

Promoting invasive species to enhance multifunctionality in a native ecosystem still requires strong(er) scrutiny

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After reviewing Thomsen et al. (2018), the four (now five) pillars of our initial critique (Sotka and Byers 2018) of Ramus et al. (2017) remain, and all relate to the analysis and over-interpretation of the data.

(1) *Important, critical ecosystem services were poorly examined or ignored.* This shortcoming led Ramus et al. (2017) and Thomsen et al. (2018) to overstate how comprehensive their multifunctionality (hereafter, MF) analysis was. Their MF analysis excluded functions and services such as primary and secondary productivity, nutrient cycling, the facilitation of microbial *Vibrio* blooms, protection from coastal erosion, and “tourism, recreation, education and research.” Two of these—primary productivity and nutrient cycling—are not simply arbitrarily chosen “other” functions (in the words of Thomsen et al.: “possible functions 12 and 13 that we could have measured”). As defined by Hooper et al. (2005), one of the seminal papers on the topic, ecosystem functions “include both sizes of compartments (e.g., pools of materials such as carbon or organic matter) and rates of processes (e.g., fluxes of materials and energy

among compartments).” That is, these are fundamental components that quantify the movement of energy and nutrients through systems. Such compartments and processes are not represented in the work of Ramus et al. (2017).

Thomsen et al. (2018) justify overlooking these central ecosystem processes by citing studies embedded in a recent MF meta-analysis (Lefcheck et al. 2015) which they state “did not report effects on either nutrient cycling or primary productivity (e.g., Gamfeldt et al. 2005; Jiang 2007; Laossi et al. 2008; Maestre and Reynolds 2007).” This explanation is insufficient, considering that the goal of Ramus et al. (2017) appears to have been to paint a comprehensive, bottom-line, ecosystem-level picture of the seaweed *Gracilaria*'s influence. Furthermore, a closer examination shows that all four of these studies recognized the importance of primary production, and measured and discussed proxies for it (e.g., the title of Laossi et al. (2008) is “Effects of plant diversity on plant biomass production and soil macrofauna in Amazonian pastures”).

The role of introduced *Gracilaria* on primary productivity or nutrient cycling was addressed in two recent articles, but neither clearly demonstrates the uniformly positive effects claimed by Thomsen et al. (2018). Davoult et al. (2017) show that “despite the invasion of a new primary producer, the productivity of the mudflat remained stable.” Thomsen et al. (2018) also state that *Gracilaria* generates “higher net

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denitrification rates (Gonzalez et al. 2013)”, but a more complete reading of that paper indicates that the net denitrification was highly temporally variable and density-dependent, such that denitrification declined at high densities. By raising these papers so prominently in their response, Thomsen et al. (2018) seem to reinforce our criticism that the impacts of *Gracilaria* on these functions are important, yet possibly variable, and ultimately missing from Ramus et al. (2017).

(2) *Multifunctionality is unsupported: re-analysis leads to a different conclusion.* Thomsen et al. (2018) are correct that one can load whichever functions one chooses into a MF analysis. However, it is also true that MF is only as comprehensive and valuable as the functions that comprise it (“the definition of multifunctionality determines how it is measured, and vice versa”; Manning et al. 2018). In the case of Ramus et al. (2017), we maintain that the inclusion and treatment of variables in the MF index were subjective and several variables remain poor proxies for ecosystem functioning. For example, Ramus et al. (2017) and Thomsen et al. (2018) subjectively or with weak justification assert that decreased dissolution of gypsum blocks reflects better protection of shorelines from storms; decreased number of ray pits yields less clam predation and thus less trophic energy transfer; degradation of *Spartina* pieces in an abnormal location yields ecologically-relevant decomposition rates; and standing density of organisms is a proxy for secondary productivity and not simply colonization of invertebrates from nearby habitats. Alternative and equally justified treatment of these processes yields a different MF interpretation (Sotka and Byers 2018).

Most importantly, we ask why MF analysis is necessary in this study? Ramus et al. (2017) quantified several individual univariate relationships of the effect of *Gracilaria* on other species and functions. Although we do not agree with the case made for advancing several of these functions, when the functions are presented individually, assessment of them is transparent, and readers can easily judge the effects of each and weigh more heavily the variables they prioritize in impact assessment. It appears unhelpful to take such well explicated relationships and obfuscate these details in a metric that is focused on statistical rather than biological effects. To us, in this case, there appears to be little to no value added by invoking MF. We believe a more powerful approach is to let the

individually explicated univariate relationships speak for themselves.

(3) *Intertidal mudflats are not a wasteland.* Thomsen et al. (2018) emphasize that Ramus et al. (2017) intended their use of the term “barren” to be synonymous with “bare” and not “poor value.” We do not know the intention of the authors, but it is clear that the use of “barren” mudflats was tightly coupled to assertions of lower value or reduced ecosystem functioning in two separate statements of Ramus et al. (2017) (first paragraph of Introduction; second paragraph of Discussion). In both cases, the authors note that *Gracilaria* generates MF when biogenic habitat is lost (i.e., when the habitat is barren). Thus, the underlying implication is that “barren” habitats have low value. We argue that invaded and uninvaded mudflats have different values and will be lower or higher depending on which functions or services are examined or emphasized.

We also maintain that the principal coastal foundation species of the southeastern United States (oysters, seagrasses and salt marshes) have “minimal spatial overlap with *Gracilaria*,” and thus *Gracilaria* does not and cannot serve as habitat replacement. Along the eastern seaboard, *Gracilaria* largely exists either as drifting mats or is anchored in place with decorator worms on mudflat beds (Thomsen and McGlathery 2005; Kollars et al. 2016; Krueger-Hadfield et al. 2016). We do not doubt that in certain areas it will drift into the subtidal zone in which seagrass occurs or into high intertidal habitats of salt marshes, where it often dies. *Gracilaria* growth and survival rates are, however, greatest in the mid- to low intertidal (Kollars et al. 2016) and these mid- to low-intertidal individuals serve as sources for drifting thalli. We concur that seagrasses, salt marshes, and oysters have historically declined from a variety of human threats in North Carolina and elsewhere. The more pertinent issue is whether these foundation species ever occurred on these intertidal mudflats. The authors provide no evidence of overlapping habitat usage between *Gracilaria* and the native foundation species and limited historical evidence to support how prominent these native species were in the local area (“...we cannot say whether seagrasses were once abundant or uncommon in the local area;” Thomsen et al. 2018).

Furthermore, if the goal is to demonstrate that *Gracilaria* may be an acceptable replacement for

oysters, seagrasses, and salt marshes that once existed in greater abundance on the southern United States coast, then experiments would be required that would compare a variety of ecosystem functions provided by intertidal *Gracilaria* to those provided by these foundation species. Ramus et al. (2017) did not do these experiments, and we restate our conclusion that they should have generated more caution in their interpretation, rather than assuming *Gracilaria* is replicating lost functions.

(4) “*Potential benefits of invasive species may have been overlooked*” is a strawman. Ramus et al. (2017) conclude that *Gracilaria* has overwhelmingly positive effects. Even if we were to accept that this were true (which we do not know, for the reasons we outline above), this result is not novel. Rather, it fits within the context of an enormous literature on aquatic and terrestrial introductions that have positive, negative and neutral effects (Sotka and Byers 2018; see a recent review by Guy-Haim et al. 2018 for introduced ecosystem engineers), including that for *Gracilaria* itself (e.g., Byers et al. 2012; Wright et al. 2014; Bishop and Byers 2015; Haram et al. 2018). We applaud the authors in becoming far more circumspect on this point in Thomsen et al. (2018) than in Ramus et al. (2017) or in their press release.¹

In response to our critique, Thomsen et al. (2018) instead focused on the novelty of their experimental design (i.e., invader density, size of experimental unit), an aspect with which Sotka and Byers (2018) did not argue.

(5) *It is premature to promote Gracilaria for use in coastal habitat restoration (our fifth critique, as paraphrased by Thomsen et al. 2018)*. We agree with the more tempered conclusion of Thomsen et al. (2018) that “*Gracilaria has both positive and negative effects and should not be promoted for restoration.*” However, we have a difficult time reconciling this with the overwhelmingly positive message that emanates from Ramus et al. (2017):

“An invasive foundation species enhances multifunctionality in a coastal ecosystem” (Title)

“invasive habitat formers may be considered as a tool to enhance multiple ecosystem functions” (pg. 1)

“managers should pragmatically acknowledge and incorporate the possibility of positive ecosystem functions delivered by nonnative foundation species into their decision making processes for conservation strategies” (pg. 4).

“...if native foundation species are absent and restoration is infeasible, then actively incorporating established nonnative foundation species into conservation and management strategies may have stronger than expected benefits for the provisioning of coastal ecosystem services.” (Concluding paragraph)

Furthermore, Ramus et al. (2017) frame the management choice on *Gracilaria* as “*passive ‘do nothing, laissez-faire’ vs. active ‘remove and replace’*” (Ramus et al. 2017), and clearly side with the former. We believe their solution of ‘doing nothing’ is akin to promotion for a spreading invader like *Gracilaria*, and thus in effect, an active management decision.

Overall, we were pleased that Thomsen et al. (2018) take a more measured, even cautious, tone about the value and restoration potential of *Gracilaria* in a manner that we felt was missing from, and that we would have appreciated in, Ramus et al. (2017). Unfortunately, Ramus et al. (2017) convey a management message that *Gracilaria* is so overwhelmingly positive to ecosystem services and for society, that the introduced species should be considered as a restoration tool. Prematurely sanctioning an invasive species for restoration can both yield poor policy and undermine future public support for science-based solutions.

References

- Bishop MJ, Byers JE (2015) Predation risk predicts use of a novel habitat. *Oikos* 124:1225–1231
- Byers JE, Gribben PE, Yeager C, Sotka EE (2012) Impacts of an abundant introduced ecosystem engineer within mudflats of the southeastern US coast. *Biol Invasions* 14:2587–2600

¹ “...What if some of those invasive species are actually benefiting native species and ecosystem services?” said Brian Silliman, Rachel Carson Associate Professor of Marine Conservation Biology at Duke’s Nicholas School of the Environment, who co-authored the study. “Our experimental study shows for the first time that this can be the case.” <https://nicholas.duke.edu/about/news/invasive-plant-species-can-enhance-coastal-ecosystems>. July 17 2017. Accessed August 22 2018.

- Davoult D, Surget G, Stiger-Pouvreau V, Noisette F, Riera P, Stagnol D, Androuin T, Poupart N (2017) Multiple effects of a *Gracilaria vermiculophylla* invasion on estuarine mudflat functioning and diversity. *Mar Environ Res* 131:227–235
- Gamfeldt L, Hillebrand H, Jonsson PR (2005) Species richness changes across two trophic levels simultaneously affect prey and consumer biomass. *Ecol Lett* 8:696–703
- Gonzalez DJ, Smyth AR, Piehler MF, McGlathery KJ (2013) Mats of the non-native macroalga, *Gracilaria vermiculophylla*, alter net denitrification rates and nutrient fluxes on intertidal mudflats. *Limnol Oceanogr* 58:2101–2108
- Guy-Haim T, Lyons DA, Kotta J, Ojaveer H, Queiros AM, Chatzinikolaou E, Arvanitidis C, Como S, Magni P, Blight AJ, Orav-Kotta H, Somerfield PJ, Crowe TP, Rilov G (2018) Diverse effects of invasive ecosystem engineers on marine biodiversity and ecosystem functions: a global review and meta-analysis. *Glob Change Biol* 24:906–924
- Haram LE, Kinney KA, Sotka EE, Byers JE (2018) Mixed effects of an introduced ecosystem engineer on the foraging behavior and habitat selection of predators. *Ecology*. <https://doi.org/10.1002/ecy.2495>
- Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr* 75:3–35
- Jiang L (2007) Negative selection effects suppress relationships between bacterial diversity and ecosystem functioning. *Ecology* 88:1075–1085
- Kollars NM, Byers JE, Sotka EE (2016) Invasive decor: an association between a native decorator worm and a non-native seaweed can be mutualistic. *Mar Ecol Prog Ser* 545:135–145
- Krueger-Hadfield SA, Kollars NM, Byers JE, Greig TW, Hammann M, Murray DC, Murren CJ, Strand AE, Terada R, Weinberger F, Sotka EE (2016) Invasion of novel habitats uncouples haplo-diplontic life cycles. *Mol Ecol* 25:3801–3816
- Laossi KR, Barot S, Carvalho D, Desjardins T, Lavelle P, Martins M, Mitja D, Rendeiro AC, Rousseau G, Sarrazin M, Velasquez E, Grimaldi M (2008) Effects of plant diversity on plant biomass production and soil macrofauna in Amazonian pastures. *Pedobiologia* 51:397–407
- Lefcheck JS, Byrnes JEK, Isbell F, Gamfeldt L, Griffin JN, Eisenhauer N, Hensel MJS, Hector A, Cardinale BJ, Duffy JE (2015) Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. *Nat Commun* 6:1–7
- Maestre FT, Reynolds JF (2007) Biomass responses to elevated CO₂, soil heterogeneity and diversity: an experimental assessment with grassland assemblages. *Oecologia* 151:512–520
- Manning P, Van Der Plas F, Soliveres S, Allan E, Maestre FT, Mace G, Whittingham MJ, Fischer M (2018) Redefining ecosystem multifunctionality. *Nat Ecol Evol* 2:427–436
- Ramus AP, Silliman BR, Thomsen MS, Long ZT (2017) An invasive foundation species enhances multifunctionality in a coastal ecosystem. *Proc Natl Acad Sci* 114:8580–8585
- Sotka EE, Byers JE (2018) Not so fast: promoting invasive species to enhance multifunctionality in a native ecosystem requires strong(er) scrutiny. *Biol Invasions*. <https://doi.org/10.1007/s10530-018-1822-0>
- Thomsen MS, McGlathery K (2005) Facilitation of macroalgae by the sedimentary tube forming polychaete *Diopatra cuprea*. *Estuar Coast Shelf Sci* 62:63–73
- Thomsen MS, Ramus AP, Long ZT, Silliman BR (2018) A seaweed increases ecosystem multifunctionality when invading bare mudflats. *Biol Invasions*. <https://doi.org/10.1007/s10530-018-1823-z>
- Wright JT, Byers JE, DeVore JL, Sotka EE (2014) Engineering or food? Mechanisms of facilitation by a habitat-forming invasive seaweed. *Ecology* 95:2699–2706