CORAL REEF ECOLOGY

Functional trade-offs in fish communities

Combining pantropical fish community surveys with bioenergetic models has revealed the global distribution of reef-fish ecosystem functions, and that trade-offs linked to demographic and trophic structure prevent any community from maximizing all functions simultaneously.

Matthew McLean

Coral reefs are declining worldwide as they suffer the combined effects of stressors such as overfishing, pollution and global warming[1]. The resilience of coral reefs depends on the integrity of key ecosystem functions that promote coral growth and recovery[2], such as herbivory (in which fish and invertebrates remove reef algae)[2]. Consequently, scientists and managers have begun to focus more on assessing and protecting coral reef ecosystem functions, particularly those provided by fishes. However, measuring ecosystem functions directly is highly challenging, and most work has used simple proxies such as species richness or biomass to represent reef fish functions[3]. Although these metrics provide a useful approximation, they assume that ecosystem functions scale linearly with biomass and that all functions can be maximized simultaneously. Writing in *Nature Ecology & Evolution*, Schiettekatte et al.[4] used bioenergetic models to move beyond simple proxies and directly estimate five ecosystem functions performed by reef fishes: nitrogen excretion, phosphorous excretion, biomass production, herbivory and piscivory (consumption of other fishes). They found that all five functions were related to biomass and showed similar geographical patterns, but that no single location displayed high levels of all functions simultaneously. The work shows that allometric relationships with biomass, and biological trade-offs between functions, prevent the existence of 'perfectly' functioning reefs, even in the most pristine locations.

Coral reefs provide crucial ecosystem services to millions of people throughout the tropics, including food security, employment and shoreline protection[5]. The strength and stability of these services depends on the biological and geochemical processes that occur within ecosystems, collectively known as ecosystem functioning[6]. On coral reefs, fishes are a primary contributor to ecosystem functioning owing to their exceptional abundance, size and diversity[7]. Fishes regulate food webs through trophic interactions, particularly via top-down control on secondary and primary consumers[8]. For instance, piscivory can enhance diversity and stabilize food webs by limiting competitive exclusion among prey[9]. Fishes also help to regulate biogeochemical cycles by consuming, transporting and excreting nutrients, in turn shaping primary productivity[10]. Some reef-dwelling fishes feed near seagrasses at night but shelter near corals during the day, where they release transported nutrients and enhance coral growth[11]. Fishes also fuel coral-reef food webs and fisheries by producing new biomass through growth and reproduction[12]. Pelagic fishes can greatly enhance biological

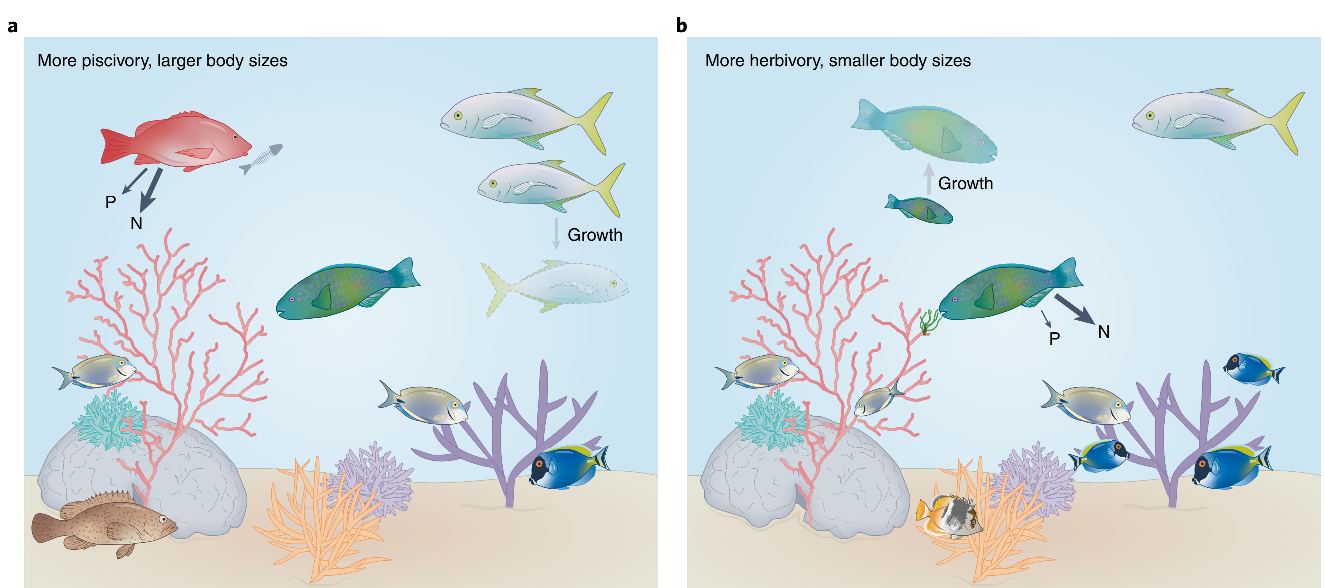

Fig. 1 | Contrasting patterns in ecosystem functions linked to differences in community structure. **a**, Schiettekatte and colleagues' findings[4] show that reef fish communities dominated by large predators have higher rates of piscivory and phosphorus excretion but lower nitrogen excretion and biomass production (due to slower mean growth rates), relative to those dominated by small herbivores. **b**, Reef fish communities dominated by small herbivores have higher herbivory, nitrogen excretion and biomass production, but lower piscivory and phosphorus excretion, relative to those dominated by large predators.

productivity on coral reefs by harnessing plankton-derived energy[13].

Although one might expect healthy reefs with high fish diversity and biomass to excel in all aspects of ecosystem functioning, Schiettekatte et al.[4] found strong negative relationships between several fish functions. The authors collected biological samples such as otoliths (ear bones), stomach contents, body stoichiometry and respiration rates for 50–100 species from reefs, mainly in French Polynesia. They then used Bayesian regression models with phylogenetic trees to extrapolate the 5 ecosystem functions for over 1,000 species, which allowed them to estimate community-level functions across 585 tropical sites. They found that phosphorus excretion was negatively correlated with herbivory, biomass production and nitrogen excretion, and piscivory was negatively correlated with herbivory and nitrogen excretion. Interestingly, these patterns were explained by the demographic and trophic structure of communities — properties that are overlooked by simple metrics such as biomass. Communities with higher mean trophic levels tend to have higher phosphorus excretion because predatory fishes consume phosphorus-rich diets (Fig. 1a). However, biomass production is often low on such reefs because larger individuals have slower growth rates. By contrast, communities with lower mean trophic levels are often dominated by small, rapidly growing herbivores, leading to higher biomass production and greater nitrogen excretion (Fig. 1b). The authors also found that phosphorus excretion was low in communities dominated by younger individuals. This, they explained, is because young, actively growing fishes retain phosphorus to build their skeletons, limiting excretion. These negative relationships reflect fundamental biological trade-offs that limit reefs from excelling at all functions simultaneously. These results also emphasize the role of fish community structure in determining overall ecosystem states. On coral reefs, primary productivity is dominated by rapidly growing benthic algae that are primarily limited by nitrogen and phosphorus availability[14]. The ratio of available nitrogen to phosphorus is also a major determinant of benthic algae composition[15]. Thus, the demographic and trophic structure of fish communities can directly shape benthic ecology and productivity through variation in nutrient cycling. This also reveals another pathway by which human impacts (particularly fishing) can indirectly modify ecosystem health and functioning.

Taking their study one step further, Schiettekatte et al.[4] examined the contribution of individual species to ecosystem functions, finding that functions were consistently driven by few dominant species that varied widely in identity among and within regions. Thus, managing fish communities to preserve ecosystem functioning will not be as simple as protecting a handful of key species. Instead, trait-based approaches may offer a potential avenue for linking management to ecosystem functioning. A recent study found that fish communities in similar environments displayed similar trait compositions, despite hosting entirely different species pools[16]. Uncovering functional traits that link species with important contributions to ecosystem functions could therefore help to identify functional groups with high conservation priority.

Schiettekatte and colleagues' work will open many doors for research into ecosystem functioning on coral reefs. Whereas previous studies have relied on easily observed proxies for ecosystem functions, these authors integrated field collections, laboratory analyses and statistical modelling to directly estimate five key ecosystem functions sustained by reef fishes. Not only do these findings highlight trade-offs in ecosystem functions, but they also reveal global hotspots of ecosystem functioning, as well as areas in need of functional restoration. Future work assessing the social and ecological conditions promoting ecosystem functioning will provide critical guidance for conservation planning. Future studies should also determine whether specific thresholds and configurations of ecosystem functions underpin reef resilience, which could provide 'functional baselines' for management. Yet, despite the advances made by Schiettekatte et al.[4], their ecosystem function estimates relied heavily on extrapolation, as the hard data used to build their bioenergetic models (such as tissue samples, stomach contents and metabolic rates) came from a limited number of species, families and locations. Thus, ongoing work is needed to build empirical databases of species-level ecosystem functions for coral reefs and other marine ecosystems. As we continue to prioritize ecosystem functioning and services in coral reef conservation, studies such as that of Schiettekatte et al.[4] will be invaluable for advancing our ability to quantify, assess and protect crucial ecosystem functions. ❐

Matthew McLean ✉
Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada.
✉*e-mail: mcleamj@gmail.com*

Published online: 04 April 2022
https://doi.org/10.1038/s41559-022-01706-1

References

1. Eddy, T. D. et al. *One Earth* **4**, 1278–1285 (2021).
2. Mumby, P. J. et al. *Science* **311**, 98–101 (2006).
3. Maire, E. et al. *Proc. R. Soc. Lond. B* **285**, 20181167 (2018).
4. Schiettekatte, N. M. D. et al. *Nat. Ecol. Evol.* https://doi.org/10.1038/s41559-022-0-01710-5 (2022).
5. Woodhead, A. J., Hicks, C. C., Norström, A. V., Williams, G. J. & Graham, N. A. J. *Funct. Ecol.* **33**, 1023–1034 (2019).
6. Naeem, S., Bunker, D. E., Hector, A., Loreau, M. & Perrings, C. *Biodiversity, Ecosystem Functioning, and Human Wellbeing: An Ecological and Economic Perspective* (Oxford Univ. Press, 2009).
7. Villéger, S., Brosse, S., Mouchet, M., Mouillot, D. & Vanni, M. *J. Aquat. Sci.* **79**, 783–801 (2017).
8. Bascompte, J., Melián, C. J. & Sala, E. *Proc. Natl Acad. Sci. USA* **102**, 5443–5447 (2005).
9. Houk, P. & Musburger, C. *Mar. Ecol. Prog. Ser.* **488**, 23–34 (2013).
10. Allgeier, J. E., Burkepile, D. E. & Layman, C. A. *Glob. Change Biol.* **23**, 2166–2178 (2017).
11. Meyer, J. L., Schultz, E. T. & Helfman, G. S. *Science* **220**, 1047–1049 (1983).
12. Brandl, S. J. et al. *Science* **364**, 1189–1192 (2019).
13. Morais, R. A., Siqueira, A. C., Smallhorn-West, P. F. & Bellwood, D. R. *PLoS Biol.* **19**, e3001435 (2021).
14. Larned, S. T. *Mar. Biol.* **132**, 409–421 (1998).
15. McClanahan, T. R., Carreiro-Silva, M. & DiLorenzo, M. *Mar. Pollut. Bull.* **54**, 1947–1957 (2007).
16. McLean, M. et al. *Proc. Natl Acad. Sci. USA* **118**, e2012318118 (2021).

Competing interests

The author declares no competing interests.