Dear Editor,

I am writing on behalf of my co-authors to submit our manuscript titled "**Shaped to kill: The evolution of siphonophore tentilla for specialized prey capture in the open ocean**" to be considered for publication in PNAS. All authors approve of the manuscript and its submission to PNAS. The manuscript is original work and has not been simultaneously submitted to any other journal. This work was uploaded as a pre-print to BioRxiv https://doi.org/10.1101/653345 earlier this year and benefited from community feedback.

We answer two closely related long-standing questions: Is predatory specialization a 'dead-end'? How does the morphology of a functionally specialized prey capture apparatus evolve with changes in dietary specialization and generalization? In addition, we inquire what evolutionary changes in organismal attributes lead to the realization of these shifts in ecological roles. We focus on siphonophores, a clade of oceanic predators with extremely diverse, highly specialized tentacle structures used exclusively for prey capture.

Our results strongly deviate from the expected trend of generalists evolving into specialists. Siphonophore generalists evolved from ancestral specialists, and all specialists evolved from ancestors specialized in a different prey type. We find strong evolutionary correlations between morphology and diet, significant support for a diet-driven evolutionary model, and significant shifts in the evolutionary rate correlation matrices across diets. These results show how the modular body plan of siphonophores can provide an escape from evolutionary constraints associated with specialization. This insight is key to our general understanding of the evolution of predation, indicating that the specialization trends observed in traditional bilaterian predators are a special case.

Our conclusions are supported by integrated analyses of new and previously published data. The major new data are a morphological characterization of the prey capture apparatus of siphonophores, the most extensive and detailed to date (229 individuals across 71 species). Collecting these new data was a major undertaking. Siphonophores are fragile animals that live far offshore and in the deep sea, and thus are extremely hard to collect. Specimen collection required SCUBA diving and the deployment of remotely operated vehicles hundreds of kilometers from shore. We expand the taxon sampling on the existing phylogeny, integrate published dietary data, and analyze it together with the new morphological data in a robust phylogenetic comparative framework.

This manuscript advances the active discussion on the evolutionary trends of trophic niche breadth, reviewed in Forister *et al.* 2012 (https://doi.org/10.1890/11-0650.1). Moreover, our findings are relevant to the discussion on the importance of organismal biology and evolutionary history in determining food web structure (Lima-Perez *et al.* 2015 https://science.sciencemag.org/content/348/6237/1262073), and to the importance of studying shifts in phenotypic integration as evolutionary mechanisms to access ecological novelties (Futuyma 2010 https://doi.org/10.1111/j.1558-5646.2010.00960.x). We believe that this manuscript is appropriate for publication in PNAS, as it challenges traditional assumptions on the evolution of niche breadth and addresses fundamental questions about how organismal evolution generates food web structure.

This work lies at the intersection between evolutionary biology, morphology, ecology, and oceanography. The structure of oceanic food webs is critical for the sustainability of marine ecosystems, commercial fisheries, and the biological carbon pump. Thus, it is critical to understand the mechanisms that determine this structure and how changing the pool of organismal traits in the community will affect its architecture. This knowledge will allow scientists to better predict the impacts of climate change, overfishing, and conservation policies on the functioning of oceanic ecosystems.

Thank you for your consideration of our manuscript.

Yours sincerely,

Alejandro Damian-Serrano