REPLY TO WILSON ET AL.:

# Feedbacks between geomorphology and fauna engineers are key to predicting coastal response to rising seas

**Sinead M. Crotty[a,1], Thomas Bianchi[b], Andrew Altieri[c], and Christine Angelini[c]**

In their letter to the editor, Wilson et al. (1) highlight their historical work demonstrating that the burrowing and grazing activities of *Sesarma reticulatum* at tidal creekheads helps drive erosion and headward elongation of creeks in US Atlantic salt marshes. Combined with our previous work mechanistically linking sea level rise, geomorphology, sediment dynamics, and the emerging keystone grazer *S. reticulatum* (2), Wilson emphasizes that future research should evaluate feedbacks between *Sesarma*, other biota, and geomorphology in the context of sea-level rise. We agree.

We further propose that future study of vegetated coastal ecosystem response to climate change broadly requires more deliberate and nuanced inclusion of fauna in order to remain relevant and accurate. We acknowledge that vegetated coastal systems are built and structurally defined by habitat-forming plants. However, ecosystem-engineering infauna and epifauna—organisms whose physical structures and/or activities alter nutrient cycling, habitat complexity, sediment transport, and other functions—often powerfully modulate ecosystem structure and stability at landscape scales (3). Despite the demonstrated importance of faunal engineers, models of accretion, migration, and creek formation widely ignore their effects. Instead, the role of sea-level rise in controlling coastal wetland vertical persistence is considered solely in the context of vegetation–geomorphology feedbacks (4).

Recent work demonstrates that fauna modify both vegetation and geomorphology—and that climate change amplifies these impacts, elevating these organisms to keystone roles (2) (Fig. 1). Examples are evident across ecosystems; herbivorous crabs, fungal-farming snails, and other consumers

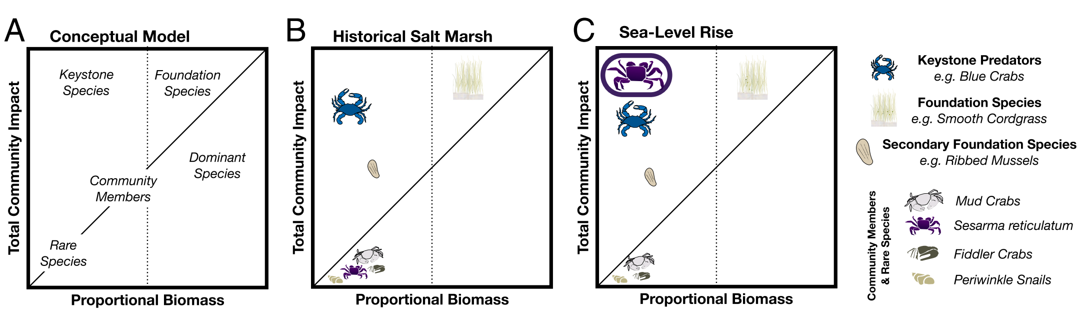


**Fig. 1. Historical and projected roles of faunal engineers. (*A*) Conceptual models of keystone species, originating in Power et al. (5), map the impact of community members as well as keystone, foundation, dominant, and rare species as a function of proportional biomass. Those species with disproportionate effects are termed keystone species (or foundation species if they are also numerically dominant) and fall above the 1:1 line. (*B*) Historical roles of marsh flora and fauna. (*C*) In the context of sea-level rise, however, the effects of *S. reticulatum* on marsh ecology and geomorphology are far greater, or disproportionate, to their population size, elevating them to keystone status.**

[a]Carbon Containment Lab, School of the Environment, Yale University, New Haven, CT 06511; [b]Department of Geological Sciences, University of Florida, Gainesville, FL 32611; and [c]Department of Environmental Engineering Sciences, University of Florida, Gainesville, FL 32611

Author contributions: S.M.C. designed research; S.M.C. performed research; S.M.C. wrote the paper; and S.M.C., T.B., A.A., and C.A. edited versions of the paper.

The authors declare no competing interest.



[1]To whom correspondence may be addressed. Email: sinead.crotty@yale.edu.

Published February 23, 2022.

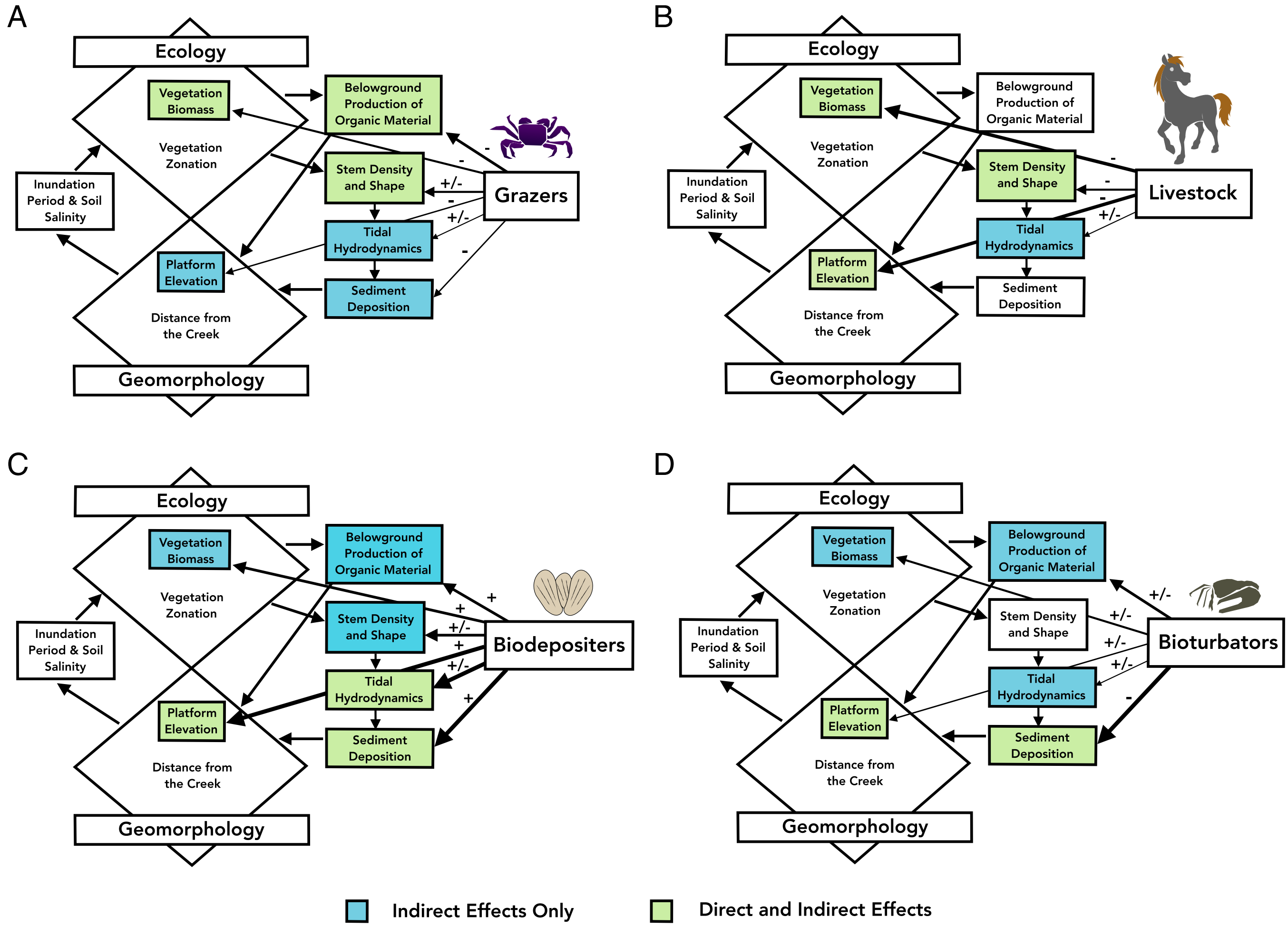


**Fig. 2.** **Fauna engineering effects on ecogeomorphology of vegetated coastal ecosystems [adapted from Fagherazzi et al. with permission from John Wiley and Sons (4)]. Conceptual model depicting the mechanisms through which (*A*) grazers, (*B*) livestock, (*C*) biodepositers, and (*D*) bioturbators alter ecogeomorphology, with indirect (blue) and direct + indirect (green) effects highlighted.**

strongly decrease plant biomass directly through grazing activities, and/or indirectly through the spread of disease (Fig. 2*A*). Effects of these consumers can drive large-scale vegetation dieback or rapid geomorphological evolution (6, 7). Likewise, trampling and grazing by larger-bodied herbivores and consumers can compact vegetation and landforms at landscape scales (8) (Fig. 2*B*).

In contrast, deposition by suspension- and filter-feeding organisms, such as bivalves and sponges, and resuspension of sediment by bioturbators, such as burrowing crabs and worms, can directly increase landform elevation and significantly alter rates of sediment import and export (9). Simultaneously, through deposition of nutrient-rich material, oxygenation of soil, and enhancement of plant growth, these faunal engineers also indirectly enhance sediment capture by plant leaves or soil accumulation via root production (9) (Fig. 2 *C* and *D*). Finally, as warming drives poleward range expansions, many of these coastal systems will also be experiencing shifts in faunal communities, further complicating community and biogeochemical dynamics (10).

In many cases, the role of fauna in mediating the structure and function of biogenic landforms is dictated by their spatial distribution—a feature that is, ironically, often predictably controlled by underlying geomorphology and associated hydrology—processes that control larval and food delivery, and spatial and temporal gradients in physical and biological stress (11). We thus concur that deeper evaluation of the relationship between fauna and geomorphology is an urgent scientific need. We further highlight that the key to this investigation will be understanding the bidirectional feedbacks among geomorphology, vegetation, and spatial patterning of fauna, and the response of such interactive effects to rising seas.

1 C. A. Wilson, Z. J. Hughes, D. M. FitzGerald, Causal relationships among sea level rise, marsh crab activity, and salt marsh geomorphology. *Proc. Natl. Acad. Sci. U. S. A.*, 10.1073/pnas.2111535119 (2022).
2 S. M. Crotty *et al.*, Sea-level rise and the emergence of a keystone grazer alter the geomorphic evolution and ecology of southeast US salt marshes. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 17891–17902 (2020).
3 C. G. Jones, J. H. Lawton, M. Shachak, "Organisms as Ecosystem Engineers" in *Ecosystem Management: Selected Readings*, F. B. Samson, F. L. Knopf, Eds. (Springer, 1996), pp. 130–147.
4 S. Fagherazzi *et al.*, Numerical models of salt marsh evolution: Ecological, geomorphic, and climatic factors. *Rev. Geophys.* **50**, RG1002 (2012).

5 M. E. Power *et al.*, Challenges in the quest for keystones: Identifying keystone species is difficult—but essential to understanding how loss of species will affect ecosystems. *Bioscience* **46**, 609–620 (1996).
6 B. R. Silliman, J. C. Zieman, Top-down control of *Spartina alterniflora* production by periwinkle grazing in a Virginia salt marsh. *Ecology* **82**, 2830–2845 (2001).
7 C. Holdredge, M. D. Bertness, A. H. Altieri, Role of crab herbivory in die-off of New England salt marshes. *Conserv. Biol.* **23**, 672–679 (2009).
8 K. E. Davidson *et al.*, Livestock grazing alters multiple ecosystem properties and services in salt marshes: A meta-analysis. *J. Appl. Ecol.* **54**, 1395–1405 (2017).
9 J. Norkko, S. E. Shumway, "Bivalves as bioturbators and bioirrigators" in *Shellfish Aquaculture and the Environment*, S. E. Shumway, Ed. (Wiley-Blackwell, 2011), pp. 297–317.
10 T. S. Bianchi *et al.*, What global biogeochemical consequences will marine animal-sediment interactions have during climate change? *Elem. Sci. Anth.* **9**, 00180 (2021).
11 S. M. Crotty, C. Angelini, Geomorphology and species interactions control facilitation cascades in a salt marsh ecosystem. *Curr. Biol.* **30**, 1562–1571.e4 (2020).