**Title:** Biological trade-offs underlie coral reef ecosystem functioning

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**One Sentence Summary:** A global assessment reveals critical trade-offs among multiple ecosystem functions performed by coral reef fishes.

**Preserving coral reef functioning is a critical challenge of the 21st century. However, a lack of quantitative assessments of multiple functions across large spatial scales has hindered local and regional conservation efforts. We integrate empirically-parametrized bioenergetic models and global community surveys to quantify five key functions mediated by coral reef fishes. We show that functions exhibit critical trade-offs driven by varying community structures, such that no community can maximize all functions. Further, functions are locally dominated by few species, but worldwide, the identity of dominant species greatly varies; more than half of the 1,110 species in our dataset are functionally dominant on a local scale. Our results underline the need for a nuanced, local, and context-dependent approach to coral reef conservation that considers multiple functions beyond the effect of standing stock biomass.**

The flow of elements through biological communities fuels all ecosystems on earth1. Harmful human dominance disrupts the natural functioning in contemperory ecosystems2. Coral reefs represent a prime example of an ecosystem that is severely impacted by anthropogenic threats such as warming, and intensive fishing pressure3,4. Drastic declines in habitat quality and fish biomass have evoked serious concerns about the persistence of coral reef functioning5,6,7. However, our knowledge on process-based functions - fluxes of elements and energy - is still in its infancy and evaluations of coral reef functioning typically rely on static proxies, such as live coral cover, standing stock biomass of reef fishes, or measures of diversity8,9,10. This sparsity of quantification of functions constitutes a severe limitation to efficient management of coral reef ecosystem functioning.7

Coral reef fishes play an essential role in coral reef functioning, because they contribute to a high proportion of consumer biomass and therefore represent essential vectors of fluxes of carbon (C), nitrogen (N) and phosphorus (P) through storage and recycling.11–13 Ecosystem functions mediated by coral reef fishes include nutrient cycling, biomass production, herbivory , and piscivory (secondary consumption)7. While the high diversity of coral reef fishes has inspired many studies with a focus on ecosystem functioning, only a handful of studies have attempted to quantify functions as continuous fluxes7. Further, studies that do quantify functions mostly focused on biomass production14,15 or fish excretion12 and suggest that functions rely on community structure. An assessment of multiple functions on a large scale is currently lacking. Consequently, trade-offs among functions, their drivers, and their vulnerability to global stressors remain poorly understood in coral reef ecosystems7.

Here, we integrate biogeochemistry and community ecology to advance our understanding of the elemental fluxes that underpin reef fish functioning. Using empirically-collected species-specific data on basic organismal processes and Bayesian phylogenetic models, we parameterize individual-level bioenergetic models to estimate five key ecosystem functions: N excretion, P excretion, biomass production, herbivory, and piscivory. We apply these bioenergetic models to 9,118 reef fish transects across 585 sites worldwide (Table S1) to: (1) quantify community-level reef fish functions and their trade-offs, (2) extract the community- and species-level effects on these functions, and (3) gauge the vulnerability of reef fish functioning in the Anthropocene.

**Results**

By combining individual-level bioenergetic models and global underwater visual transect data, we quantified five key ecosystem functions mediated by coral reef fishes across the globe. We estimated the average functions per locality as well as a combined measure of multifunctionality by running a multivariate Bayesian regression model (Fig. 1, Table S2). Functions across localities show similar spatial patterns, yet a high level of function does not nescessarily ensure a high level of another function. For example, Trindade in the South Atlantic Ocean has high values for N excretion, P excretion, and piscivory, but average values for biomass production. A measure of multifunctionality thus does not appropriately represent the state of all functions.

Biomass is the most commonly employed indicator of coral reef functioning7,8, and we demonstrate a predictably strong relationship between fish biomass and all five functions by running multivariate mixed effect Bayesian model (Fig. 1). Specifically, the effects of the log-transformed biomass on log-transformed functions were 0.932 (95%CI: 0.929; 0.934), 1.051 (1.047; 1.056), 0.771 (0.764; 0.780), 0.940 (0.923; 0.957), and 0.668 (0.635; 0.702) for N excretion, P excretion, production, herbivory, and piscivory, respectively. We also incorporated sea surface temperature (sst) because it affects the metabolic and growth rates of fishes, which scales up to the community16. We found positive effects of sst on N excretion, production, and herbivory, and negligible effects of sst on P excretion and piscivory (Table S3).

The above-mentioned multivariate model also allowed us to estimate the correlations between functions, independent of the effects of biomass and sst. Specifically, we estimated correlations between functions on three levels: the locality effects, the site effects, and the residual variations (Fig. 2, fig. S1). The correlations mostly overlapped across the three levels for a given pair of functions. We found consistently negative trade-offs between P excretion and N excretion, P excretion and biomass production. Further, there were slightly weaker negative correlations between piscivory and N excretion and between piscivory and herbivory. As a consequence of the negative correlations, a fish community cannot have high values for all functions simultaneously.

To explore what drives the residual variation and trade-offs of functions beyond the effects of biomass and sst, we conducted a multivariate Bayesian mixed effect model by adding ten variables that describe the community structure: species richness and the median, lower, and upper 95% quantiles of size, immaturity, and trophic level of the individuals inside a community. We found that the community structure drives the observed trade-offs (Fig. 3; Table S4).

We then questioned if functions tend to be driven by specific species across sites. We quantified the degree of dominance inside each community on the site-level and found that functions are on average characterized by a high level of dominance, i.e. in most communities, a small proportion of species perform most of a function (Fig. 4a). As a comparison, we simulated random communities ranging from 5 to 50 species which yielded an average of 0.506. We also calculated the proportion of species that is dominant in at least one transect (i.e. species that contribute more than a community in which each species contributes equally). We found that most species play a dominant role, and 70% of all species contributed disproportionally to a function in at least one community (Fig. 4b). Finally, we investigated how often species are dominant across their range and found that very few species are dominant throughout their range (Fig. 4c). Together, this means that functions inside communities tend to be driven by few dominant species, but that the identity of these dominant species varies highly across communities.

**Discussion**

By quantifying five key functions mediated by coral reef fishes, we demonstrate that ecosystem-wide functioning is mainly driven by fish biomass, yet biomass alone does not fully capture functional variability across communities. While biomass is one of the most commonly employed indicator of coral reef functioning7,8, our analyses suggests that biomass alone does not sufficiently characterize functioning. We demonstrate strong trade-offs among the five functions, independent of biomass. Using biomass as a proxy for functioning can therefore mask fundamental differences in critical community-level functions. Furthermore, for a given value of biomass, no reef can yield above average values across all five functions. While many reefs may stand out as hotspots for one function, none can maximize all functions simultaneously.

Fish community structures drive the observed trade-offs among functions which can be explained by organismal physiology and life-history traits of the individuals inside communities17,18. For example, we observed a clear trade-off between P excretion and biomass production which is largely driven by the age and trophic community structure. Communities dominated by fishes with high trophic levels are characterized high P excretion rates because predatory fishes have a P-rich diet12. In contrast, biomass production is high in communities dominated by fishes with low trophic levels because herbivores tend to have higher growth rates19. Moreover, communities dominated by mature fishes have high values of P excretion because growing fishes are more likely to retain P to form P-rich bones17,20. while communities dominated by immature fishes maximize biomass production. Furthermore, metabolic theory predicts that small-bodied individuals have higher mass-specific metabolic rates, leading to elevated consumption rates and disproportionate contributions to functions that rely on rapid energetic turnover such as herbivory, piscivory, production, and N excretion15,21,22.

Our results also reveal that functions consistently hinge on a few dominant species, but the identities of local, dominant species vary strongly across sites23. Locally, specific high-performing taxa may disproportionately impact rates of functioning at the community level due to high biomass or abundance24. Despite high species richness on coral reefs, researchers often report the existence of functionally-dominant “key species”25. While few high-performing taxa indeed dominate functioning in each site, there are no species that are dominant across their entire range. In addition, more than half of all species contributed disproportionally to a specific function in at least one site inside their range. There are thus no widespread key species to target for conservation, rather, the functional role and conservation priority of species should be investigated at a local scale.

Our global analysis of multiple functions suggests pathways in which human-induced shifts in reef fish community structure may impact coral reef ecosystems (Fig. 5). Fishing and climate-induced coral loss have caused declines in reef fish biomass and shifts in community structure26,27, and our findings suggest that these changes will have effects on ecosystem functioning. Intensive fishing and associated reductions in biomass of large fishes alters the size, age, and trophic structure of fish communities27. When accounting for the effect of biomass, these community shifts can enhance nitrogen excretion and production15, but negatively impact phosphorus excretion, herbivory, and piscivory. Further, declines in coral cover related to climate change are often associated with a shift toward herbivores, which may deter algal domination28. Simultaneously, herbivores have a minor contribution to P excretion12,17, so a shift to herbivore dominance and the subsequent decline of community-level P excretion may change the balance of nutrient cycling on coral reefs, potentially favoring algal growth in comparison with corals29.

Conserving biomass, diversity, and ecosystem functions are important objectives of most conservation initiatives8. While safeguarding fish biomass enhances functioning, the trade-offs between key functions reveal a critical challenge for coral reef conservation, where actions to enhance one function may negatively impact another. For example, the establishment of marine protected areas, which are one of the primary conservation tactics for coral reefs30. may protect herbivorous species and thus provide benefits for herbivory. However, marine protected areas do not protect reefs from the pervasive effects of climate change30, and community shifts towards herbivore domination may result in the decline of P excretion. Thus, measuring conservation success with biomass or solely one function (e.g. herbivory) can mask the collapse of other essential functions. It is necessary to gauge the state of reef ecosystems based on multiple, complementary, process-based functions, yet our comprehension of process-based functioning of coral reefs or what a “functional” coral reef really means is still in its infancy7. To appropriately manage coral reef functioning with respect to local needs and stressors, future studies should seek to establish functional baselines for global coral reefs. Until then, our study suggests that coral reef fish functions can be managed by enhancing standing stock biomass, protecting local key species, and promoting a balanced community structure.

Overall, using coral reef fishes, we demonstrate that the variability in processes that govern the elemental cycling presents an unrecognized challenge for protecting ecosystem functioning. Management strategies that call for the enhancement of coral reef functioning via an economic mindset (i.e. where higher functioning is better) are not feasible. Instead, conserving coral reef ecosystem functioning will require a more nuanced approach that considers processes that vary beyond the effect of standing stock biomass and are subject to variable, local trade-offs, drivers, and anthropogenic threats.

**References**

1. Welti, N. *et al.* Bridging food webs, ecosystem metabolism, and biogeochemistry using ecological stoichiometry theory. *Frontiers in Microbiology* **8**, 1298 (2017).

2. Ceballos, G. *et al.* Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Science Advances* **1**, 1–5 (2015).

3. Hughes, T. P. *et al.* Global warming and recurrent mass bleaching of corals. *Nature* **543**, 373–377 (2017).

4. Pauly, D. *et al.* Towards sustainability in world fisheries. vol. 418 689–695 (2002).

5. Bellwood, D. R., Streit, R. P., Brandl, S. J. & Tebbett, S. B. The meaning of the term ‘function’ in ecology: A coral reef perspective. vol. 33 948–961 (2019).

6. Williams, G. J. *et al.* Coral reef ecology in the Anthropocene. *Functional Ecology* **33**, 1014–1022 (2019).

7. Brandl, S. J. *et al.* Coral reef ecosystem functioning: Eight core processes and the role of biodiversity. *Frontiers in Ecology and the Environment* **17**, 445–454 (2019).

8. Cinner, J. E. *et al.* Meeting fisheries, ecosystem function, and biodiversity goals in a human-dominated world. *Science* **368**, 307–311 (2020).

9. Mouillot, D. *et al.* Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. *Proceedings of the National Academy of Sciences of the United States of America* **111**, 13757–62 (2014).

10. Mora, C. *et al.* Global Human Footprint on the Linkage between Biodiversity and Ecosystem Functioning in Reef Fishes. *PLoS Biology* **9**, e1000606 (2011).

11. McIntyre, P. B. *et al.* Fish distributions and nutrient cycling in streams: can fish create biogeochemical hotspots. *Ecology* **89**, 2335–2346 (2008).

12. Allgeier, J. E., Layman, C. A., Mumby, P. J. & Rosemond, A. D. Consistent nutrient storage and supply mediated by diverse fish communities in coral reef ecosystems. *Global Change Biology* **20**, 2459–2472 (2014).

13. Barneche, D. R. *et al.* Scaling metabolism from individuals to reef-fish communities at broad spatial scales. *Ecology Letters* **17**, 1067–1076 (2014).

14. Morais, R. A. & Bellwood, D. R. Pelagic Subsidies Underpin Fish Productivity on a Degraded Coral Reef. *Current Biology* **29**, 1521–1527.e6 (2019).

15. Morais, R. A., Connolly, S. R. & Bellwood, D. R. Human exploitation shapes productivity–biomass relationships on coral reefs. *Global Change Biology* **26**, 1295–1305 (2020).

16. Barneche, D. R. *et al.* Body size, reef area and temperature predict global reef-fish species richness across spatial scales. *Global Ecology and Biogeography* **28**, 315–327 (2019).

17. Schiettekatte, N. M. D. *et al.* Nutrient limitation, bioenergetics and stoichiometry: A new model to predict elemental fluxes mediated by fishes. *Functional Ecology* **34**, 1857–1869 (2020).

18. Schramski, J. R., Dell, A. I., Grady, J. M., Sibly, R. M. & Brown, J. H. Metabolic theory predicts whole-ecosystem properties. *Proceedings of the National Academy of Sciences* **112**, 2617–2622 (2015).

19. Morais, R. A. & Bellwood, D. R. Global drivers of reef fish growth. *Fish and Fisheries* **19**, 874–889 (2018).

20. Hood, J. M., Vanni, M. J. & Flecker, A. S. Nutrient recycling by two phosphorus-rich grazing catfish: The potential for phosphorus-limitation of fish growth. *Oecologia* **146**, 247–257 (2005).

21. Barneche, D. R. & Allen, A. P. The energetics of fish growth and how it constrains food-web trophic structure. *Ecology Letters* **21**, 836–844 (2018).

22. Brandl, S. J. *et al.* Demographic dynamics of the smallest marine vertebrates fuel coral reef ecosystem functioning. *Science* **364**, 1189–1192 (2019).

23. Lefcheck, J. S. *et al.* Tropical fish diversity enhances coral reef functioning across multiple scales. *Science Advances* **5**, (2019).

24. Topor, Z. M., Rasher, D. B., Duffy, J. E. & Brandl, S. J. Marine protected areas enhance coral reef functioning by promoting fish biodiversity. *Conservation Letters* **12**, e12638 (2019).

25. Bellwood, D. R., Hughes, T. P. & Hoey, A. S. Sleeping Functional Group Drives Coral-Reef Recovery. *Current Biology* **16**, 2434–2439 (2006).

26. Darling, E. S. & D’agata, S. Coral Reefs: Fishing for Sustainability. vol. 27 R65–R68 (2017).

27. Graham, N. A. J. *et al.* Human Disruption of Coral Reef Trophic Structure. *Current Biology* **27**, 231–236 (2017).

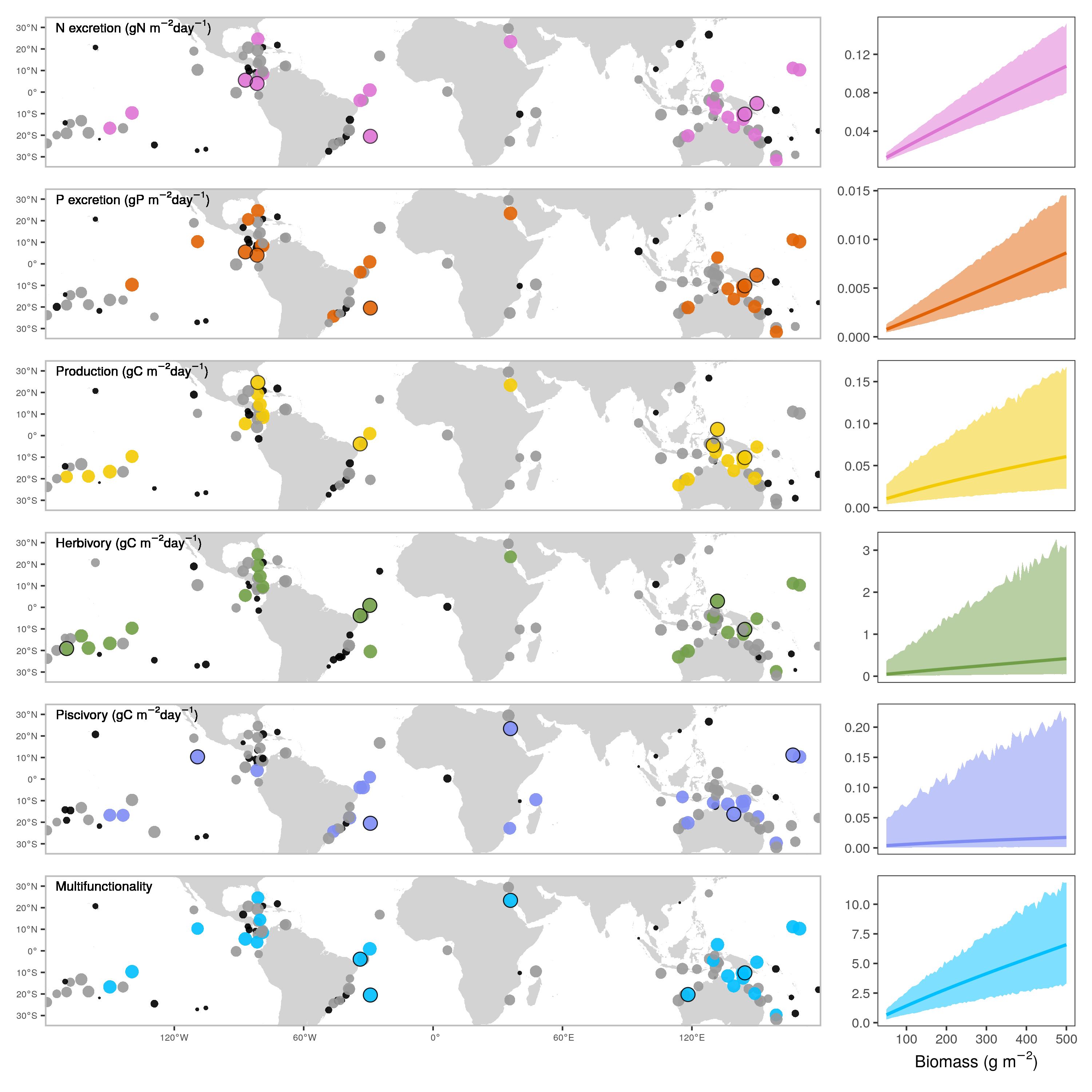
28. Graham, N. A. J. *et al.* Dynamic fragility of oceanic coral reef ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 8425–8429 (2006).

29. Burkepile, D. E. *et al.* Nutrient supply from fishes facilitates macroalgae and suppresses corals in a Caribbean coral reef ecosystem. *Scientific Reports* **3**, 1493 (2013).

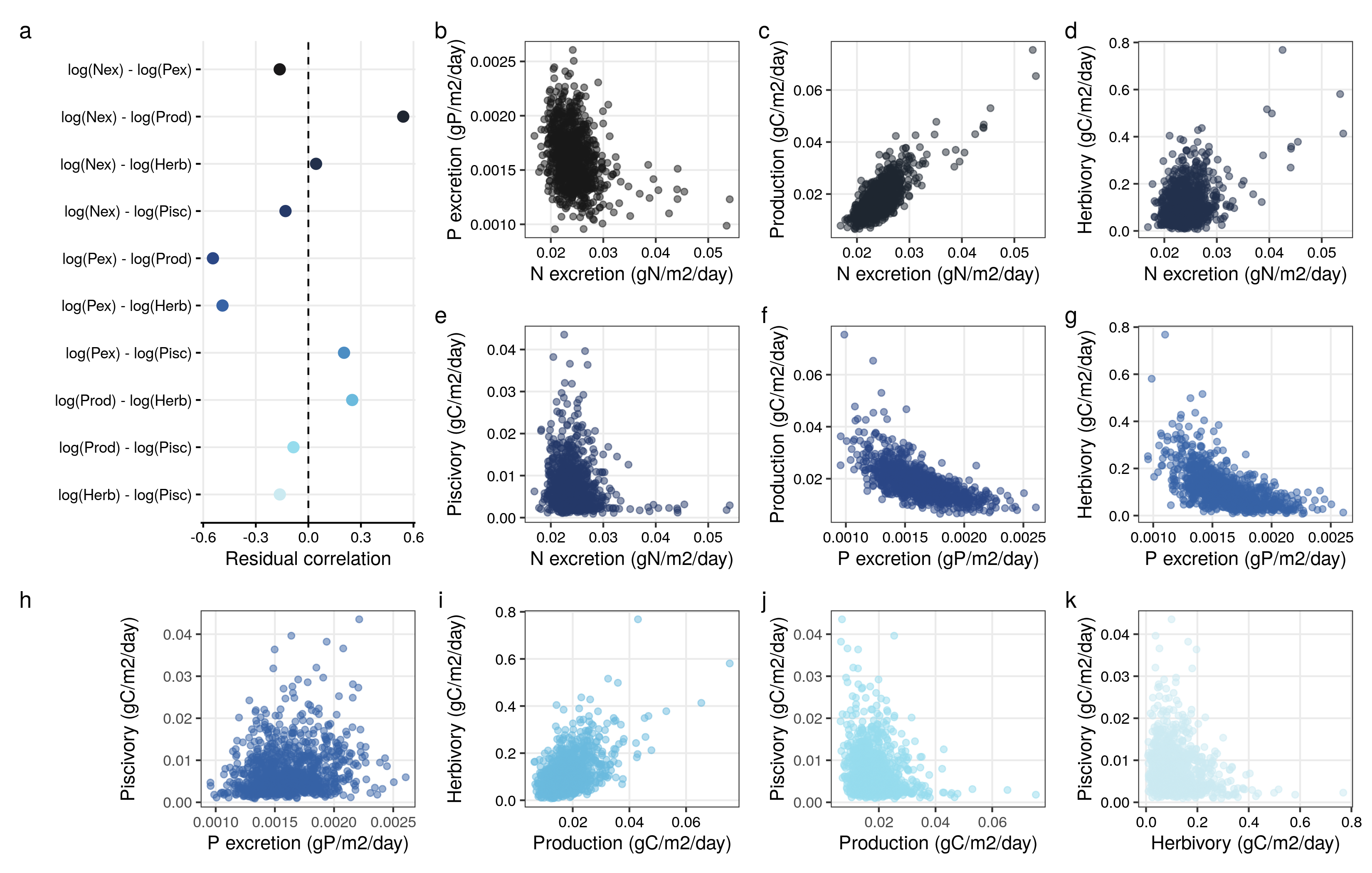
30. Graham, N. A. J. *et al.* Changing role of coral reef marine reserves in a warming climate. *Nature Communications* **11**, 1–8 (2020).

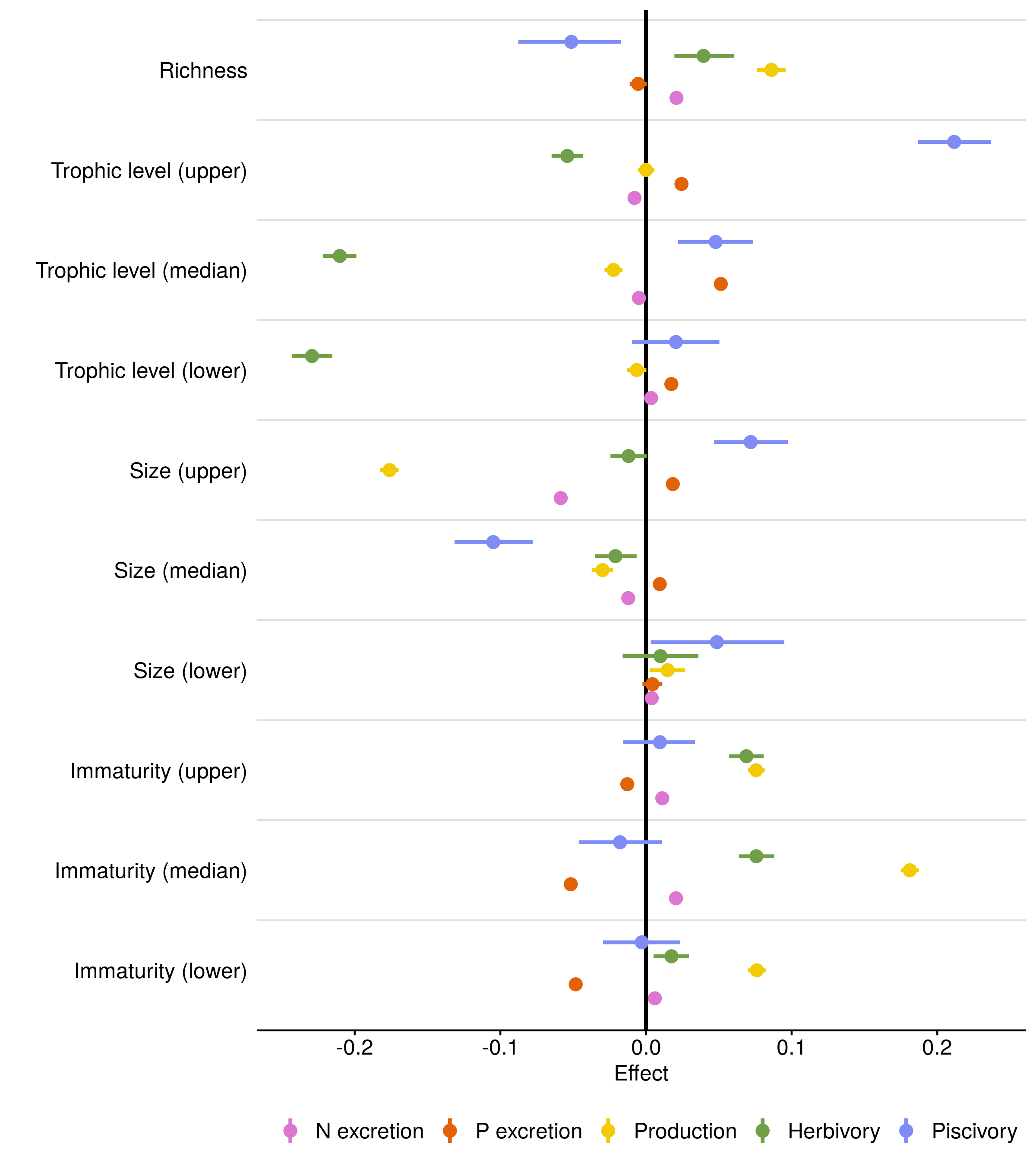
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**Figures**

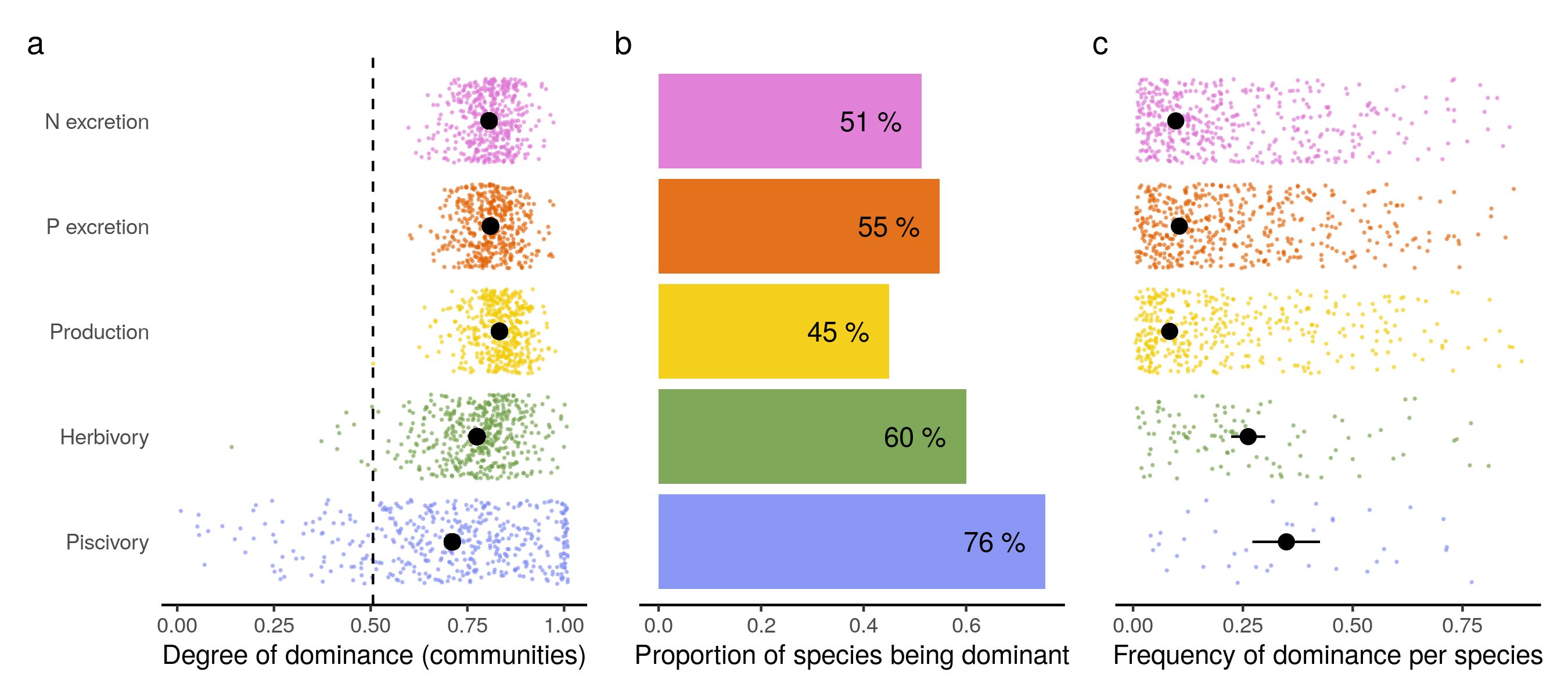


**Fig. 1: Maps of five key ecosystem functions and multifunctionality, and their relationships with biomass.** Left: Dots indicate localities of field surveys, with dot sizes representing the ranked values of the locality-level predictions of functions, and color scales showing categorical assignments (black = lower 25%, grey = 25-75%, color = >75%). Black circular outlines highlight the five localities with the highest values of each function. Multifunction represents the weighted average of the five standardized functions. Right: The predicted values for functions and multifunction with increasing biomass. The lines represent the average predicted value and the shaded areas show the 95% credible interval of he predictions.

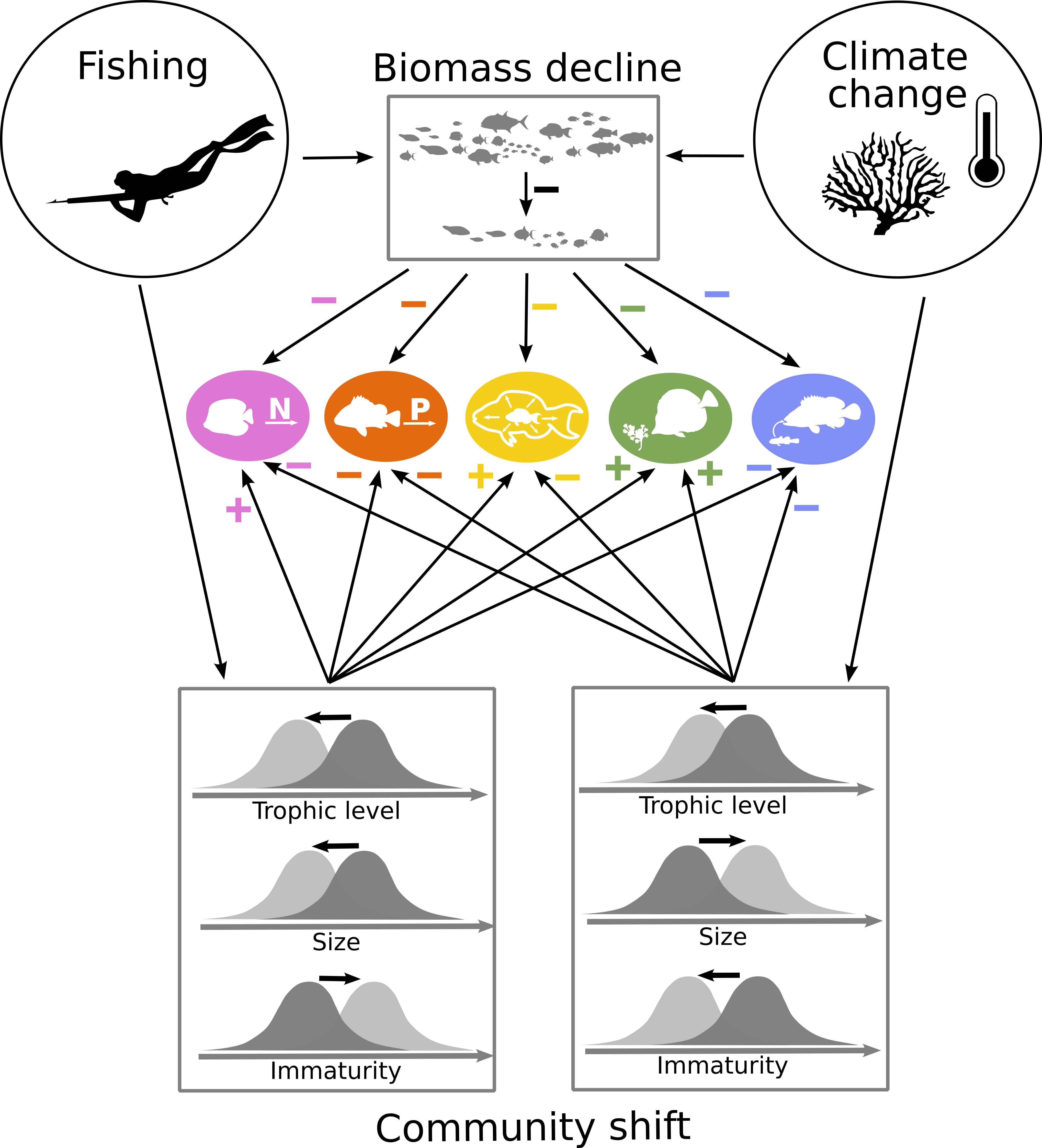
**Fig. 2: Correlations among five functions while accounting for biomass and sea surface temperature.** a: Modeled correlation coefficients of residual errors. Dots represent the average and lines represent the 95%CI. b-k: Scatter plots of the mean residual error of the functions to demonstrate the correlations.



**Fig. 3. Effects of ecological community variables on five functions.** Dots indicate fixed effect values from Bayesian linear regressions that examine effects of species richness, trophic level, size, and immaturity of fishes. To represent both the median and the spread of trophic level, size, and immaturity across individuals inside a community, we included lower and upper 95% quantile values of these three traits as community variables. All data were log-transformed and standardized to compare across functions and variables (see Table S2 for parameter values on non-standardized data). Dots represent the average effect size estimate, and horizontal lines indicate the 95% credible interval. Immaturity is defined as the derivative of the Von Bertalanffy growth model for a given size, and the higher this value, the younger the individual.



**Fig. 4: Local dominance in species contributions for five ecosystem functions on coral reefs.** a: The degree of dominance of communities for each function on the site-level. Colored dots represent the raw values and the black dots and lines display the mean and 95% credible intervals of the average degree of dominance, respectively. Degrees of dominance range between zero (all species contribute equally) and one (a single species is the sole contributor to a given function). The vertical dashed line shows the average of the degree of dominance of 1,000 randomly simulated communities. b: Bar plot showing the proportion of species that are dominant in at least one site relative to the total number of species. In the case of herbivory and piscivory, the total number of herbivores and piscivores, respectively, is used. c: Species-specific frequencies of dominance in each function across all sites, ranging from zero (species are never dominant) to one (dominant wherever present). A species is categorized as dominant in a community if its contribution to a function is higher than a scenario in which all species are equal (i.e. one divided by the number of species that contribute to the function).



**Fig. 5. Vulnerability of five critical functions to fishing and climate change-induced coral loss.** Conceptual scheme showing the potential ways in which fishing and climate change may affect functions through their effects on biomass and community structure.