

A seaweed increases ecosystem multifunctionality when invading bare mudflats

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Introduction

One of the most successful marine invaders worldwide is the seaweed *Gracilaria vermiculophylla* (Gulbransen et al. 2013; Hu and Juan 2014; Thomsen et al. 2016b). A

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highly variable abundance of *Gracilaria* in many different invaded habitats and bioregions has motivated researchers to quantify impacts on a variety of ecological response variables (Gulbransen and McGlathery 2013; Thomsen et al. 2013; Davoult et al. 2017). Ramus et al. (2017) therefore used a manipulative field experiment to test for density-dependent effects of *Gracilaria* on 11 ecosystem functions (see Fig. 1 for a description of the functions). From their experiment and analyses, Ramus et al. concluded that in comparison to bare mudflats, *Gracilaria* increases multiple ecosystem functions (Figs. 2H and S2E in Ramus et al. 2017).

Ramus et al. were particularly interested in the seven functions that were measured monthly from the beginning of the experiment, whereas the remaining four functions were measured only near the end of the experiment (hereafter referred to as ‘7’ and ‘7 plus 4’ measured functions). Results from analyses of 7 and 7 plus 4 functions were shown in the manuscript and online supplement, respectively, with each function being analyzed individually and in concert using the ‘averaging’ and ‘threshold’ approaches to quantifying multifunctionality, as described by Byrnes et al. (2014b). In their paper, Ramus et al. adopted the definition that multifunctionality is ‘the simultaneous performance of multiple functions’ (Byrnes et al. 2014b) and investigated different processes that ‘simultaneously affect the multitude of ecosystem functions present in nature’ (Lefcheck et al. 2015). These definitions emphasize that many, rather than specific types of, functions can be analyzed in a single

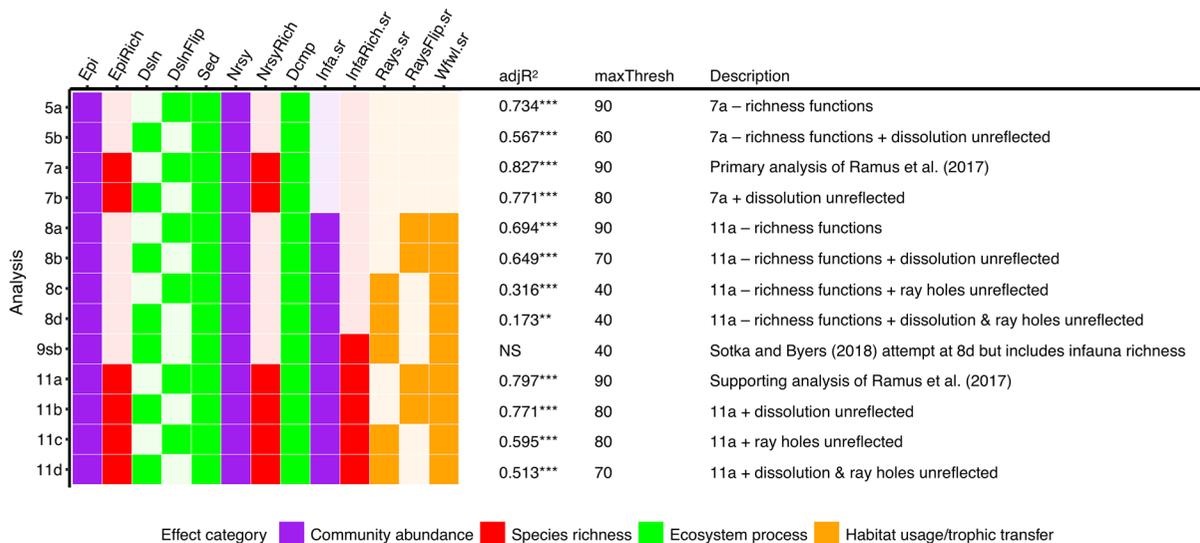


Fig. 1 Summary of ecosystem multifunctionality analyses (reanalyzed from Dataset S1 in Ramus et al. 2017). Analyses are described by the number of functions included and a letter to denote the variant. Column names: Epi, mean abundance of epifauna ($\# \text{ m}^{-2}$); EpiRich, mean richness of epifauna taxa (m^{-2}); Dsln, mean chalk dissolution expressed as mass lost (g day^{-1}); DslnFlip, mean reflected chalk dissolution; Sed, mean sediment stabilization expressed as the change in height in cm per month ($\Delta \text{cm month}^{-1}$); Nrsy, mean abundance of nursery species ($\# \text{ m}^{-2}$); NrsyRich, mean richness of nursery taxa (m^{-2}); Dcmp, mean decomposition of *Spartina* stems expressed as mass lost (g month^{-1}); Infa.sr, the mean abundance of infauna ($\# \text{ L}^{-1}$); InfaRich.sr, the mean number of infauna taxa (L^{-1}); Rays.sr, the mean number of ray holes ($\#$

$\text{m}^{-2} \text{ day}^{-1}$); RaysFlip.sr, the reflected mean number of ray holes; and Wfwl.sr, the mean abundance of waterfowl ($\# \text{ m}^{-2} \text{ h}^{-1}$); adjR², the proportion of variance in the response variable explained by *Gracilaria* cover in estimated model, adjusted for the number of parameters used in the model (stars denote significance level: ***0.001, **0.01); maxThresh, the maximum threshold fit with a significant relationship; Description, a description of the different combinations and reflections of functions included. The suffix ‘.sr’ denotes supporting responses measured at the end of the experiment. See online Appendix A for model selection tables. These analyses support the conclusion that *Gracilaria* enhances ecosystem multifunctionality when invading bare mudflats

statistical framework, and do not require that the measured functions are nonindependent (Byrnes et al. 2014b; Lefcheck et al. 2015).

Here, we welcome Sotka and Byers (2018) critique of our paper and thank them for providing us with an opportunity to clear up misunderstandings and re-evaluate what is known about *Gracilaria*'s ecological effects on bare mudflats. Sotka and Byers outlined five critiques of Ramus et al. Those were: (1) ecosystem functions deemed important by Sotka and Byers were not measured, (2) data did not support the conclusion that *Gracilaria* increases multifunctionality, (3) bare mudflats are not wastelands of poor value, (4) facilitation by nonnative species is not novel, and (5) it is premature to promote *Gracilaria* for use in coastal habitat restoration (the final critique did not have a heading but was repeated in the title, introduction, and discussion of their paper). We rebut these five critiques

beginning with point 2 because this point criticizes our scientific data analysis, whereas the other critiques address opinions.

***Gracilaria* increases ecosystem multifunctionality on bare mudflats**

Sotka and Byers argue that we did not provide sufficient evidence to conclude that *Gracilaria* increases ecosystem multifunctionality because (1) the criteria for the inclusion of functions was subjective, (2) certain response variables should not have been reflected, (3) abundance and richness functions are nonindependent, and thus should not have both been included in analyses, and (4) an analysis of a different subset of functions and reflections of functions therein did not show a significant positive

relationship between *Gracilaria* abundance and average multifunctionality.

First, the selection of responses included in our multifunctionality analysis was objective. All seven intensively measured responses were included in the main analysis and the four less intensively measured responses were added in the supplementary analysis (Figs. 2 and S2 in Ramus et al. 2017). We see nothing wrong in analyzing all our data with two complementary analyses.

Second, we stand by our arguments for inverting dissolution and the number of ray holes. We reflected them following recommendations of Byrnes et al. (2014b) because we considered response variables in relation to functions that underpin coastal ecosystem services, as described by Barbier et al. (2011). Based on the ecosystem services described therein, we noted that coastal protection and erosion control both covary with flow velocity (which correlates with dissolution rates; Thompson and Glenn 1994), and that decreased predation by rays should facilitate commercially and recreationally important bivalves, like clams, mussels, and oysters, similar to how *Gracilaria* facilitates other animals on bare mudflats (Nyberg et al. 2009; Thomsen et al. 2010; Byers et al. 2012; Cordero et al. 2012; Johnston and Lipcius 2012; Cordero and Seitz 2014; Guidone et al. 2014; Wright et al. 2014; Bishop and Byers 2015; Kollars et al. 2016; Davoult et al. 2017). We therefore reflected dissolution and the number of ray holes accordingly.

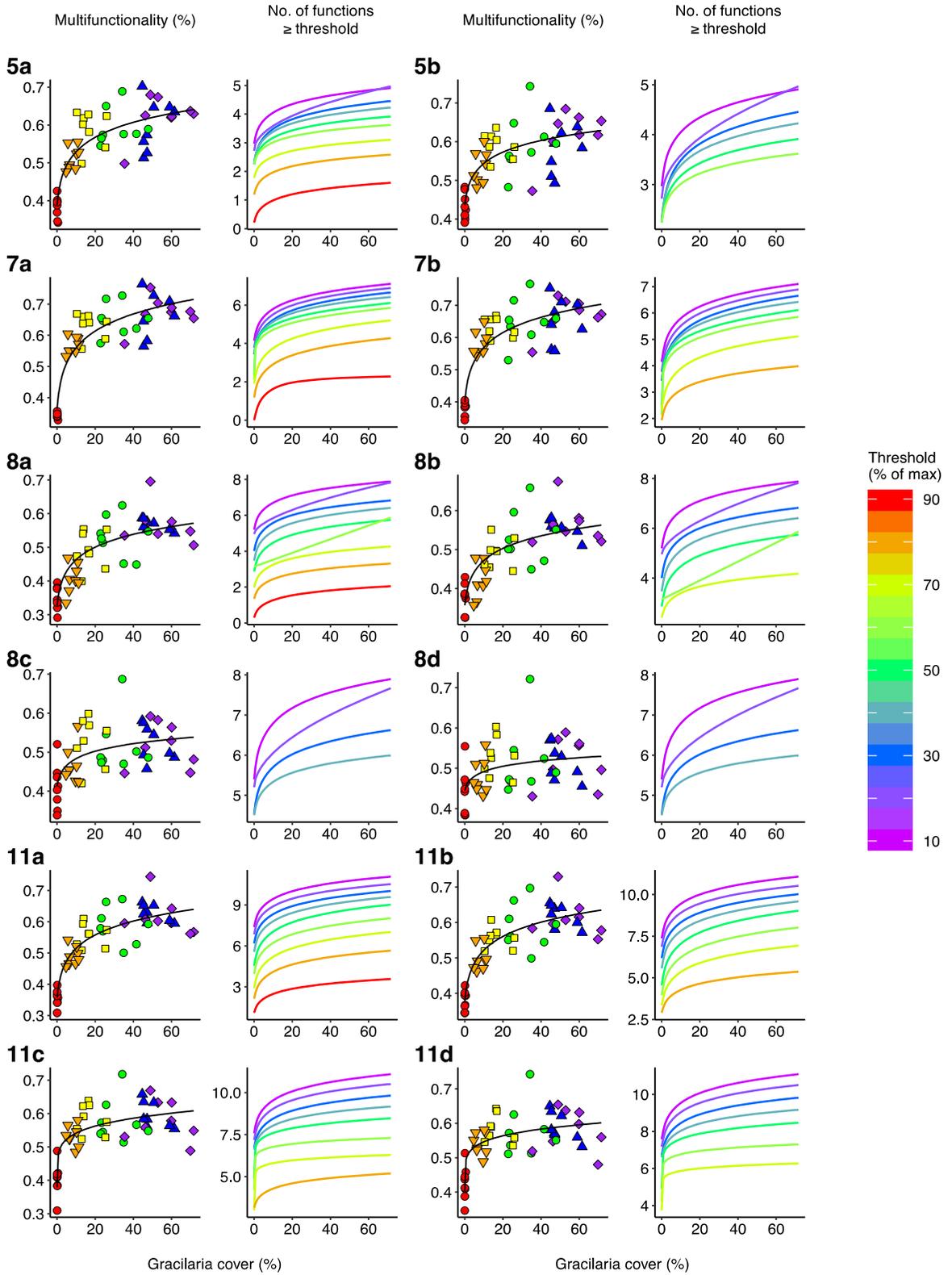
Third, standard approaches to quantifying multifunctionality “make no assumptions of independence between functions” because these indices focus on “the yields of individual function themselves” (p. 113 in Byrnes et al. 2014b). It is noteworthy that Sotka and Byers, in their own reanalysis of 9 of the functions that we measured (Fig. 1, 9sb), included both the abundance and taxonomic richness of infauna even though these two functions are autocorrelated in space and time (both metrics are calculated from the same sample). Indeed, a recent meta-analysis demonstrates that nonindependent functions are commonly measured and included together in analyses (Lefcheck et al. 2015). For example, although above and below ground biomass of individual plants scales isometrically (Cheng and Niklas 2006), both of these functions were included in many of the analyzed studies (Lefcheck et al. 2015). Moreover, several published experiments (e.g., BIODEPTH, Cedar Creek, Jena)

included, like Ramus et al., both abundance and richness functions. More specifically, however, Ramus et al. argued that both abundance and richness were included in multifunctionality analyses because they underpin different ecological processes. For example, abundances more often correlate with processes such as carbon sequestration, productivity, respiration, and the maintenance of fisheries, whereas richness better reflects genetic, functional, and morphological diversity, evolutionary history, taxonomic complementarity (different taxa support different functions; Hensel and Silliman 2013), and redundancy (different taxa support similar functions).

While we stand by our ecological arguments and original analyses, a new sensitivity analysis (Figs. 1, 2) shows that our results are robust to the number and reflection of functions included (see Byrnes et al. 2014a for a related discussion about misunderstandings of multifunctionality indices). Several reanalyses with unreflected functions revealed similar, significant results, and demonstrate that the conclusion of Ramus et al. is not only robust, but also parsimonious. Thus, irrespective of issues related to data nonindependence, included functions, and reflection, Ramus et al.’s analysis of multifunctionality was appropriate and unequivocal.

Interestingly, the analysis of Sotka and Byers also supports this conclusion because multifunctionality was higher in plots containing *Gracilaria* than those without *Gracilaria* (Fig. 1b in Sotka and Byers 2018). While the nonsignificant p value in their analysis was calculated from a regression, most invasion impact studies compare only invaded and noninvaded habitats (see online Appendix B and C). We therefore tested their analysis of 9 ecosystem functions using a standard invaded versus non-invaded comparison. This analysis shows that even for the specific combination of functions hand-picked by Sotka and Byers, *Gracilaria* significantly increased average multifunctionality in comparison to bare mudflats (t test, $P = 0.006$, $t = -2.85$; Levene’s test, $P = 0.86$; average multifunctionality in: uninvaded mud = 0.47 ± 0.02 SE, $n = 8$; invaded mud = 0.53 ± 0.01 , $n = 40$).

Finally, the experimental results of Ramus et al. are corroborated by a substantial and growing body of work on this invasive seaweed. In comparison to bare mudflats, *Gracilaria*-invaded mudflats typically have higher abundance and diversity of mobile epifauna



◀ **Fig. 2** Relationships between the percent cover of the non-native seaweed *Gracilaria vermiculophylla* and ecosystem multifunctionality indices for different combinations and reflections of functions [reanalyzed from Dataset S1 in Ramus et al. (2017)]. Analyses are described by the number of functions included and a letter to denote the variant (see Fig. 1 for a description and summary of the functions included). Left column: multifunctionality index, the average of the standardized functions in percent. Right column: the raw number of functions exceeding threshold levels in each plot against *Gracilaria* cover, for thresholds ranging from 10% (magenta) to 90% (red) of the maximum indicated on the color scale. Points are the multifunctionality index versus the average *Gracilaria* cover of each plot ($n = 48$). Colors and symbols correspond to the six seaweed density treatments (number of stakes arranged in squared grids: red circles = 0, orange triangles = 9, yellow squares = 36, green circles = 100, blue triangles = 225, purple diamonds = 400). Best-fitting models determined by AICc are shown where significant at the 0.05 level. These analyses support the conclusion that *Gracilaria* enhances ecosystem multifunctionality when invading bare mudflats

(Thomsen 2010; Byers et al. 2012; Gulbransen et al. 2013; Wright et al. 2014; Davoult et al. 2017) and sessile epibiota (Thomsen et al. 2006, 2010); higher abundance of sediment meiofauna (Davoult et al. 2017); higher survival of juvenile animals (Wright et al. 2014; Bishop and Byers 2015), including economically important blue crabs (Falls 2008; Johnston and Lipcius 2012) and bay scallops (Cordero et al. 2012; Cordero and Seitz 2014); higher net denitrification rates (Gonzalez et al. 2013); increased substrate for egg laying snails (Guidone et al. 2014); increased primary productivity, sediment chlorophyll-a, and net community production (Davoult et al. 2017); higher subsidy and transport of animals and plant material to adjacent salt marshes (Thomsen et al. 2009a; Gulbransen and McGlathery 2013); and increased buffering of temperature extremes, as well as reduced desiccation stress (Wright et al. 2014). Here we also highlight the recent results of Davoult et al. (2017), who found that in comparison to bare mudflats, 56 out of 60 reported effects were higher on mudflats invaded by *Gracilaria*.

Taken together, the analyses of Ramus et al. (2017), our new analyses presented here (Figs. 1, 2), Sotka and Byers's reanalysis of our data (aforementioned t test), and the studies reviewed above, all support Ramus et al.'s conclusion that *Gracilaria* increases multifunctionality in comparison to bare mudflats.

Future studies should measure more ecosystem functions

Next, Sotka and Byers critique that the results of Ramus et al. did not support increased multifunctionality because nutrient cycling or primary productivity was not measured (i.e., as possible functions 12 and 13 that we could have measured). To put the analysis of Ramus et al. into a broader context, however, many of the research papers included in a recent meta-analysis of ecosystem multifunctionality (Lefcheck et al. 2015) quantified less functions, included many covarying and nonindependent responses (e.g., above and below ground biomass, abundance and richness), and did not report effects on either nutrient cycling or primary productivity (e.g., Gamfeldt et al. 2005; Jiang 2007; Maestre and Reynolds 2007; Laossi et al. 2008). The approaches and methodologies used, as well as the number and types of functions measured by Ramus et al., therefore sit safely within the body of work that has analyzed ecosystem multifunctionality. Nevertheless, we concur with Sotka and Byers' sentiment about the importance of measuring 'more functions', and therefore reiterate our original conclusion that future studies should "measure more ecosystem functions" (p. 8582 in Ramus et al. 2017).

Mudflats are not wastelands of poor values

Third, Sotka and Byers misinterpreted our sentence that "*Gracilaria* can provide multiple functions by creating novel habitat in an otherwise barren sedimentary landscape" (Ramus et al. 2017, p. 8581) to imply that Ramus et al. believe that mudflats are 'wastelands' of 'poor value'. Yet Ramus et al. make no mention of the words 'poor value' or 'wastelands' as is asserted by Sotka and Byers. Rather, Ramus et al. used the terms 'barren' and 'bare' interchangeably to juxtapose the physical differences between sedimentary (or rocky) systems that lack conspicuous, three-dimensional structures above the benthic surface and those dominated by large biological organisms, such as mangroves, corals, seagrasses, kelps, seaweeds, or other foundation species (i.e., with conspicuous, three-dimensional biogenic structure protruding above the benthic surface). Moreover, the usage of the term 'barren' is relatively common in the literature with many examples from ecology (e.g., Lindeboom and

Sandee 1989; Rowley 1989, 1990; Valentine and Johnson 2005; Santos et al. 2011), geology (e.g., Hays 1965; Whyte 1971; Alho 2003), and palaeontology (e.g., Ruddiman et al. 1980; Kellogg and Kellogg 1987; Löffler 1997; Alho 2003), representing research papers that, like us, do not imply that low complexity habitats are “wastelands of poor value”. Indeed, these juxtapositioned terms are commonly used by ecologists across fields, including Sotka and Byers, who have compared vegetated habitats created by ecosystem engineers to ‘bare’ (as opposed to ‘barren’) sedimentary habitats on numerous occasions (e.g., Wright et al. 2014; Bishop and Byers 2015; Kollars et al. 2016).

In this section, Sotka and Byers also question the relevance of discussing our results in the context of lost or present native foundation species, stating that there is “...minimal spatial overlap with *Gracilaria*...”. While this may be the case for the specific system in which they have worked, this assertion is misleading when considered in a broader context. First, the argument that *Gracilaria* occurs at different elevation in the intertidal than native foundation species is incorrect. *Gracilaria* often co-occurs with (and thus likely affects) a wide variety of native foundation species, including gardening polychaetes (Thomsen and McGlathery 2005; Thomsen et al. 2010; Kollars et al. 2016), oysters (Thomsen 2004; Thomsen and McGlathery 2006; Thomsen et al. 2007a), salt marshes (Thomsen et al. 2009a; Gulbransen and McGlathery 2013), canopy-forming seaweeds (Hammann et al. 2013), mussels (Thomsen et al. 2007b, 2013), and seagrasses (Thomsen et al. 2010, 2013; Hoeffle et al. 2011, 2012; Cacabelos et al. 2012; Gulbransen et al. 2013). Second, research carried out on bare mudflats has implications for nearby foundation species because storms and tidal currents cause *Gracilaria* to fragment (Thomsen 2004) and subsequently export and deposit fronds to habitats where hydrodynamic forces are reduced (e.g., around oyster reefs, seagrass beds, and salt marshes; see previous references). These resultant ‘spill-over’ effects, documented through tagging experiments, can, for example, result in faunal exchanges when organisms inhabiting *Gracilaria* on mudflats are transported through advection to salt marshes (Thomsen et al. 2009a), as well as increased local nutrient concentrations when *Gracilaria* eventually decomposes (Gulbransen and McGlathery 2013). Finally, we note that native foundation species, including

gardening polychaetes, oysters, and salt marshes, occur near our study site (and are therefore likely to be affected by *Gracilaria*), and that herbarium collections (see online Appendix D) document the presence of seagrasses in the local area in the past. While we cannot say whether seagrasses were once abundant or uncommon in the local area, they were nonetheless common enough to warrant collection and preservation—and thus represent yet another native foundation species, that, had they not disappeared, would have also interacted with *Gracilaria*.

More studies should quantify facilitation processes as well as test for large scale density-dependent effects on multifunctionality

In the fourth critique, Sotka and Byers argue that Ramus et al. misrepresented the literature about past facilitation research. However, Ramus et al. cited the same review about invasion–facilitation research (Rodriguez 2006) that Sotka and Byers referenced to argue that facilitation research was ignored (p. 8580 in Ramus et al. 2017; we also note that we cited other papers documenting facilitation by invasive foundation species). More importantly, however, Ramus et al. (2017, p. 8580) argued that published invasion impact studies typically “...consider only one or few related response variables when assessing the impacts of invaders...”, “...are conducted on small spatial scales...”, and “...rarely incorporate multiple abundance levels...”. So, in order to explicitly address these research gaps, Ramus et al. described a field experiment that manipulated six invader densities in 25 m² plots, assessed impacts on 7 (or 7 plus 4) ecosystem functions, and analyzed responses variables in a single framework using standardized approaches to quantifying multifunctionality. Given that the research gaps outlined above were underappreciated by Sotka and Byers (and possibly by other readers), we examined if these study attributes are common in the marine invasion literature by comparing Ramus et al.’s experiment to 100 representative published papers that also manipulated the abundance of marine invaders in field experiments and quantified impacts on resident species (see online Appendix B and C). For each of these 100 papers, we extracted data on the number of manipulated densities, plot sizes, whether abiotic responses were included in addition to

biological responses, and whether ‘impact’ was analyzed with multifunctionality metrics (Byrnes et al. 2014b). We also recorded if the title or abstract described whether the focal invader (1) mainly facilitated resident species, (2) both facilitated and inhibited resident species, or (3) inhibited or had no or extremely variable effects on resident species. This literature review not only confirms that Ramus et al.’s experimental approach was unique, but also re-emphasizes that major research gaps exist related to multifunctionality, large spatial scales, and a wide range of realistic abundances when assessing the impact of an invader (online Appendix B and C). For example, only one of the 100 studies manipulated larger plots (Schmidt and Scheibling 2007), only one study manipulated more invader densities (Kotta et al. 2006), relatively few studies included abiotic measurements or emphasized facilitation effects, and not a single study analyzed results with multifunctionality metrics.

Nonnative *Gracilaria* has both positive and negative effects and should not be promoted for restoration

Finally, Sotka and Byers criticize that Ramus et al. ‘promoted’, ‘recommended’, and ‘endorsed’ *Gracilaria* for restoration. However, Ramus et al. did not use any of these terms in their manuscript or in the online supplement. Instead, we state (in a box on p. 8580) that “in areas where native foundation species have been lost, invasive habitat formers may be considered as a tool to enhance multiple ecosystem functions”. It is plausible that this sentence inspired Sotka and Byers to argue that “Ramus et al. ... concluded that this and other invasive engineering species should more frequently be considered as candidate species to restore ecosystem function of degraded habitats”. However, our box-sentence was meant to reflect that holding back eradication could also be considered a management tool. In other words, Ramus et al.’s discussion of management implications was not about promoting (i.e., adding) *Gracilaria* to new habitats, but rather whether agencies should invest large amounts of limited conservation resources to remove *Gracilaria* from already invaded habitats. Ramus et al. have previously discussed both the positive and negative effects of invasive species (e.g., Thomsen et al. 2009b, 2011, 2014, 2016a), and many

of these points were reiterated in Ramus et al. (2017). For example, Ramus et al. stated that *Gracilaria* could (1) have negative effects on ecosystem functions that were not measured, (2) increase global homogenization, (3) have unknown long-term evolutionary consequences, (4) have negative impacts on cryptic and rare endemic species, (5) decrease the likelihood of native habitat restoration success, and (6) accumulate in extreme densities, where it may enhance the risk of local anoxia that can cause mortality of fish and benthic invertebrates (e.g., Thomsen and McGlathery 2006; Thomsen et al. 2009b, 2012a, b; Martínez-Lüscher and Holmer 2010; Hoeffle et al. 2011; Holmer et al. 2011; Hammann et al. 2013; Gonzalez et al. 2014). Ramus et al. also pointed out that native foundation species, like oysters, seagrasses, and marshes typically (1) have more stable biomass across seasons than *Gracilaria*, thereby providing more stable ecosystem functions, (2) have stronger legacy effects, as relic bivalves and macrophyte rhizomes can accumulate over time, and (3) do not cause large scale anoxia events and associated faunal die-offs. Taken together, these points represent a rather extensive list of ‘cons’ in the ‘pro vs. cons’ debate about whether it is prudent or not to remove *Gracilaria* from already invaded habitats (Ramus et al. 2017).

Furthermore, if eradication of *Gracilaria* is to be considered as a viable management strategy, it is also relevant to review past attempts to eradicate widely distributed invasive seaweeds—all of which, to our knowledge, have failed. This includes multimillion dollar programs to remove *Undaria pinnatifida* from the Chatham Islands, Stewart Island, and Fjordland (Wotton et al. 2004; Hewitt et al. 2005; Hunt et al. 2009; South et al. 2017), as well as *Sargassum muticum* from the United Kingdom (Farnham and Jones 1974; Gray and Jones 1977; Critchley et al. 1986). Lessons learned from these failures, in conjunction with *Gracilaria*’s wide distribution along the Atlantic Coast of the United States, high abundance in many different coastal habitats, ability to withstand stress and regrow from small fragments, and morphological similarity to native *Gracilaria* species (Thomsen and McGlathery 2007; Gulbransen et al. 2013; Nejrup et al. 2013; Hu and Juan 2014), suggest that attempts to permanently eradicate *Gracilaria* would not only be difficult and expensive, but also carry a high risk of failure. So, in contrast to the claim that Ramus et al. ‘promoted’ *Gracilaria* for use in

restoration, Ramus et al. instead listed potential negative effects of *Gracilaria* and how native foundation species, like seagrasses, marshes, and oysters (i.e., with shells or perennial clonal growth-strategies and below ground biomass) can provide more stable ecosystem functions.

Conclusions

Reanalysis of Ramus et al.'s data confirmed that *Gracilaria* increases average multifunctionality in comparison to bare mudflats (Figs. 1, 2), a finding that is supported by other studies showing higher functional responses on invaded versus noninvaded mudflats. While Ramus et al. did not measure nutrient fluxes or primary productivity, their study still analyzed multifunctionality appropriately. In contrast to Sotka and Byers's claim, Ramus et al. neither stated, nor believe, that mudflats are wastelands of poor value. A review of 100 field experiments investigating the impacts of marine invaders highlights that the approach of Ramus et al. was unique compared to past research. This is not only because facilitation was emphasized, but also because the experiment manipulated many densities in large plots and assessed impacts on many individual functions as well as integrative metrics of multifunctionality. Finally, Ramus et al. discussed many processes by which *Gracilaria* could have both negative and positive effect on ecosystem functions, as well as the pros and cons of strategies to remove *Gracilaria* from already invaded locations, thereby differing from the claim that Ramus et al. promoted *Gracilaria* for restoration. We conclude that the seaweed *Gracilaria*, bounded by Ramus et al.'s measurements and spatiotemporal, experimental, and ecological context, increases multifunctionality when invading bare mudflats.

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