

Correction

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An invasive foundation species enhances multifunctionality in a coastal ecosystem

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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. We manipulated the abundance of the nonnative, habitat-forming seaweed *Gracilaria vermiculophylla* in large plots (25 m²) on southeastern US intertidal landscapes to assess impacts on multiple ecosystem functions underlying coastal ecosystem services. We document that in the absence of native habitat formers, this invasion has an overall positive, density-dependent impact across a diverse set of ecosystem processes (e.g., abundance and richness of nursery taxa, flow attenuation). Manipulation of invader abundance revealed both thresholds and saturations in the provisioning of ecosystem functions. Taken together, these findings call into question the focus of traditional invasion research and management that assumes negative effects of nonnatives, and emphasize the need to consider context-dependence and integrative measurements when assessing the impact of an invader, including density dependence, multifunctionality, and the status of native habitat formers. This work supports discussion of the idea that where native foundation species have been lost, invasive habitat formers may be considered as sources of valuable ecosystem functions.

exotic plant | ecosystem engineer | novel facilitation | conservation | biodiversity

The large-scale degradation of marine ecosystems is unequivocal (1–4). Recent assessments suggest that ~20% of coral reefs (5), 30% of seagrasses (6), 45% of salt marshes (7), and 90% of oyster reefs (8) have been lost worldwide, implying that many coastal ecosystems around the world have been converted from complex biogenic habitats to barren sedimentary systems. Because a significant proportion of society depends on these coastal ecosystems to generate >10¹⁴ USD in services each year through storm protection, food production, and tourism (1, 9), conservation resources of >10⁹ USD are spent globally each year in an attempt to reverse the decline of these coastal foundation species (10, 11). Yet many efforts to restore coastal habitats have achieved only limited success despite high investment per hectare (12–14). It is therefore pertinent that research examine different means by which the loss of marine foundation species can be offset in order to provide society with the goods and services needed to prosper.

Nonnative species often threaten biodiversity (15) and incur substantial costs (16), but recent reviews have also pointed out their potential value for conservation (17, 18). Related analyses also suggest biases that favor finding negative effects, and, as a consequence, the potential benefits of invasive species may have been overlooked (19, 20). For example, most studies (i) examine impacts when invasive species are displacing functionally similar native species (21–24), (ii) consider only one or few related response variables when assessing the impacts of invaders (19, 20), (iii) are conducted on small spatial scales (e.g., in aquatic systems typically ≤1 m²; refs. 25 and 26), and (iv) rarely incorporate multiple abundance levels, despite the fact that impacts depend fundamentally on the abundance of the invader (26, 27).

Because managers often need to conserve ecosystem functions where native foundation species have been lost (e.g., kelp forest

retreat due to warming waters, coral reef loss due to multiple stressors, oyster reef decline due to overharvesting and diseases, seagrass loss to eutrophication and warming; refs. 5, 8, 14, 28, 29), recognizing that nonnative species may enhance ecosystem functions could influence management decisions (17, 18). For example, in coastal areas that have experienced degradation of native foundation species, such as on coral reefs (5, 30), seagrass beds (6), and oyster reefs (8, 12), invasive foundation species could have significant positive effects, particularly if they replace and substitute ecological functions that have otherwise been lost (18, 21, 22, 31). With the exception of highly managed systems, such as agricultural fields, society values ecosystems that simultaneously provide many different and complementary functions and services (1, 9). In order to facilitate informed management decisions, impacts of invaders should therefore, whenever possible, be assessed on multiple ecosystem functions (32), at realistic spatial scales (e.g., landscape; refs. 26 and 33), and across a wide range of realistic invader abundances (26, 27, 34). Only then will managers have critical information needed to better predict when and where invasion impacts will be positive vs. negative.

To address this research gap, we focused on the nonnative seaweed *Gracilaria vermiculophylla* (hereinafter *Gracilaria*) that has invaded shallow soft-bottom lagoons and estuaries throughout coastlines of the North Atlantic (35). *Gracilaria* is expected to have negative ecological effects where native foundation species are present (24), but where native habitat formers are absent or have declined, *Gracilaria* can generate mosaics of vegetated habitats that could constitute hotspots of ecosystem functions (23). An initial survey of two sites along the North Carolina coast revealed high abundance and variability in *Gracilaria* cover (mean ± SD, 14 ± 23%, but also often with 100% cover; Fig. 1A–C). In North

Significance

The accelerating loss of coastal foundation species impairs the delivery of vital ecosystem services on which nearly half the human population depends. Recognizing how loss of habitat-forming species such as seagrasses and oysters can be offset is therefore essential. This paper demonstrates that in areas where native foundation species are absent, nonnative habitat formers can amplify the production of diverse ecosystem functions that underpin provisioning of services to humans, such as food production. Our findings suggest that in areas where native foundation species have been lost, invasive habitat formers may be considered as a tool to enhance multiple ecosystem functions.

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The authors declare no conflict of interest.

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Data deposition: The plot-level data used to generate all analyses and figures of this paper are tabulated in [Dataset S1](#) and have been made available digitally via GitHub (<https://github.com/apramus/invFxfunc>).

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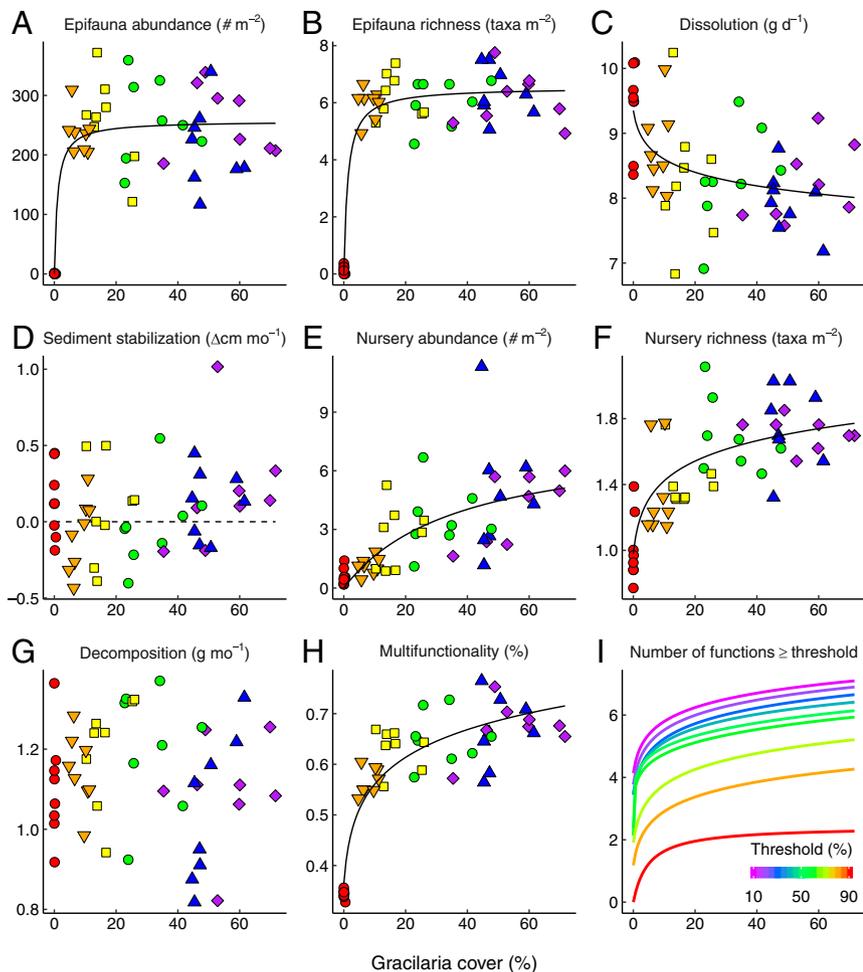


Fig. 2. Density-dependent impacts of an invasive foundation species on coastal ecosystem functions. (A) Epifauna abundance. (B) Number of epifauna taxa. (C) Gypsum dissolution (a proxy for flow attenuation; data were reflected before calculating multifunctionality, so that reduced dissolution corresponded to increased flow attenuation). (D) Sediment stabilization, the change in substrate elevation per month. Values above the dashed line represent accretion, whereas those below represent erosion. (E) Abundance of nursery species, i.e., mobile macrofauna and juvenile species of commercial importance. (F) Taxonomic richness of nursery species. (G) Decomposition (biomass of *Spartina* stems lost). (H) Multifunctionality index; the average of the seven standardized functions in percent. (I) 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 below. Points are time-averaged responses of each function vs. the average *Gracilaria* cover of each plot ($n = 48$). Colors and symbols correspond to the six 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). The best-fitting models determined by AICc are shown where significant ($F_{1,46} \geq 17.61$; $P < 0.001$). In I, the form of the relationship was logarithmic up to the 40% threshold (blue-green), then changed to a power function at 50% (green), back to logarithmic at 70% (yellow), and then to a hyperbolic function at 90% (red).

(23, 31, 42, 44, 45), although those studies quantified impacts from only a few experimental densities and on smaller spatial scales. Our results are also consistent with a growing body of work demonstrating the importance of positive interactions in ecological communities, especially under conditions of elevated physical stress that dominate degraded coastal habitats targeted for restoration (31, 38, 46). Furthermore, we note that *Gracilaria* represents a typical foundation species (*sensu* ref. 47) because it increases biodiversity through habitat formation and delivers multiple ecosystem functions, analogous to trees in forests (48), salt marshes (38), oyster reefs (8, 12), seagrasses (6), mussel beds (46), and many other sessile taxa (1, 9). Our results therefore support the need for an experimental and comprehensive examination of invasive species' effects before ascribing a sign (+ or -) to their overall impact (18, 19).

Although we did not identify the underpinning mechanisms by which *Gracilaria* increases ecosystem multifunctionality, our results suggest that, by forming a complex biogenic habitat, *Gracilaria* (i) occupies the fundamental niche of a foundation species, (ii) directly increases biodiversity, (iii) indirectly increases ecosystem functioning (via its effect on biodiversity), and (iv) thereby provides density-dependent functions comparable to those of functionally similar natives (20–22, 31, 44, 45).

It is possible that *Gracilaria* has negative effects on ecosystem functions that were not measured here (24) or that could emerge if *Gracilaria* were to accumulate in very large densities in stagnant waters (49). However, we found no negative effect of *Gracilaria* on either infauna or waterfowl activity, and only a weak negative effect on ray foraging activity even at the highest densities (*SI Text* and *Fig. S2*; these additional functions were measured only at the end of the experiment and thus were excluded from the formal

analysis). It is likely that decreased ray foraging could facilitate commercially and recreationally important bivalves like clams, mussels, and oysters, similar to how *Gracilaria* modifies other predator-prey interactions in this system (50).

Ecologists are becoming increasingly aware that native foundation species provide ecosystem functions in nonlinear ways (39–41). Our experimental findings demonstrate similar nonlinearity in ecosystem functions provided by a nonnative foundation species that has invaded thousands of kilometers of coastline throughout the Northern Hemisphere. We also found that the slopes and saturation points in these nonlinear functions vary widely for different ecosystem functions. Scale dependency is likely an important factor contributing to this variation. For example, functions such as wave attenuation and sediment stabilization may manifest on larger scales and at higher densities (39), whereas functions associated with biodiversity, such as productivity and nursery habitats, appear to operate on smaller scales and at lower densities (i.e., with early thresholds as shown here and in ref. 41). Although curve shapes of multifunctionality are likely to depend on the functions included in the analysis, our supplementary analysis (adding four processes measured at the end of our experiment) showed similarly curved functional responses, suggesting that our results are robust (*Fig. S2*). Nevertheless, to better understand the impacts of nonnative coastal foundation species, future studies should manipulate more densities (including both high and low extremes) and measure more ecosystem functions across different environmental gradients (e.g., salinity, depth, latitude).

Management Implications. Human activities are accelerating the losses of species that provide the foundation for coastal habitats, including seagrasses, oysters, and salt marshes (3, 4, 6–8, 12),

and, consequently, the services that these species provide (1, 2, 9). Restoration is an important tool for mitigating coastal degradation, but despite recent advances (e.g., ref. 38), current practices have yet to succeed at scales sufficiently large to match the scale of degradation. For example, a recent synthesis (13) suggests relatively low survival of restored seagrasses (41%), salt marshes (65%), and oyster reefs (56%) in the short-term (≤ 2 y) despite mean restoration costs of \sim \\$700,000, \\$1,040,000, and \\$860,000 (2010 USD) per hectare for these three coastal habitats, respectively (Table S2). Moreover, these appraisals do not take into account that (i) the cost and success of simultaneously eradicating nonnative analogs is uncertain (51); (ii) coastal management is becoming increasingly complicated as global anthropogenic stressors, such as climate change, eutrophication, and overharvesting, alter the context for future native and invasive species interactions (52–54); and (iii) managers and researchers often do not know whether invasive foundation species are drivers, passengers, or back-seat drivers of ecological change, even though each of these scenarios requires a unique management and restoration approach (55, 56). Currently, it appears that replacement of many native by nonnative foundation species, such as Wadden Sea mussels by invasive oysters and Mediterranean seagrasses by the nonnative seaweed *Caulerpa*, are driven more by external factors such as warming and eutrophication than by competitive interactions among foundation species (57–59).

Based on our case study, we recognize several advantages and disadvantages associated with passive “do nothing, laissez faire” vs. active “remove and replace” approaches to the management of invasive foundation species. For this *Gracilaria* invasion in an area where native foundation species have severely declined, our results suggest that a passive approach could help sustain fishery outputs, invertebrate biodiversity, and erosion control, without causing reductions in extant native foundation species. Akin to other invasions, however, *Gracilaria* may still increase “global homogenization” (60) and could have unknown long-term evolutionary consequences (61). In addition, *Gracilaria* could potentially (i) have negative impacts on cryptic and rare endemic species (which would require a massive sampling effort to detect), (ii) decrease the likelihood of native habitat restoration success, and (iii) accumulate in extreme densities, where it may enhance the risk of local anoxia that can cause mortality of fish and benthic invertebrates (49, 62). For an active remove and replace strategy, managers, in contrast, would seek to remove *Gracilaria* and restore economically and culturally important native foundation species to regain their associated benefits that support high biodiversity, sustainable fisheries, and regulation of erosional forces caused by wind and waves. Native oysters, seagrasses, and marshes typically have more stable biomass across seasons than *Gracilaria*, thereby providing more stable ecosystem functions. These native foundation species also have stronger legacy effects, as relic bivalves and macrophyte rhizomes can accumulate over time and thereby enhance ecological functions over longer time scales (63, 64). Finally, in contrast to *Gracilaria* and other invasive seaweeds, native marshes, oysters, and seagrasses have not been shown to cause large-scale anoxia events and associated faunal die-offs.

Nevertheless, despite the benefits of a remove and replace strategy, this approach has clear associated risks and costs. First, the initial economic cost is fantastically high, and both the removal of invasive species and subsequent restoration of native species carry a high risk of failure. The remove and replace approach may also result in reintroduction, and will necessitate long-term monitoring and management of restored natives (13, 51). Clearly, more research is needed to provide better data for evaluating these management approaches. For example, it will be important to study (i) facilitative vs. antagonistic impacts of *Gracilaria* on seagrasses, oysters, and marshes, and whether these native foundation species can recolonize invaded areas; (ii) long-term multigenerational impacts of *Gracilaria* on invertebrates, fish, and birds to, for example, document whether this invasion leads to evolutionary traps or whether there are cryptic native

species that are lost or decimated following the invasion (61); and (iii) economic, environmental, and cultural costs and benefits associated with the contrasting management schemes (16). However, until such research has been carried out, 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 (17, 18), especially when native foundation species are absent and eradication and restoration is infeasible.

Conclusions. Our large-scale field experiment documented positive density-dependent relationships between *Gracilaria* abundance and many individual and integrative ecosystem functions. Consequently, 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. We hope that this work will stimulate new thinking and innovative research on the impacts of nonnative foundation species, which are likely to become increasingly common community members in our rapidly changing world.

Materials and Methods

Study System. The experiment was carried out on intertidal mud and sandflats located within the Zeke’s Island National Estuarine Research Reserve (NERR), a shallow lagoon-like estuarine complex in the lower Cape Fear River, NC (Fig. S3). Tides are semidiurnal and range from 1.1 to 1.7 m above mean lower low water (MLLW). Salinity ranges from 20 to 35 ppt depending on rainfall and tidal currents. Like much of the Atlantic coast of the southeastern US, this estuary was once dominated by such species as salt marsh cordgrass (*Spartina alterniflora*) in the high-intertidal zone, oyster reefs (*Crassostrea virginica*) in the mid-intertidal zone, and mudflats in the low-intertidal zone, in which *Gracilaria* is becoming increasingly common (23). The infaunal polychaete *Diopatra cuprea* is relatively common in some locations and can facilitate *Gracilaria* by incorporating fronds into its tube caps (31, 65). At the study site, *Gracilaria* forms extensive meadows and is typically the only macrophyte on the intertidal flats (Fig. 1 A–C); the ephemeral green seaweed *Ulva* spp. is sometimes found in low abundance in spring.

To investigate the potential extent of *Gracilaria* impacts, we quantified *Gracilaria* cover along 14 intertidal line transects in Zeke’s Island NERR (33.95 N, 77.94 W) and eight transects in Masonboro Island NERR (34.14 N, 77.85 W) during 2013. Cover was quantified during low tide in 10–15 0.25-m² quadrats positioned haphazardly (>1 m apart) along each transect running from high to low intertidal (~ 0 m MLLW) perpendicular to the water line. Replicate transects were separated by at least 5 m. *Gracilaria* cover was scored within each quadrat using a modified Braun–Blanquet method, in which the quadrat was divided into a 5 \times 5 grid and each square was scored as 0 for $<50\%$ cover or 1 for $>50\%$ cover. In instances where the cumulative score was 0 despite the presence of a small frond of algae in the quadrat, it was scored as 0.5. The cumulative scores of each quadrat were divided by the total possible score (i.e., 25) and multiplied by 100 to obtain *Gracilaria* cover in percent. The mean cover across all transects and sites was 13.8% (SD = 23.3%, $n = 304$), suggesting high variability of *Gracilaria*, consistent with previous reports (35).

Experiment. We manipulated *Gracilaria* cover across six density treatments ($n = 8$ per treatment) in a large-scale field experiment using 25-m² plots (Fig. 1 D–F). We selected three low-intertidal flats spanning >1 km in the reserve that differed in terms of area, flow regimes, *Gracilaria* cover, grain size, and proximity to the *Spartina* salt marsh. The three flats represented the continuum of estuarine habitats where *Gracilaria* naturally occurs in this area. We established the 48 plots along the mean low water line at 5-m intervals by adding 3-m steel rebar 1.2 m into the substrate at each plot corner. Treatments were randomly assigned to the plots to avoid potentially confounding small-scale effects of site (and all plots had only a few *Diopatra* tubes). *Gracilaria* was fixed in a plot with metal “U-pegs” (constructed from clothes hangers; ref. 66) by physically staking handful-sized “clumps” of loose thalli to the sediment surface. Pegs were flushed with the sediment surface to avoid above-surface experimental artifacts. Thus, our six treatments were based on the total number of pegs per 25 m² (arranged in squared grids) as follows: 0 (0 \times 0), 9 (3 \times 3), 36 (6 \times 6), 100 (10 \times 10), 225 (15 \times 15), and 400

(20 × 20). We acknowledge that *Gracilaria* density thereby covaried with peg density; however, all pegs were flushed with or slightly below the sediment surface and thus did not affect any ecosystem functions above the sediment surface. More importantly, all peg densities were relatively low, corresponding to a maximum of 16 pegs per m² (a maximum of 4 pegs per epifauna quadrat and no pegs in any infaunal cores). Specific tests of peg artifacts comparing 1-m² plots with 0 vs. 16 pegs (without any *Gracilaria*) demonstrated that even at the highest densities used in our experiment, pegs had no effect on the abundance and taxonomic richness of epifauna or infauna, decomposition, dissolution, bird or ray feeding activities, or average multifunctionality (one-way ANOVA, $P \geq 0.38$ for all responses; Table S3).

Gracilaria was collected from nearby locations and added to plots in the U-peg grids in August 2013 (Fig. 1 D and E). Treatments were maintained and response variables were quantified approximately monthly from September 2013 to June 2014 (treatments were maintained and measured at total of 10 times). At each plot visit, we quantified the cover of *Gracilaria* (in 10 randomly placed 0.25-m² quadrats per plot) and seven ecosystem functions (see the next section for details) before maintaining *Gracilaria* densities by replenishing U-pegs devoid of *Gracilaria* and manually removing *Gracilaria* from control plots.

To examine the effect of *Gracilaria* on epifauna, we positioned a 0.25-m² quadrat in the center of each plot and collected all *Gracilaria* and associated epifauna into a zip-top bag. Thus, here epifauna refers to organisms associated with both *Gracilaria* and the sediment surface (23). In the laboratory, *Gracilaria* was rinsed in freshwater and shaken for ~1 min to remove epifauna, which were captured in a 500- μ m sieve. The wet biomass of *Gracilaria* was quantified after centrifugation to remove excess water. Epifauna were identified and enumerated to broad taxonomic groupings (typically family level) under a stereomicroscope (~18 \times ; Nikon SMZ800). For simplicity, all faunal data were standardized to unit area. Taxonomic richness was rescaled to unit area using the species–area relationship and assuming a conservative z value of 0.15 (67).

To quantify whether *Gracilaria* attenuates hydrodynamic forces, we used gypsum dissolution blocks (68). Gypsum dissolves at a rate proportional to water velocity and thus represents an integrated proxy for tidal currents and wave exposure (69). We created gypsum blocks as hemispheres ($\phi = 6.5$ cm) from dental plaster (Die Keen; Heraeus Kalzer), covered on the bottom with two layers of polyurethane to ensure that an equal surface area would be subject to dissolution (70). Gypsum blocks were dried at 60 °C for a minimum of 24 h, after which the initial mass was recorded and one block was deployed flush with the substrate surface in the center of each plot for 4 d. Following retrieval, the gypsum blocks were dried and reweighed, and the dissolution rate was calculated as grams of gypsum dissolved per day. Because lower dissolution rates indicate greater flow reduction, dissolution rate was calculated using the equation $-f_i + \max(f_i)$, so that greater flow reduction corresponds with a positive contribution to ecosystem functioning (32).

To examine the effect of *Gracilaria* on sediment stabilization, we marked all corner poles at 20 cm above the substrate surface in August 2013, then measured the distance between the marking and the substrate surface with a ruler to the nearest 0.5 cm at the end of each month. We calculated the monthly (30 d) change in height in cm by subtracting the final distance from the initial distance to the substrate (using the average of the four corners per plot) and correcting for the time interval between measurements. Accretion and erosion are represented as positive and negative values, respectively.

To assess the effectiveness of *Gracilaria* as a nursery habitat for commercially and recreationally important species, we sampled the entire plot using a 1.2-m-high × 6.7-m-wide nylon seine net (The Fish Net Company; mesh size 3.175 mm) during a falling tide (Fig. S1). On completion of a pass, we swiftly pulled the net taught, tilted it into a horizontal position, and lifted it from the water into an adjacent boat (RV Adelaide) in a single motion. Organisms (>1 cm) retained on the boat were identified to the family level and enumerated before being returned to the water. Abundances were reported per unit area (dividing by 25 m²), and richness data were rescaled to unit area using the species–area relationship and assuming a conservative z value of 0.15 (67).

We quantified the effect of *Gracilaria* on decomposition processes as described previously (71). Standing dead *Spartina* stems were collected from

adjacent salt marshes, washed, and dried at 60 °C for a minimum of 72 h (until no further weight loss occurred). We pooled multiple stems to achieve an initial mass of 7.0 ± 0.5 g and placed them inside a mesh litter bag, which was closed and deployed on the sediment surface in the center of each plot. Bags were retrieved just before the next treatment maintenance. Remaining stem material was washed, dried, and weighed, and the decomposition rate was recorded as the mass lost in grams per month.

Data Analysis. We calculated the average response of each function in each plot using the full 10-mo dataset (48 plots sampled each month; Dataset S1), such that each plot is represented by a single value in each plot of Fig. 2. We analyzed the abundance and taxonomic richness (of epifauna and nursery species) as separate functions because abundance more directly affects services like carbon sequestration and the maintenance of fisheries, whereas richness reflects taxonomic complementarity (i.e., different taxa support different functions; e.g., ref. 71) and redundancy (i.e., different taxa support similar functions), which can affect the resilience of ecosystem processes. To assess whether *Gracilaria* cover enhances the simultaneous performance of all seven measured functions, we used the *multifunc* package (version 0.7.0; <https://github.com/jebyrnes/multifunc>) and the averaging and single threshold approaches outlined previously (32). The averaging approach determines the average level of a suite of functions by standardizing each function to a common scale and taking their mean. After reflecting dissolution (presented in its raw form in Fig. 2C) to represent a positive contribution to functioning, we calculated an average multifunctionality index (in %) for each plot (Fig. 2H). Here we assume that high values of each of our functions correspond to high ecosystem functioning (i.e., higher values of sediment stabilization denote a higher level of performance for this function). The average multifunctionality index can be interpreted as the average level of all seven functions; however, this index cannot be used to interpret whether all functions are being performed simultaneously at a high level, given that functions performed at low levels can be averaged out by those performed at high levels. Thus, we also tallied the number of functions, at their standardized function value, in each plot that surpassed each of nine threshold levels (10%, 20%, 30%, 40%, 50%, 60%, 70%, 80%, and 90% of maximum functioning). Threshold index scores, which range from none to all seven functions, can be interpreted simply as the number of functions performed above a given threshold level in a plot (Fig. 2I).

Because recent experiments and ecological theory suggest that relationships between the structure and function of coastal habitats are characterized by thresholds and nonlinear limiting functions (39–41), we analyzed the relationship between *Gracilaria* cover and each response variable individually by comparing five models (41, 72). Using nonlinear least squares (73), we fit null, linear, log, hyperbolic, and power relationships for each response using the average *Gracilaria* cover (in %) of each plot as the explanatory variable. Model selection was based on AICc (74, 75). For each response variable, we compared the null model (i.e., just the intercept, a straight horizontal line representing the mean response) with the model of best fit using one-way ANOVA. We report the significance of the *Gracilaria* cover treatment as the probability (P) of obtaining the model, given that the null hypothesis is true. Model fits, AICc values, AICc weights, and parameter estimates for each ecosystem function and multifunction response variable are reported in Dataset S2. All analyses were conducted in R version 3.3.1 (76).

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