁₀ (Phosphate)	Salinity	-0.681	0.049	0.000
log ₁₀ (Phosphate)	Temperature (mean)	-0.853	0.067	0.000
log ₁₀ (Phosphate)	log ₁₀ (PAR)	-0.290	0.040	0.000
log ₁₀ (Phosphate)	Temperature (range)	-0.036	0.019	0.061
log ₁₀ (Phosphate)	log ₁₀ (Population index)	-0.035	0.027	0.197
log ₁₀ (Phosphate)	Depth	0.000	0.008	0.992
log ₁₀ (Nitrate)	log ₁₀ (PAR)	-0.884	0.044	0.000
log ₁₀ (Nitrate)	Salinity	-0.638	0.055	0.000

log ₁₀ (Nitrate)	Temperature (mean)	-0.842	0.075	0.000
log ₁₀ (Nitrate)	Temperature (range)	-0.156	0.021	0.000
log ₁₀ (Nitrate)	Depth	0.030	0.008	0.000
log ₁₀ (Nitrate)	log ₁₀ (Population index)	-0.086	0.030	0.004

114

115

116 **Table S1b:** Standardized coefficients (scaled by mean and variance) from the global model
 117 predicting fish biomass including only fishes >35 cm in total length.

Predictor	Estimate	Standard error	P-value
log ₁₀ (Estimated richness)	0.357	0.040	0.000
Depth	0.153	0.024	0.000
Functional diversity	0.142	0.029	0.000
log ₁₀ (Population index)	-0.280	0.057	0.000
Temperature (mean)	-0.250	0.108	0.021
Temperature (range)	-0.102	0.049	0.038
log ₁₀ (PAR)	0.144	0.089	0.106
Salinity	-0.091	0.071	0.204
log ₁₀ (Chlorophyll)	0.040	0.050	0.418
log ₁₀ (Nitrate)	0.045	0.068	0.507
log ₁₀ (Phosphate)	0.008	0.074	0.916

118

119

120 **Table S1c:** Standardized coefficients (scaled by mean and variance) from the global model
 121 predicting fish biomass including only temperate sites.

Predictor	Estimate	Standard error	P-value
Functional diversity	0.234	0.025	0.000
Temperature (range)	-0.257	0.038	0.000
log ₁₀ (Estimated richness)	0.155	0.029	0.000
Depth	0.110	0.021	0.000
Temperature (mean)	0.431	0.090	0.000
Salinity	-0.156	0.061	0.011
log ₁₀ (Population index)	-0.083	0.035	0.020
log ₁₀ (Nitrate)	0.170	0.075	0.023
log ₁₀ (Chlorophyll)	0.053	0.035	0.132
log ₁₀ (Phosphate)	-0.049	0.079	0.532
log ₁₀ (PAR)	0.044	0.083	0.597

122
 123

124 **Table S1d:** Standardized coefficients (scaled by mean and variance) from the global model
 125 predicting fish biomass including only tropical sites.

Predictor	Estimate	Standard error	P-value
Functional diversity	0.301	0.041	0.000
log ₁₀ (Estimated richness)	0.166	0.041	0.000
log ₁₀ (Population index)	-0.292	0.076	0.000
Depth	0.074	0.031	0.016
Salinity	-0.233	0.110	0.035
log ₁₀ (Chlorophyll)	-0.131	0.067	0.051
Temperature (mean)	0.105	0.104	0.313
log ₁₀ (PAR)	0.048	0.073	0.512
log ₁₀ (Nitrate)	-0.051	0.107	0.635
log ₁₀ (Phosphate)	-0.020	0.109	0.858
Temperature (range)	0.015	0.084	0.861

126

127

128 **Table S1e:** Standardized coefficients (scaled by mean and variance) from the global model
 129 predicting fish biomass including only top carnivores.

Predictor	Estimate	Standard error	P-value
Functional diversity	0.206	0.022	0.000
log ₁₀ (Population index)	-0.128	0.038	0.001
log ₁₀ (Chlorophyll)	0.118	0.036	0.001
Depth	0.047	0.017	0.007
Salinity	-0.098	0.045	0.032
log ₁₀ (Nitrate)	0.101	0.050	0.045
log ₁₀ (Estimated richness)	0.041	0.029	0.159
log ₁₀ (PAR)	0.080	0.066	0.230
Temperature (range)	-0.034	0.041	0.404
Temperature (mean)	0.052	0.077	0.495
log ₁₀ (Phosphate)	-0.036	0.054	0.502

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 131

132 **Table S1f:** Standardized coefficients (scaled by mean and variance) from the global model
 133 predicting fish biomass including only benthic carnivores.

Predictor	Estimate	Standard error	P-value
Functional diversity	0.128	0.024	0.000
Depth	0.096	0.020	0.000
Temperature (range)	-0.207	0.046	0.000
log ₁₀ (Population index)	-0.172	0.053	0.001
log ₁₀ (Chlorophyll)	0.081	0.043	0.060
Salinity	-0.115	0.070	0.100
Temperature (mean)	-0.155	0.104	0.135
log ₁₀ (Nitrate)	0.086	0.063	0.173
log ₁₀ (Estimated richness)	-0.044	0.034	0.188
log ₁₀ (PAR)	0.093	0.090	0.305
log ₁₀ (Phosphate)	-0.042	0.074	0.571

134
 135

136 **Table S1g:** Standardized coefficients (scaled by mean and variance) from the global model
 137 predicting fish biomass including only herbivores.

Predictor	Estimate	Standard error	P-value
Functional diversity	0.123	0.019	0.000
Temperature (range)	-0.168	0.034	0.000
log ₁₀ (Chlorophyll)	-0.095	0.031	0.002
Depth	0.037	0.014	0.008
log ₁₀ (Estimated richness)	0.063	0.024	0.010
log ₁₀ (Phosphate)	-0.118	0.050	0.018
log ₁₀ (PAR)	0.125	0.060	0.036
log ₁₀ (Population index)	-0.059	0.035	0.095
Temperature (mean)	-0.078	0.083	0.348
log ₁₀ (Nitrate)	-0.037	0.044	0.401
Salinity	-0.024	0.056	0.669

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 139

140 **Table S1h:** Standardized coefficients (scaled by mean and variance) from the global model
 141 predicting fish biomass including only planktivores.

Predictor	Estimate	Standard error	P-value
Depth	0.168	0.015	0.000
log ₁₀ (Estimated richness)	0.159	0.024	0.000
Functional diversity	0.053	0.018	0.003
log ₁₀ (Population index)	-0.070	0.038	0.063
Temperature (range)	-0.058	0.037	0.123
log ₁₀ (Nitrate)	-0.052	0.050	0.302
Temperature (mean)	0.090	0.088	0.305
log ₁₀ (Phosphate)	0.054	0.054	0.317
log ₁₀ (PAR)	0.039	0.068	0.566
log ₁₀ (Chlorophyll)	-0.015	0.034	0.662
Salinity	0.014	0.051	0.792

142
 143

144 **Table S1i:** Standardized coefficients (scaled by mean and variance) from the global model
 145 predicting fish biomass including only invertivores.

Predictor	Estimate	Standard error	P-value
Functional diversity	0.128	0.024	0.000
Depth	0.096	0.020	0.000
Temperature (range)	-0.207	0.046	0.000
log ₁₀ (Population index)	-0.172	0.053	0.001
log ₁₀ (Chlorophyll)	0.081	0.043	0.060
Salinity	-0.115	0.070	0.100
Temperature (mean)	-0.155	0.104	0.135
log ₁₀ (Nitrate)	0.086	0.063	0.173
log ₁₀ (Estimated richness)	-0.044	0.034	0.188
log ₁₀ (PAR)	0.093	0.090	0.305
log ₁₀ (Phosphate)	-0.042	0.074	0.571

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 147

148 **Table S1j:** Standardized coefficients (scaled by mean and variance) from the global model
 149 predicting fish biomass at the ecoregion level.

Predictor	Estimate	Standard error	P-value
log ₁₀ (Population index)	-0.192	0.054	0.001
Temperature (range)	-0.231	0.075	0.003
Functional diversity	0.168	0.064	0.012
log ₁₀ (Chlorophyll)	0.193	0.079	0.018
Depth	0.156	0.066	0.023
log ₁₀ (Estimated richness)	0.202	0.132	0.132
Temperature (mean)	0.154	0.136	0.264
log ₁₀ (Nitrate)	-0.061	0.095	0.521
log ₁₀ (Phosphate)	-0.063	0.101	0.535
Salinity	0.011	0.064	0.870
log ₁₀ (PAR)	-0.016	0.099	0.871

150

151 **Table S1k:** Standardized coefficients (scaled by mean and variance) from the global model
 152 predicting fish biomass at the site level using raw (observed) species richness.

Predictor	Estimate	Standard error	P-value
log ₁₀ (Observed richness)	0.7887	0.0331	0.0000
Depth	0.0933	0.0132	0.0000
Functional diversity	0.0910	0.0176	0.0000
Temperature (range)	-0.1665	0.0329	0.0000
log ₁₀ (Population index)	-0.1575	0.0385	0.0000
Temperature (mean)	-0.2238	0.0795	0.0050
Salinity	-0.1397	0.0519	0.0072
log ₁₀ (Chlorophyll)	0.0576	0.0295	0.0508
log ₁₀ (PAR)	0.0708	0.0643	0.2711
log ₁₀ (Phosphate)	-0.0214	0.0523	0.6830
log ₁₀ (Nitrate)	0.0116	0.0456	0.7995

153

154 **Table S2:** Effects of species richness on resistance of fish biomass to changing climate and
 155 human impacts. Cells show standardized partial regression coefficients of interactions between
 156 estimated richness and sea surface temperature (SST, mean and range) and log human population
 157 index from global hierarchical models of reef fish log biomass. Bold black terms indicate
 158 significant ($P < 0.05$) stabilizing effects on biomass, i.e., richness reduces the effect of the
 159 stressor. Gray terms are not significant at $P < 0.05$.

160

Response (biomass)	SST mean	SST range	population
all fish (global)	-0.127	0.128	0.014
all fish (temperate)	-0.158	0.075	-0.001
all fish tropical)	-0.031	0.030	0.030
top carnivores (global)	0.012	0.080	-0.022
top carnivores (temperate)	0.007	0.047	0.001
top carnivores (tropical)	-0.107	0.045	-0.050
large fish (global)	0.010	0.040	0.008
large fish (temperate)	0.003	0.000	0.034
large fish (tropical)	-0.093	0.040	-0.022

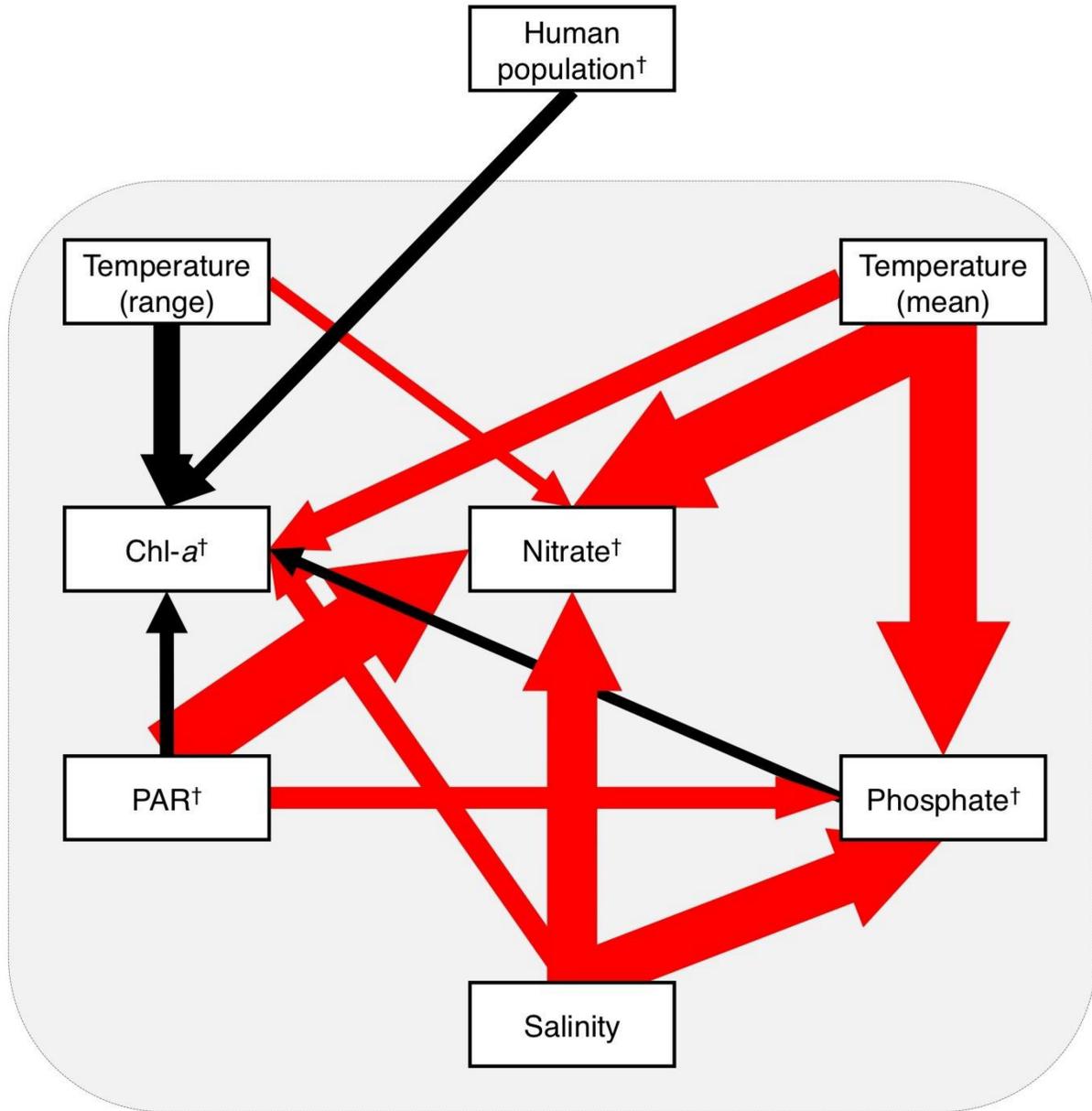
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162

163 **Table S3:** Functional traits used in the analysis of functional diversity (adopted from ref. 38).

Trait	Category	Units
Maximum length	Body size	Continuous (cm)
Trophic breadth	Trophic niche	Number of prey phyla consumed (1-8)
Trophic group	Trophic niche	Browsing herbivore, scraping herbivore, benthic invertivore, planktivore, higher carnivore
Water column position	Behavior	Benthic, demersal, site-attached pelagic, roaming pelagic
Gregariousness	Behavior	Singleton, paired to forming small schools, always schools
Diel activity pattern	Behavior	Nocturnal, diurnal
Preferred substrate	Habitat use	Hard substrate, soft sediment
Habitat complexity requirements	Habitat use	Low, medium, high

164



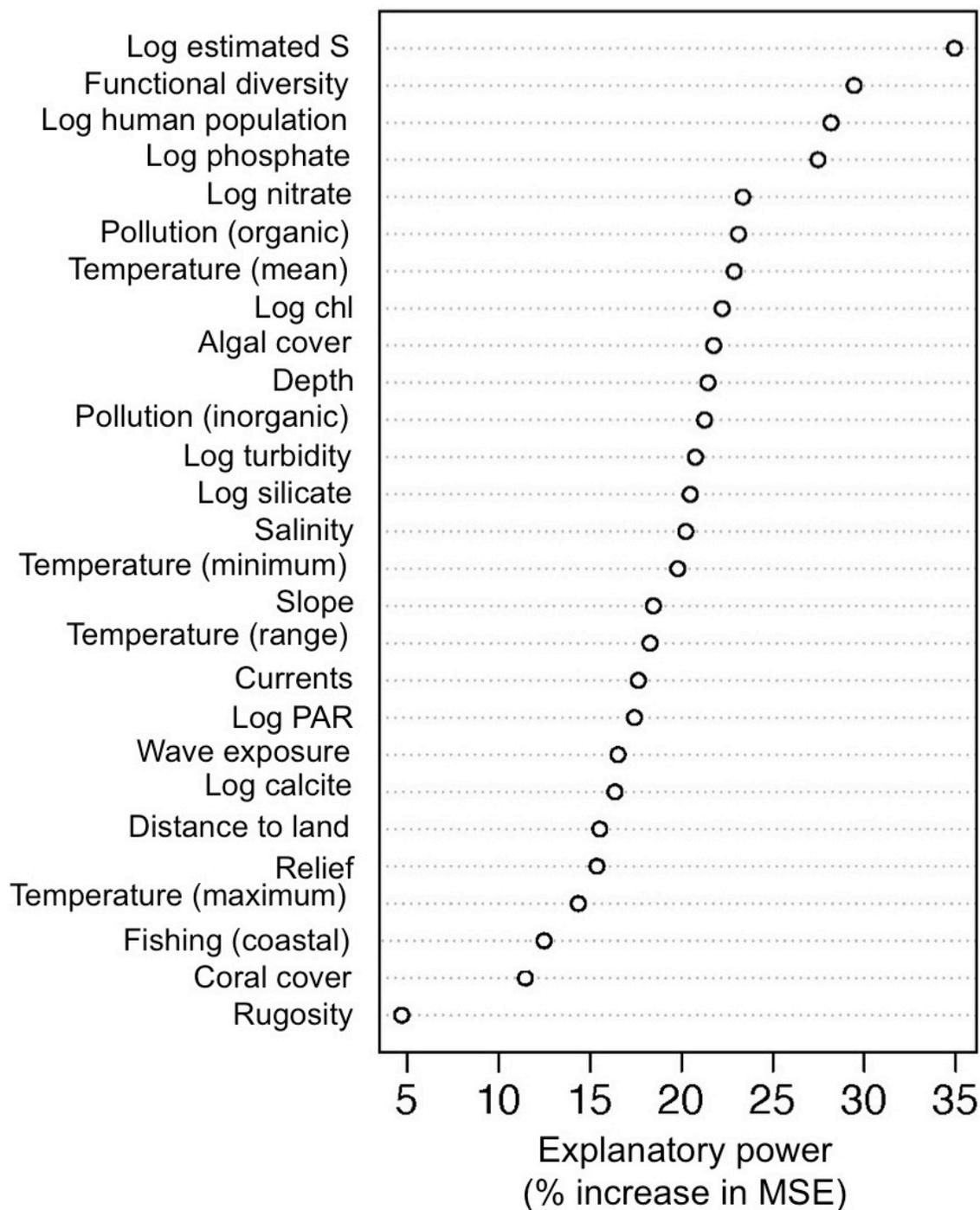
165

166 **Figure S1:** Path diagram of relationships among abiotic forcing factors, and human population,

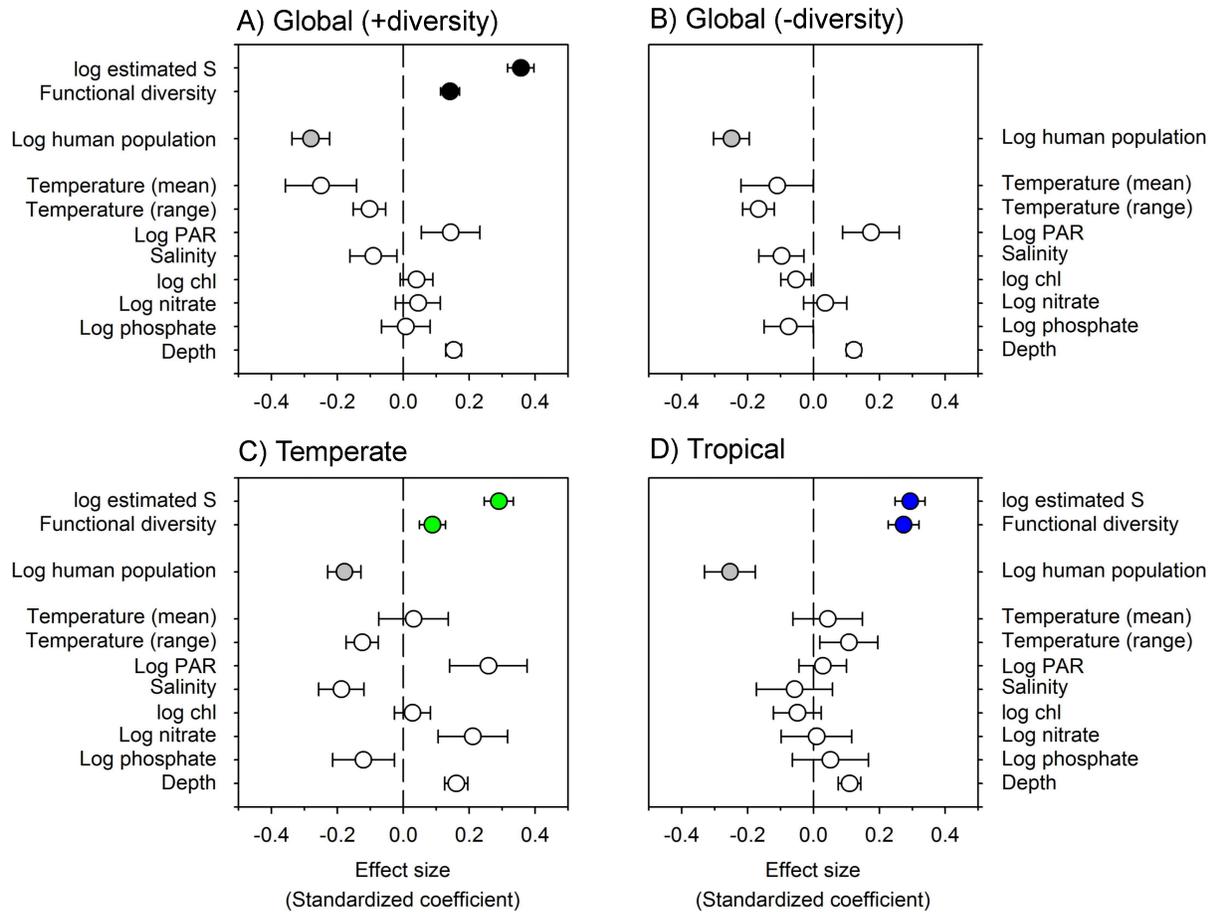
167 influencing fish diversity and biomass (Fig. 1). Paths of $\beta < 0.05$ are not shown. Gray box

168 surrounds abiotic variables plus phytoplankton (Chl-*a*). † = \log_{10} -transformed.

169



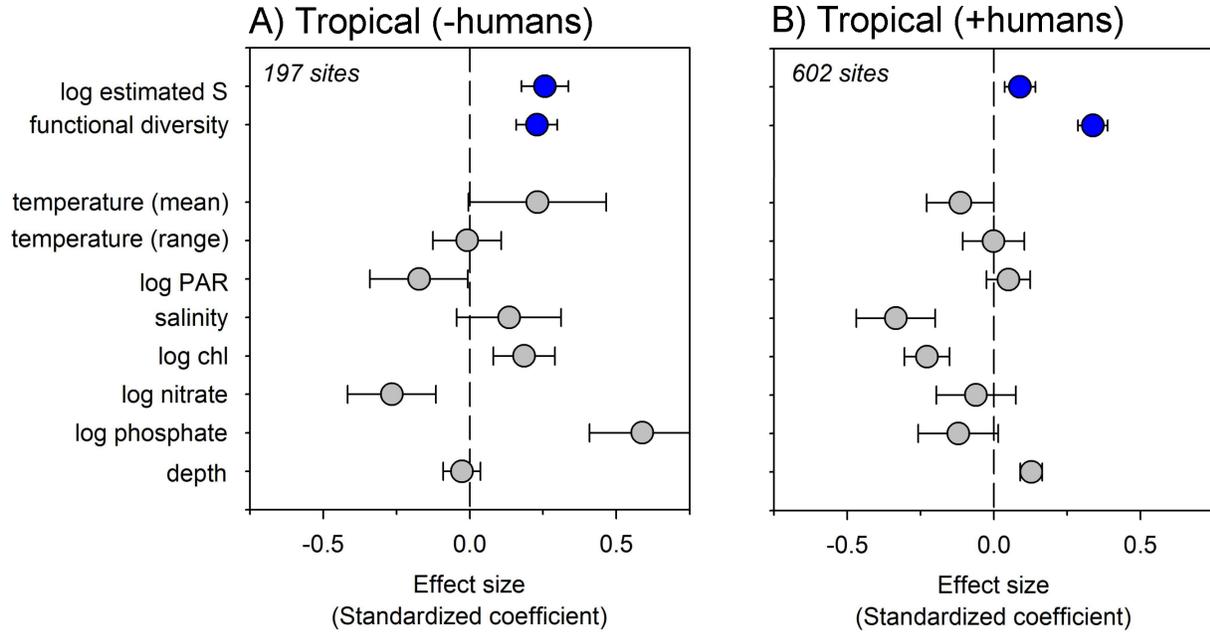
170
 171 **Figure S2:** Results of random forest analysis of the relative importance of two diversity
 172 components (functional diversity and estimated species richness), human population density, and
 173 25 environmental variables to global reef fish biomass.



174

175 **Figure S3:** Relative influence of biodiversity and environmental factors on log biomass of large
 176 (> 35 cm) reef fishes. Effect size estimated as standardized partial regression coefficients from
 177 hierarchical linear models at the global level (A) with and (B) without diversity as predictors, and
 178 separately for (C) temperate and (D) tropical sites.

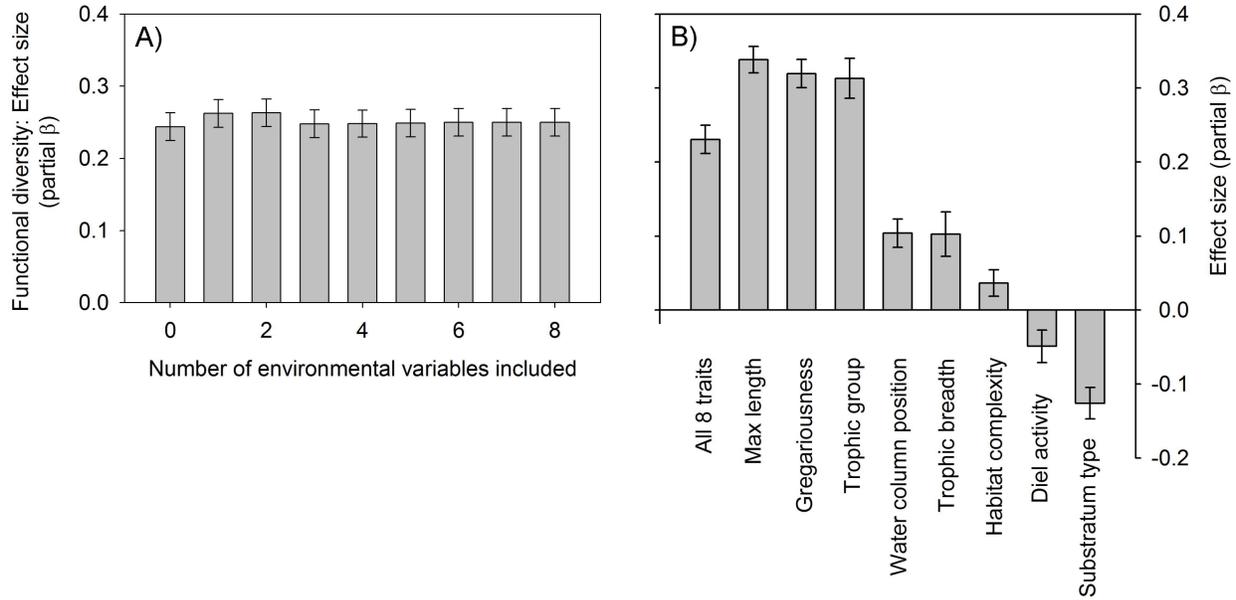
179



180

181 **Figure S4:** Relative influence of biodiversity and environmental factors on log biomass of
 182 tropical reef fishes in the (A) absence and (B) presence of human population. Effects sizes are
 183 standardized partial regression coefficients from hierarchical linear models estimated separately
 184 for tropical sites without vs with human influence.

185



186

187 **Figure S5:** Effects of model construction on robustness of estimated diversity effects on reef fish

188 community biomass. (A) Estimated effect of functional diversity in hierarchical mixed models

189 including functional diversity alone (0) versus 1-8 environmental variables, added in decreasing

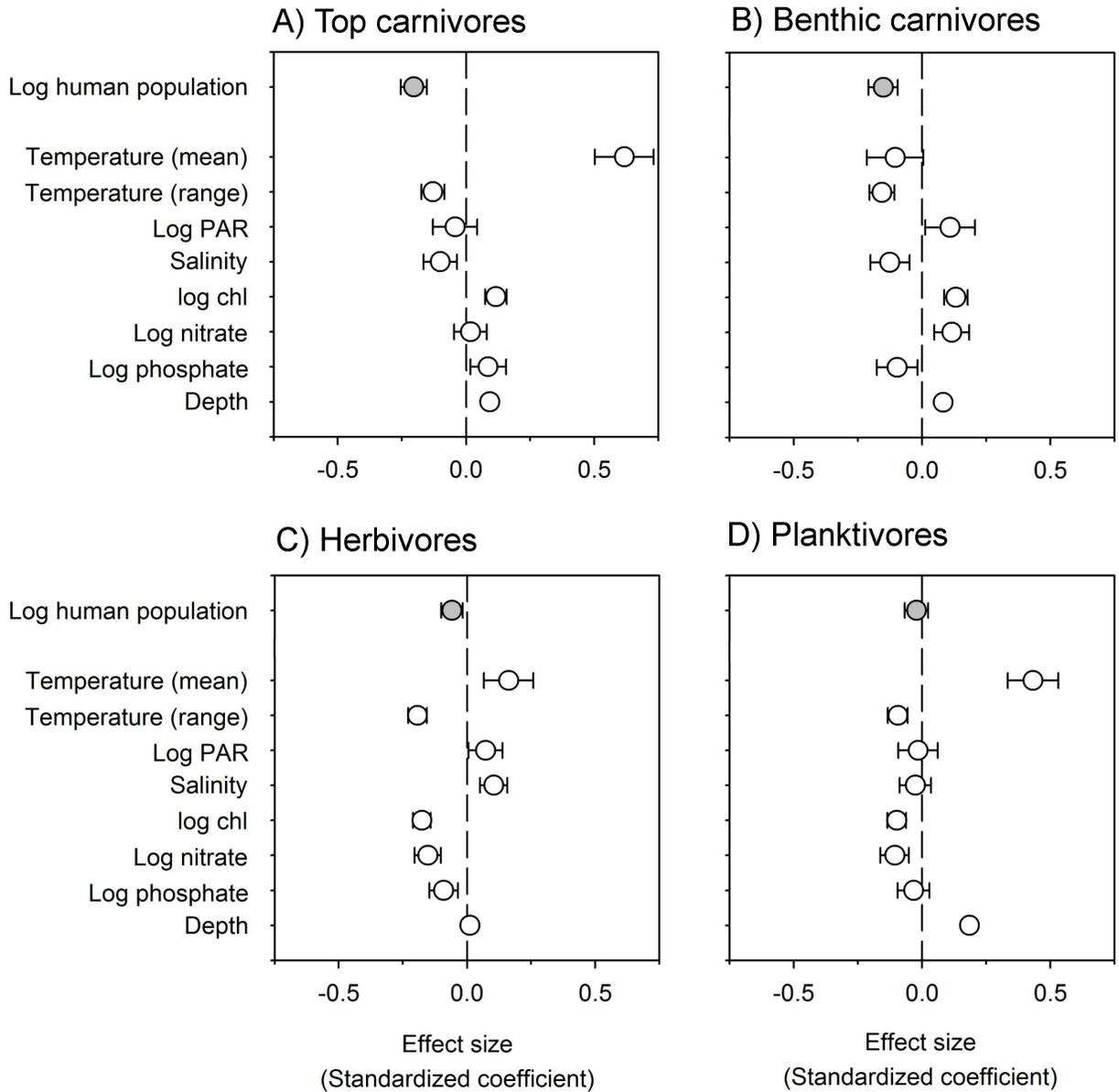
190 order of effect size. (B) Relative importance of component traits to estimated effect of functional

191 diversity on fish community biomass; effect size of functional diversity is calculated from all

192 eight traits versus from each individual component trait in the context of the global hierarchical

193 model.

194



195

196 **Figure S6:** Relative influence of human population and environmental factors on log biomass of

197 different trophic groups of reef fishes. Effects sizes are standardized partial regression

198 coefficients from hierarchical linear models estimated separately by trophic level. This analysis

199 omits diversity as a predictor in order to include all sites, including those with no fishes at that

200 trophic level.

201