Grateful for the dead: the widespread importance of dead foundation species for biodiversity, ecosystem function, and resilience.

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Abstract

Foundation species such as corals, trees, and bivalves enhance ecosystem function and biodiversity by creating habitat for associated organisms, ameliorating stress, and modifying energy flow. However, theory generally ignores their ecological functions after death. Here we review the traits and functions of dead foundation species relative to their living counterparts, and the processes that control their persistence. We also conduct a meta-analysis to quantify where the effect of dead foundation species on community functions is unique or redundant to their living counterparts. We focus on marine ecosystems due to the greater diversity of foundation species they support and the increasing prevalence of mass-mortality events in these systems. Our study reveals how foundation species continue to provide important functions after death and exhibit new functions that are distinct from when they are alive. We develop a framework using broad, trait-based functional differences among types of dead foundation species to predict whether they will promote stability by enhancing ecosystem resilience or promote shifts to alternate states. Our synthesis establishes how an understanding of the ecological importance of dead foundation species can assist in predicting system trajectories, enhance restoration and conservation efforts, and contribute to ecological theory on habitat heterogeneity and ecosystem function.

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Dear Dr. Jonathan Chase,

Please consider our resubmission of the enclosed manuscript, "Grateful for the dead: the widespread importance of dead foundation species for biodiversity, ecosystem function, and resilience" that my co-authors and I have prepared for publication as a *Reviews and Synthesis*article in *Ecology Letters* .

We anticipate that this topic will be of general interest to the readership of *Ecology Letters.* Dead foundation species (FS), an important subset of ecosystem engineers, have long been recognized for their ubiquity

and importance across ecosystems worldwide. However, their ecological functions after death have not been systematically examined in marine systems. We consider this a significant knowledge gap, expecially considering the global increase in mortality rates of FS as a result of anthropogenic stressors. Whether the ecosystem functions of FS change or persist following mortality are of widespread interest to community and ecosystem ecologists, fisheries scientists, conservation biologists, natural resources management, and biogeochemists. Here, we synthesize this overlooked component of ecosystem function.

Our study has widespread relevance for predicting ecosystem trajectories amidst global change. We reveal through meta-analysis and literature review that dead FS continue to provide important and unique functions after death, often host higher biodiversity of organisms than their living counterparts, and increase habitat heterogeneity throughout ecosystems. Live and dead FS are often differentially affected by abiotic and biotic stressors, and the loss of dead structures can initiate regime shifts. We offer a conceptual framework for predicting when dead FS are likely to facilitate system recovery, or promote system decline. By using a trait-based approach to highlight the functions provided by dead FS, we expect our paper will contribute to general ecological theory and improve the ability of ecologists and management to predict thresholds and tipping points for ecosystems.

The following scientists could serve as potential reviewers of this manuscript:

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Thank you for your time and consideration of our work for publication.

Sincerely,

Patrick H. Saldaña

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