Biol Invasions (2019) 21:19–25
https://doi.org/10.1007/s10530-018-1822-0

INVASION NOTE

Not so fast: promoting invasive species to enhance multifunctionality in a native ecosystem requires strong(er) scrutiny

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Received: 14 September 2017 / Accepted: 19 August 2018 / Published online: 27 August 2018

Abstract Since at least the 1980s, ecologists have argued that restoring ecosystem functioning in highly degraded areas is the "acid test" for ecological understanding (Bradshaw 1987). Ecosystem engineers and foundational species are often considered pivotal in the restoration of degraded areas (Suding et al. 2004; Byers et al. 2006), as by definition, they "engineer" biotic structure that serves as habitat. For decades, ecologists have debated when and where we may promote non-native engineers instead of native engineers for restoration. Entering into this long-standing debate, Ramus et al. (2017) reported the results from a field experiment in North Carolina with the Japanese seaweed *Gracilaria vermiculophylla* and concluded that this and other invasive engineering species should more frequently be considered as candidate species to restore ecosystem function of degraded habitats. Here, we argue that it is premature to suggest we understand the effects of the non-native *Gracilaria* on the native estuarine system well enough to promote this invader as a lynchpin of restoration efforts. Our argument is fourfold: (1) The net ecosystem effects of *Gracilaria* remain unknown because Ramus et al. overstated or did not examine the ability of the invasive seaweed to perform key services. (2) The conclusion of enhanced multifunctionality is highly dependent on several subjective, poorly justified decisions regarding the treatment of variables. (3) Contrary to the claim by Ramus et al., the mudflats where *Gracilaria* resides are not a barren sedimentary landscape without its presence. Finally, (4) Ramus et al. rely on a well-worn "strawman" approach that ignores decades of ecological research. No doubt, there are systems in which non-native engineers benefit local ecosystem functioning, but any recommendation to use a non-native in such a capacity should require careful and thorough evaluation.

Keywords Macroalgae · Multifunctionality index · Positive effects · Restoration ecology

Important, critical ecosystem services were poorly examined or ignored

Ramus et al. (2017) failed to support their conclusions of net positive ecosystem impacts because critical ecosystem functions were poorly tested or ignored. For example, the paper does not quantify primary productivity or nutrient cycling, two of the most

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fundamental ecosystem processes. Primary productivity of neither the alga (Byers et al. 2012) nor the microphytobenthos was measured, even though the latter can be substantial (Dame et al. 2000). Similarly, effects on nutrient cycling were ignored. *Gracilaria*, like other seaweeds, exudes dissolved organic matter which fosters blooms of microbes such as *Vibrio* bacteria that cause shellfish poisoning (Gonzalez et al. 2014), alters net denitrification rates (Gonzalez et al. 2013), and provides nitrogen for higher trophic levels (Gulbransen and McGlathery 2013).

Decomposition rate was used as a proxy for nutrient cycling, but the test was inappropriate. Specifically, the authors measured decomposition of *Spartina* cordgrass on *Gracilaria* mudflats in the lower intertidal zone, but this is rarely where the positively buoyant *Spartina* wrack is deposited. We also note that nearly all variables (with the exception of infaunal macroinvertebrates) focused on above-ground processes, and ignored below-ground processes (e.g., microbial productivity, bioturbation, redux potential, etc.). Overall then, the seaweed's effects on productivity and nutrient cycling are potentially large but unquantified.

Whether *Gracilaria* affects productivity of animal associates is a more complicated question. To be sure, *Gracilaria* patches have greater densities of invertebrate associates (Johnston and Lipcius 2012; Wright et al. 2014; Kollars et al. 2016): e.g., Byers et al. (2012) concluded that "…for certain taxa, (*Gracilaria*'s) effects are positive." Additionally, and as demonstrated by Ramus et al. for the first time, greater densities of fishes (as a group) also occur in *Gracilaria* patches than on bare mudflats. However, while snap-shot estimates of larger, highly mobile fishes were presented as proxies for secondary productivity, this approach does not distinguish between enhanced system-wide productivity and a transient, spatial redistribution (attraction) of mobile animals. The distinction between attraction and production has profoundly different implications for valuing a structure or habitat, and it has vexed fisheries managers of artificial reef programs for decades (Pickering and Whitmarsh 1997). It is similarly uncertain for *Gracilaria* as well.

Even if snap-shot estimates of animal associates truly represent enhanced production facilitated by this invader, a statistically-positive effect of this diverse group does not necessarily translate into a positive effect for ecosystem functioning and services. This is because direct and indirect species interactions can profoundly change the strength and direction of functioning. For example, even if the total abundance rises, there will be different system-wide outcomes if the invader enhances native predators versus competitors versus herbivores (Noonburg and Byers 2005), and the net outcome of these changes may or may not be positive for the system and society.

The paper does not convincingly demonstrate other effects on ecosystem services, despite its assertions. Ramus et al., Table S1 states a positive role of non-native *Gracilaria* in coastal protection. Although they found that artificially-secured *Gracilaria* attenuated water flow up to ~ 15%, this was measured with dissolution blocks under typical tidal and current surges. It is impossible to translate this measurement into protection from coastal storms, which have forces that are orders of magnitudes greater than typical conditions. Moreover, native seagrasses and salt marshes attenuate larger wave energy because they are rooted, while *Gracilaria* has no roots (Kollars et al. 2016). Thus, appropriate tests are needed before meaningful coastal protection by *Gracilaria* can be concluded. We are also puzzled by their assertion that *Gracilaria* provides benefits of "Tourism, recreation, education and research" as listed, without justification, by Ramus et al. in Table S1.

Multifunctionality is unsupported: re-analysis leads to a different conclusion

In addition to the incomplete set of ecosystem functions Ramus et al. used to calculate impacts of *Gracilaria* on multi-functionality, decisions over how to treat and include other variables were highly subjective. Four of the positive response variables used were epifaunal abundance and epifaunal richness and nursery species abundance and nursery species richness (see also Byers et al. 2012; Johnston and Lipcius 2012; Kollars et al. 2016 for similar positive results). Collinearity of these response pairs is highly significant ($p < 0.001$ in correlation of the two epifaunal variables and correlation of the two nursery variables). The strong correlative relationships are likely for real biological (i.e., mechanistic) reasons, and thus, treating them as independent within a multifunctionality index ostensibly overweights positive effects and is poorly justified.

Two variables (water flow and ray foraging intensity) decrease with *Gracilaria*, but the authors subjectively decided to mathematically invert them ("reflect" in the parlance of multifunctionality methodology) so they appear positive, even though the effect of these changes on ecosystem services is ambiguous. For example, we posit that the decline in ray foraging with *Gracilaria* could be viewed as a true negative effect (i.e., dense alga inhibits energy transfer to higher trophic levels), instead of a positive effect, as the authors argue without evidence. Likewise, decreased water flow might (arguably) facilitate shoreline protection, but could also reduce mixing of water, oxygen, food, and propagules and thus comprise a net negative effect. In addition to these subjective decisions, the authors relegated four more variables to the Appendix because only 3-month, and not 10-month, averages of them were possible.

The impacts of these subjective decisions are nontrivial because the multi-functionality index is sensitive to which variables are used and the directions of their responses (Byrnes et al. 2014). We re-analyzed both the multifunctionality index and the related threshold analysis using all of the available data in Ramus et al. (including the 4 functions in their Appendix) with two exceptions: we used only epifaunal and nursery abundance (and thus removed the two respective co-varying richness functions), and we used the measured declines in water flow (inferred from dissolution rates) and in ray predation rates instead of reflected functions. In this new, and equally justified analysis, the positive effect of *Gracilaria* on multifunctionality disappears (original analysis $r^2 = 0.832$ vs new analysis $r^2 = 0.127$; Fig. 1a vs b). Moreover, in the threshold analysis of Ramus et al., *Gracilaria* cover positively related to the number of functions

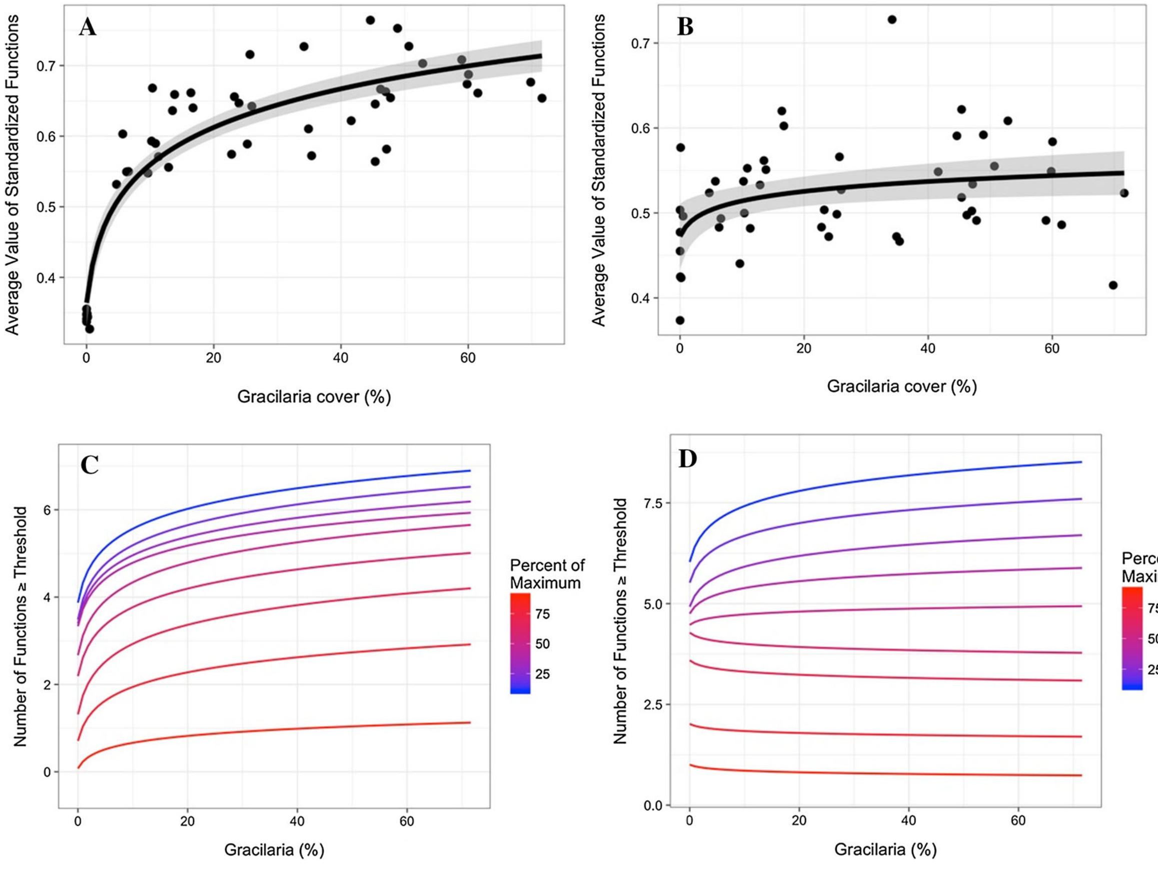

Fig. 1 The effect of variable manipulation on inference of standardized multifunctionality index (**a**, **b**) and a threshold function analysis (**c**, **d**) of Byrnes et al. (2014). **a**, **c** are recapitulations of Figure 2H and I of Ramus et al. (2017) using 7 variables. **b** and **d** are our re-analyses of 9 variables

maintained at all thresholds (10–90%) (Fig. 1c). In our re-analysis, this positive effect of *Gracilaria* on multifunctionality declined to zero, and had an apparently negative effect at thresholds above 50% (Fig. 1d). Thus, our treatment of variables utilized subjective but justifiable decisions and yielded a different conclusion (i.e., the "positive" effect was weak to absent).

Intertidal mudflats are not a wasteland

Ramus et al. (2017) argue that "*Gracilaria can provide multiple ecosystem functions by creating novel habitat in an otherwise *barren* sedimentary landscape*" (our emphasis). Intertidal mudflats are not "barren," nor of poor value. Rather, mudflats have their own unique and diverse set of invertebrate, microalgal and detrital communities; often provide important ecological goods and services; and are specialized habitats for some organisms such as shorebirds (Lenihan and Micheli 2001; Byers and Grabowski 2014). The enormous and costly efforts in both San Francisco and Willapa Bays on the US west coast to eliminate invasive *Spartina* hybrids from intertidal mudflats attest to their value (Williams and Grosholz 2008).

Furthermore, the mudflats upon which *Gracilaria* resides do not necessarily exist because native foundation species previously occupied them and have now disappeared. The authors cite statistics on historic declines in native foundational species—oysters, *Spartina* cordgrass, and seagrasses. However the numbers and statistics are for broader spatial scales (i.e., states), and do not necessarily hold at the level of individual estuaries or mudflats, such as the one in which they worked.

Importantly, the native foundation species they list would have minimal spatial overlap with *Gracilaria,* which occupies a different microhabitat. Specifically, the area where *Gracilaria* resides and Ramus et al. conducted the field experiment, is the low intertidal zone—an area lower in the intertidal relative to *Spartina* and most oysters, and higher than the exclusively subtidal seagrasses. Thus, *Gracilaria* cannot act as a habitat replacement for claimed extirpated native foundation species and cannot serve as model for such a system.

"Potential benefits of invasive species may have been overlooked" is a strawman

In framing the impetus for their study, Ramus et al. promote a strawman by arguing that positive effects of introduced species are rarely considered, especially in the context of restoring community or ecosystem function (e.g., "While invasive species often threaten biodiversity and human well-being, their potential to enhance functioning by offsetting the loss of native habitat has rarely been considered."; 1st sentence of the Abstract). This assertion is a misrepresentation of the literature. Non-native species have been long recognized as having negative, neutral and positive effects (Ewel and Putz 2004; Rodriguez 2006; Ruesink et al. 2006; Pintor and Byers 2015; Haram et al. in press). In addition to their benefits as agricultural crops and livestock (Pimentel et al. 1999), non-native species have been promoted for decades as possible restoration tools (Sousa et al. 2009; Wan et al. 2009; Schlaepfer et al. 2011; Jacobs et al. 2015). Their benefits have included food and wood production, habitat engineers, nursery provisioning, nutrient sequestration, biological control of pests, and erosion abatement. We outline a few of these studies, especially as they pertain to providing missing habitat functions, below.

In coastal zones, non-native oysters, including the ubiquitous Japanese oyster, *Crassostrea (*now *Magallana) gigas*, have also been recognized for several positive effects (Ruesink et al. 2005). Fernandez et al. (1993) showed that shells of *C. gigas* have been used as shelters to protect economically valuable juvenile Dungeness crabs (*Cancer magister*). In addition to habitat effects, the biofiltration of dense populations of invasive bivalves, including the zebra mussel, *Dreissena polymorpha*, has been used to clean water (Reeders et al. 1989; Phelps 2005). The seaweed *Undaria pinnatifida* was accidentally introduced into many nearshore systems worldwide, and in a review of the vast literature on *Undaria,* Epstein and Smale (2017) conclude that "*the presence of a habitat forming, primary producer with a broad ecological niche and potential commercial value, may deliver significant economic and even environmental benefit*" (p. 8638).

Vascular marsh plants have a long history of translocation to stabilize shorelines and bioremediate sediment and thus improve habitat. In Europe, the marsh reed *Phragmites* was used as a bioengineer to protect shorelines (Bakker 1960), oxidize sediments (Armstrong and Armstrong 1988), and remove heavy metals (Peverly et al. 1995). The marsh cordgrass, *Spartina* spp., invasive in several areas worldwide, remediates heavy metals, especially mercury (Kraus et al. 1986) and can serve as a carbon sink (Kennedy et al. 2017). Several non-native cordgrass species have been planted for shoreline stabilization and remediation in Europe, San Francisco Bay, China (Campbell et al. 2009) and Australia (Kennedy et al. 2017). Levin and Crooks (2012) point out that sea-level rise will increase interest and pressure to use the sediment accreting and protective services provided by non-native plant species (Weis and Weis 2003; Ewel and Putz 2004; Meyerson et al. 2009).

Perhaps some of the strongest examples in the area of habitat replacement come from terrestrial forests, where non-native trees are widely recognized for positive effects and have been used to restore function where native habitat has been lost (e.g., Knoke et al. 2014; Gerard et al. 2015; Jacob et al. 2017). These species colonize environmentally-stressful habitats and restore nitrogen stocks (MacDicken 1994). Several non-native species provision important habitats. Jacob et al. (2017) found that non-native fruit trees planted by farmers in deforested areas attract seed dispersers and create microclimates that help native seedlings to establish. Non-native *Eucalyptus* trees in California harbor monarch butterflies, a native species of high conservation concern (Griffiths and Villablanca 2015).

Thus, despite the strawman asserted by Ramus et al., the literature reveals many introduced species with positive outcomes for local economies and environments. However, any efforts to restore native systems with non-native species require careful consideration, experimentation and synthetic analysis before they are endorsed. Ramus et al. do acknowledge possible negative effects of *Gracilaria* (p. 4) on "cryptic and rare endemic species,…on the likelihood of native habitat restoration success, and…the risk of local anoxia." However, there is no further mention of these unmeasured effects, and instead, the authors proceed with a recommendation to use *Gracilaria* in restoration.

History is replete with examples of invaders prematurely promoted for restoration that ended up doing more harm than good, e.g., kudzu (*Pueraria montana*), ice plant (*Carpobrotus edulis*), multiflora rose (*Rosa multiflora*). Even the vascular marsh plants (e.g., *Spartina*) mentioned above have not been universally positive and expressed several strong negative ecological effects after deliberate introduction. Thus, we strongly caution against hastily endorsing a non-native species for restoration. The history of biological control provides a useful analogy. Biocontrol has been transformed over the past couple of decades from a "laissez-faire" approach to a more thoughtful, data-rich approach that emphasizes environmental safety (Strong and Pemberton 2000). The same standards should be mandated for non-natives used for restoration purposes. Because of unintended consequences, unstudied aspects, and the precautionary principle, it behooves us to use the best science in our evaluations of each non-native species, and not rush to judgement with hastily or subjectively analyzed data.

In sum, we cannot agree with the conclusion that non-native *Gracilaria* should be promoted for boosting local ecosystem services. Rather, we believe the data of Ramus et al. depict a non-native species with a mix of positive, negative, and neutral effects. More broadly, we plea that recommendations in both restoration and invasion ecology be based on sound science, and that authors in both fields frame their data to best represent the current state of understanding. As highlighted by veterans of the policy debate on climate change (Smith and Stern 2011), the strong promotion of weakly supported conclusions has the potential to yield poor policy and undermine future public support for science-based solutions.

Acknowledgements We thank two anonymous reviewers for thoughtful comments that improved this manuscript.

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