



# Little giants: a rapidly invading seagrass alters ecosystem functioning relative to native foundation species

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## Abstract

The spread of invasive species is a major component of global ecological change and how and when to manage particular species is a difficult empirical question. Ideally, these decisions should be based on the specific impacts of invading species including both their effects on native competitors and how they may or may not play similar roles in broader ecosystem functioning. *Halophila stipulacea* is an invasive seagrass currently spreading through the Caribbean, and as seagrasses are foundation species, the effects of invasion have the potential to be particularly far-reaching. To evaluate the impacts of *H. stipulacea* we quantified spread and potential for displacement of native seagrasses as well as the effects of invasion on multiple ecosystem processes, particularly resource support for higher trophic levels and habitat creation. Long-term monitoring suggested that *H. stipulacea* likely displaces some native seagrasses (*Syringodium filiforme* and *Halodule wrightii*), but not others. *Halophila stipulacea* had lower *N* and protein levels and higher *C:N* ratios than native seagrasses, and as such is a poorer quality resource for consumers. We also observed significantly lower consumption of *H. stipulacea* than the native *S. filiforme* but limited differences compared to *Thalassia testudinum*. We found *H. stipulacea* created a more nutrient limited environment than *T. testudinum* and there were significantly distinct invertebrate assemblages in native- and invasive-dominated seagrass beds, but no difference in species richness or invertebrate biomass. These results suggest that the spread of *H. stipulacea* would impact a variety of ecological processes, potentially restructuring seagrass ecosystems through both direct impacts on environmental conditions (e.g., nutrient availability) and indirect food web interactions.

**Keywords** Invasive species · Impacts · Management · Caribbean · Foundation species · Trophic support · Habitat creation

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## Introduction

It is generally assumed that the establishment and spread of an invasive species is likely to drive major shifts in biodiversity and ecosystem functioning (Hejda et al. 2009; Pyšek et al. 2012; Gallardo et al. 2015). Yet, there is some debate about the ubiquity of harmful effects of invasive species (e.g., Gurevitch and Padilla 2004; Stohlgren and Rejmánek 2014), the potential for beneficial effects (Rodríguez 2006;

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Ramus et al. 2017), and whether it is useful or appropriate to include a species' geographic history (i.e., whether it is native or exotic) in conservation decision-making (Davis et al. 2011; Buckley and Catford 2016). The arrival of exotic species in a new habitat can have a range of impacts from minimal, when they naturalize but remain rare or are ecologically similar to native species they displace (Schlaepfer et al. 2011), to drastic, if populations expand and monopolize space (Blossey et al. 2001; Schooler et al. 2006) or become strong trophic interactors (Albins and Hixon 2013). Exotic species that displace native foundation species may be more likely to have major impacts on the communities where they establish, and thus act as "invasive" species (sensu Davis and Thompson 2000; Richardson et al. 2000), because of the key roles played by the original foundation species (Ellison et al. 2005; Rohr et al. 2009). But it is unclear if invasive species that replace foundation species always drastically restructure the ecosystem or if they can provide similar services to native species (Katsanevakis et al. 2014).

While invaders may displace native species, in some cases they can produce similar ecosystem functions (Vilà et al. 2011). For example, invasive plants can provide habitat similar to native species resulting in limited effects on associated communities (Grutters et al. 2015; Nelson et al. 2017; Salisbury et al. 2017) or even increasing diversity (Dijkstra et al. 2017). In cases, where the simple presence of plants modify environmental processes such as water flow (Cornacchia et al. 2018) or substrate stabilization (Heffernan 2008), the presence of invasive species may have similar effects. In more extreme scenarios, where certain native species and their ecological functions have been lost, the inclusion or maintenance of non-native species may be an acceptable alternate solution for restoration (Schlaepfer et al. 2011). Thus, while invasions clearly have the potential to drastically restructure communities (Sanders et al. 2003; Baxter et al. 2004), the extent of their impacts are often difficult to quantify. It is particularly challenging to predict the potential effects of invasive species that may play ecologically similar roles to native species. This challenge is exacerbated when invasion impacts are measured through a single or small set of metrics that limit the ability to assess a species' full effect (Simberloff 2014). In light of extensive invasions, the difficulty of removing invaders, and the continuing controversy around the management of introduced species (Davis et al. 2011; Simberloff 2014), it is becoming apparent that a species being non-native may not be a sufficient threshold for management intervention. Thoughtful management-driven decision-making should include explicit evaluation of the variety of impacts that invasive species are likely to have on particular ecosystems to determine an optimal course of action (Hobbs et al. 2009; Strayer 2012).

Seagrasses are a foundation species in many coastal marine ecosystems (Bruno et al. 2003); as such, replacement

by an invasive species could have particularly important impacts on the community, though this depends on their potential functional equivalence. Seagrasses play a key structuring role in marine communities by providing habitat and resources for other species (Orth et al. 1984; Whitfield 2017) as well as changing water flow patterns and increasing sediment stabilization (Adams et al. 2016). Seagrasses also influence nutrient cycling, which can have impacts on other attached and planktonic species (Ziegler 1999). They provide a key trophic resource for mega-faunal species such as sea turtles and marine mammals as well as many invertebrate species (Heck et al. 2008). Seagrass beds can be critical nurseries for marine fishes, including several economically important species (Beck et al. 2001; Parsons et al. 2018). Seagrasses also provide a wide array of broader ecosystem services including coastal protection, water purification, carbon sequestration, and tourism (Barbier et al. 2011). Because of these significant roles of foundation species (both as habitat and as a trophic resource), even small differences between native and invasive seagrass species could have broad, and potentially detrimental, consequences (Thomsen et al. 2010; Moore and Duffy 2016).

In much of the Caribbean, seagrass beds are dominated by the native species *Thalassia testudinum* and *Syringodium filiforme* (Williams 1990). Recently *Halophila stipulacea*, a seagrass originally from the Indian Ocean and Red Sea, has invaded and spread through the eastern Caribbean region (Willette and Ambrose 2009; Willette et al. 2014). In the Caribbean Sea, *H. stipulacea* can rapidly expand (Willette and Ambrose 2012), and while short statured, it can grow in high-density mats that modify environmental conditions (van Tussenbroek et al. 2016). This spread has been recognized as potentially problematic both because it may restructure seagrass communities (Willette and Ambrose 2009; van Tussenbroek et al. 2016) and because *H. stipulacea* has expanded into regions that had previously been devoid of seagrass, possibly driven by release from control by herbivores, and may encroach and threaten nearby coral reefs (Steiner and Willette 2015). While native seagrasses are important food resources, differences in stoichiometry (e.g., nitrogen and phosphorus abundance or C:N ratios) or defensive compounds between *H. stipulacea* and native species may functionally lead to lower resource availability after invasion even if overall seagrass abundance does not change. However, little work has been done to explicitly evaluate potential impacts of invasion by *H. stipulacea* and some uncertainty exists as to the overall effects and in what ways it differs from or plays similar roles to native seagrasses (Rogers et al. 2014; Viana et al. 2019).

To evaluate the potential for and ecological consequences of a shift in foundation species to an invasive competitor we evaluated local spread and ecological effects of *H. stipulacea* in a system with an incipient invasion, the Virgin Islands

National Park (St. John, USVI). Firstly, we evaluated overall shifts in community composition by analyzing seagrass assemblage data from long-term monitoring locations for indications of displacement of native seagrasses. We then compared trophic support provided by different species by measuring chemical composition and nutritional quality of native and invasive seagrasses. To evaluate consumption and top-down control we quantified herbivory rates on multiple seagrass species in different habitats. Lastly, to assess differences in the habitat creation functions of native and invasive seagrasses we measured the abundance and diversity of invertebrate communities and nutrient availability in native and invasive seagrass beds. Together these analyses offer a broad assessment of ways in which invasion by *H. stipulacea* in Caribbean seagrass communities may substitute for native seagrasses or restructure the community.

## Methods

### Site description

All work was conducted around St. John, US Virgin Islands, in waters protected as part of the Virgin Islands National Park. *Halophila stipulacea* was first reported in Menebeck Reef, St. John in 2012 (Willette et al. 2014), but has subsequently spread to numerous locations around the island. Long-term monitoring studies were conducted in 4 bays on the north side of the island and we focused experimental work on two bays on the southern side of the island which have significant populations of *H. stipulacea*: Great Lameshur Bay and Saltpond Bay (Fig. 1). Great Lameshur Bay has extensive seagrass beds that include monospecific stands of *H. stipulacea*, mixed beds with native and invasive seagrasses, and beds dominated by *T. testudinum*. Focal

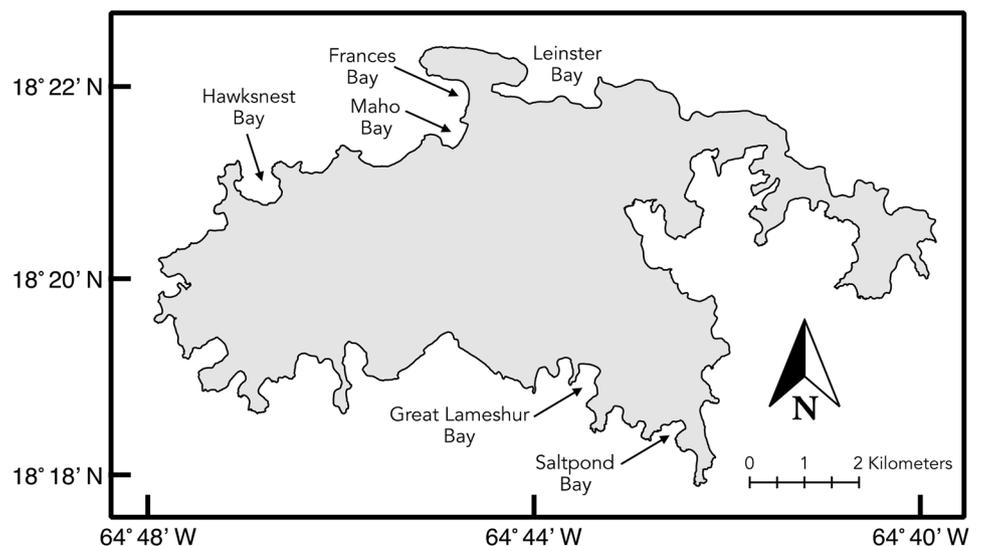
seagrass beds were in water depths of 4–7 m, but seagrasses are found at depths over 20 m. In addition, coral communities were present near the edges of bays or near rocky outcroppings which provided hard substrate and were surrounded by a reef “halo”, a band of sandy habitat clear of seagrass or macroalgae (3–7 m wide).

### Long-term monitoring of seagrass cover

Permanent mooring lines were installed within Virgin Island National Park by the National Park Service (NPS) at popular anchoring sites within bays along St. John in 1999 and 2000. Coincident with their establishment the NPS also initiated a seagrass monitoring effort, where seagrass abundance was quantified at randomly selected mooring areas in four bays, Hawksnest, Maho, Frances, and Leinster (Fig. 1). Five mooring buoys were selected in each bay (except for Frances Bay, where only four buoys were selected). At each selected buoy, four 25-m transects extending out from the mooring anchor along randomly selected fixed headings were chosen and the number of seagrass shoots were counted at ten 20 cm × 20 cm quadrats placed at randomly selected locations along the transect line (monitoring positions were originally randomly assigned, but the same locations were then resurveyed for subsequent measurements). Observers recorded total shoot count per quadrat for each of five seagrass species: *Thalassia testudinum*, *Syringodium filiforme*, *Halodule wrightii*, *Halophila decipiens* and *Halophila stipulacea*. Observations were generally made twice a year, in April/May and again in November/December, from 2000 to 2016, though from 2015 sampling effort was focused on the April/May sampling.

Because these monitoring transects were originally established for a separate purpose than measuring the effects of invasions on seagrass community composition, evaluation of

**Fig. 1** Map of St. John with all research locations. Long-term monitoring was conducted in the 4 bays on the north side of the island (Hawksnest, Frances, Maho, and Leinster) and experimental work was focused on Great Lameshur Bay and Saltpond Bay



overall temporal patterns is relatively uninformative, thus we developed an alternative analytical approach. We calculated changes in abundance of each seagrass species from one time point to the next for each sampling location. We then estimated the relationship between the change in abundance of *H. stipulacea* with change in abundance of each native seagrass species (in separate analyses) with the hypothesis that a significant negative correlation would be observed if native species are being displaced. Because many locations and time points did not have either *H. stipulacea* or all of the native seagrass species, we also constrained the data used in each analysis to only locations and time points that had *H. stipulacea* and the native seagrass of interest present in either the current or directly prior time point. This would remove locations where there was no opportunity for the species to interact (and thus any variability would have come from other drivers). After constraining the data in this way there was an insufficient number of locations to estimate a relationship between *H. stipulacea* and *T. testudinum*, but we were able to calculate relationships for each other native seagrass (*S. filiforme*  $n=402$ ; *H. wrightii*  $n=49$ ; *H. decipiens*  $n=84$ ). We estimated relationships using linear mixed effects regression with the lmer function (from the lme4 package; Bates et al. 2015) with change in *H. stipulacea* abundance as a fixed effect and bay as random effect parameter to address spatial autocorrelation between samples. Normality and heteroscedasticity of the data were evaluated by visual assessment of qqplots and residual vs fitted plots. Statistical significance of fixed effects was calculated with the “summary.merModLmerTest” function from the lmerTest package (Kuznetsova et al. 2017) using the Satterthwaite method for approximating degrees of freedom to calculate *p*-values. All analyses were conducted using R version 3.5.1 (R Core Team 2018).

## Herbivory

We conducted two herbivory assays (in July 2014 and January 2017) to compare relative consumption rates as an estimate of top-down control of *H. stipulacea* and the native seagrass species *S. filiforme* and *T. testudinum*. These experiments were conducted across different habitat types (seagrass beds, reef halo and coral reef, which were expected to reflect a gradient in herbivory pressure) to explore if relaxation of herbivore control could drive expansion of invasive seagrass beds. For each experiment we collected the appropriate seagrass species from near the experimental location, cleaned the samples of sediment, invertebrates, and visible epiphytes, spun them in a salad spinner for 1 min, and cable-tied the seagrasses into bundles of known weights (3 g for the 2014 experiment and 5 g for the 2017 experiment). Samples were then outplanted into different habitats by attaching the bundles to a line that was fixed along the

benthos. This was done in a manner so that the plant material sat close to the benthos in a relatively natural position, though not replanted into the substrate, and not floating up into the water column. In the 2014 experiment, we compared herbivory rates between a coral reef, a *T. testudinum*-dominated seagrass bed and the sand halo between the reef and seagrass and replicated the experiment in Great Lameshur Bay and Saltpond Bay. In 2017, we conducted the experiment using the same habitats, but only in Great Lameshur Bay, and included an *H. stipulacea*-dominated seagrass bed as well as a *T. testudinum*-dominated seagrass bed. Native and invasive samples were haphazardly placed along lines separated by a minimum of 0.5 m and with a replication of 10 samples for each species and location combination. Samples were left out for ~1 day (27 h in Saltpond Bay in 2014, 19 h in Great Lameshur bay in 2014, and 24 h in Great Lameshur bay in 2017, but all treatments for a location were collected at the same time and for analyses all experiments were treated as running for 1 day) and then were recovered, respun, and reweighed to measure changes in biomass. All seagrass species had substantial consumption in at least some conditions suggesting the tethering methodology did not dissuade herbivore activity. Changes in biomass were compared between species and habitats (as fixed effects and with an interaction; samples with the native seagrass species and from the reef habitat were treated as the intercept condition) using a linear mixed effects model for the 2014 experiment (with bay included as a random effect) and with a simple linear model for the 2017 experiment (when all samples were in a single bay). Linear models were fit and analyzed using the “lm” and “summary.lm” functions from the stats package and linear mixed effects models were estimated using the “lmer” and the “summary.merModLmerTest” functions as described above.

## Chemical composition

To compare the chemical composition of seagrasses that determine their quality as food resources, we collected tissue samples of *T. testudinum*, *S. filiforme*, *H. stipulacea*, and *H. wrightii* from Saltpond Bay, where all species were in a mixed community and in close proximity. Three composite samples of each species were analyzed; to provide sufficient biomass for analysis, multiple shoots, likely from multiple individuals growing adjacent to each other, were combined. Intact green blades were separated from the root/rhizome, rinsed in fresh water, cleaned of visible epiphytes, and dried at approximately 60 °C. Samples were ground, homogenized, and analyzed for total carbon, total nitrogen, phosphate phosphorus, C:N ratio, and total crude protein, all of which reflect nutritional quality. We also quantified total phenols, which are considered important defensive compounds for deterring herbivory (Hay and Fenical

1988). Samples were analyzed by the UC Davis Analytical Laboratory via combustion and conductivity detection using standard laboratory methods (<https://anlab.ucdavis.edu/methods-of-analysis>). For each compositional metric, values were compared between the 4 seagrass species using a linear model with the “lm” and “summary.lm” functions and treating values for *H. stipulacea* as the intercept condition.

### Invertebrate community composition

To evaluate the potential impacts of invasion on invertebrate communities using seagrass beds as habitat we quantified the invertebrate communities within seagrass beds dominated by *H. stipulacea* and *T. testudinum* in January 2017 in Great Lameshur Bay. These experiments were conducted by making small bags of seagrass litter that we deployed into seagrass beds dominated by different species. While this approach reduces some differences in stature or spatial complexity of different seagrass species, invertebrates were able to colonize the litterbags providing a partial sample of the types of invertebrates living within each seagrass bed. While this method is biased toward sampling smaller invertebrates and grazers or detritivores, within that subset it offers an even comparison between seagrass bed types. For each litter bag 15 g samples of fresh green biomass of the appropriate seagrass species were placed in 10 cm × 10 cm pouches made of “vexar” plastic mesh with ~ 1 cm mesh openings. Ten bags each of *H. stipulacea* and *T. testudinum* litter were attached 0.5 m apart on a nylon rope and deployed into seagrass beds dominated by the same species. Ten additional mixed species samples were created by cable-tying two pouches (each with 7.5 g of a different seagrass) side by side which were then deployed into a mixed composition seagrass bed (with both *H. stipulacea* and *T. testudinum*). Litter bags remained in the water for 4 days and then were removed by gently placing an individually-labeled plastic bag around the pouch, cutting the pouch from the nylon rope, and returning the closed bag with all contents to the lab for sorting. While the length of time that samples were in the water was limited, other studies have shown substantial colonization within 1 week (e.g., Ferreira et al. 2012) and minimally this approach offers an even comparison between habitat types though its sensitivity would likely have been higher if samples had been deployed longer.

In the lab, invertebrates from each sample were separated from the plant material, stored in 100% ethanol, and then identified to the lowest resolvable taxonomic level based on visual inspection of morphology. Taxa that were clearly distinct, but that we were unable to identify to species, were treated as morphotaxa so they could be included in diversity analyses. All analyses were based simply on species numbers rather than any measures of relatedness; therefore, actual species identities are not strictly necessary and

morphotaxa offer a conservative approach as similar species are more likely to be miscategorized as a single taxa rather than individuals of a single species being identified as different species (Oliver and Beattie 1996).

Differences between sampled invertebrate communities were evaluated with multiple approaches. Total invertebrate biomass and invertebrate species richness were compared between the *H. stipulacea*-dominated, *T. testudinum*-dominated, and mixed seagrass beds using linear models, as above. A generalized linear model with a gamma distribution (using the “glm” function with the seagrass habitat treated as the intercept condition) was utilized for the biomass data to address a lack of normality observed from evaluation of the qqplot. Multivariate community composition was visualized using non-metric multidimensional scaling (nMDS) with the “metaMDS” function from the vegan package (Oksanen et al. 2019) using Bray–Curtis dissimilarity as the distance metric and projecting into two dimensions. In addition, differences in multivariate invertebrate species composition between seagrass bed types were evaluated using the “mvabund”, “manyglm”, and anova.manyglm functions from the mvabund package (Wang et al. 2012) with the “montecarlo” resampling method (with 10,000 bootstrap iterations) used to calculate the p-value.

### Nutrient availability

To evaluate if invasion by *H. stipulacea* modifies environmental conditions by shifting nutrient levels, we conducted nutrient availability bioassays in native and invasive seagrass beds in Great Lameshur Bay (in January 2017), using the same locations as the herbivory assays. Because macroalgae are sensitive to ambient nutrient conditions and fast growers, measuring algal nutrient limitation can provide an effective bioassay for general nutrient availability in a system (Kamer et al. 2004; Muthukrishnan et al. 2016). To conduct these bioassays we used a common macroalga, *Sargassum* sp, which was collected from the same bay, cleaned of sediment and epiphytes, wet weighed into 3 g subsamples, and placed in cages made of window screening. To test for algal nutrient limitation, we enriched half the samples with 20 g of Osmocote slow release fertilizer (14%N:14%P:14%K) placed inside a diffuser made from a nylon stocking and included with the algae in the screen cages with increased growth in enriched samples indicating nutrient limitation of the algae. To limit flux of nutrients, enriched samples were placed at least two meters away from ambient samples (Carreiro-Silva et al. 2005; Fong et al. 2018). Ten replicates each of enriched and unenriched samples were placed into seagrass beds dominated by *T. testudinum* and *H. stipulacea*. Samples were recovered and reweighed after 5 days and percent change from initial biomass was calculated. Differences between seagrass beds and the effect of nutrient enrichment

were analyzed using a linear model with change in algal biomass as the response variable, seagrass type and nutrient enrichment as fixed effects and an interaction between seagrass type and nutrient enrichment. The analysis was conducted with the “lm” and “summary.lm” functions and unenriched samples from the native seagrass bed used as the intercept condition.

## Results

### Long-term monitoring of seagrass cover

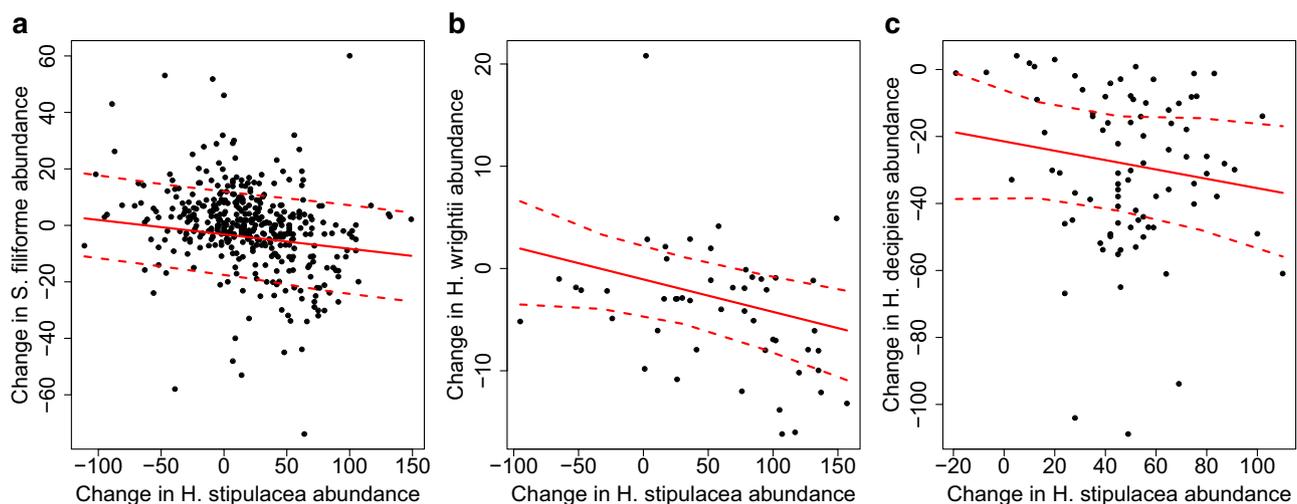
Monitoring data showed that overall seagrass distributions were very patchy as any given species was only found at a small number of the total locations. Of a total of 21,813 quadrats *Thalassia testudinum* was observed in 59, *Syringodium filiforme* in 6509, *Halodule wrightii* in 2793, *Halophila decipiens* in 806 and *Halophila stipulacea* 1272. When *H. stipulacea* was observed at the same location as a native

seagrass, there was a variable but consistent negative relationship between changes in abundance of *H. stipulacea* and the native species (Fig. 2, Table 1). This relationship was statistically significant for both *S. filiforme* and *H. wrightii*, while the relationship with *H. decipiens* was similar but not statistically significant.

### Herbivory

In the initial herbivory assay, where *H. stipulacea* was compared against *S. filiforme* (July 2014), loss of biomass was often 50–100% greater for the native species (Fig. 3). But significant differences were only seen in the reef and halo habitats, which had consumption rates much higher than the seagrass bed (Table 2a). In the seagrass habitat, consumption was uniformly low for both species. General patterns across habitat types and species were relatively consistent between bays though absolute consumption rates differed.

In the second herbivory experiment, where *H. stipulacea* was compared against *T. testudinum*, consumption patterns

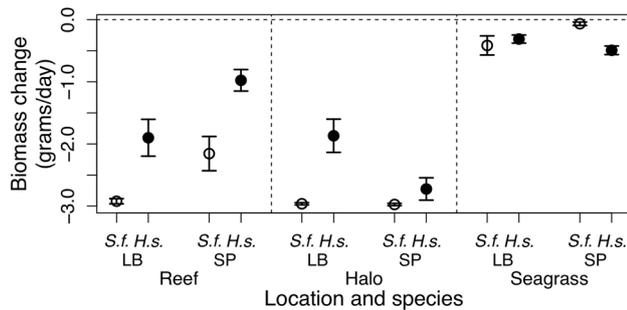


**Fig. 2** Relationships between the change in *H. stipulacea* abundance and the change in abundance of native seagrasses between successive time-points from long-term monitoring plots. Results for **a** *S. filiforme*, **b** *H. wrightii*, and **c** *H. decipiens* are shown in separate panels

**Table 1** Results of fixed effects from statistical models based on long-term monitoring data estimating the change in abundance (shoots per quadrat) of individual native seagrass species with change

in abundance of *H. stipulacea* as a predictor. Results from separate models for a) *S. filiforme*, b) *H. wrightii*, and c) *H. decipiens* are included

Native seagrass species	Parameter	Estimate	Std. Error	<i>t</i> -value	<i>p</i> -value
a) <i>S. filiforme</i>	Intercept	− 3.174	7.003	− 0.453	0.729
	<i>H. stipulacea</i> change	− 0.051	0.016	− 3.112	0.002
b) <i>H. wrightii</i>	Intercept	− 1.068	1.824	− 0.585	0.608
	<i>H. stipulacea</i> change	− 0.032	0.014	− 2.222	0.031
c) <i>H. decipiens</i>	Intercept	− 21.468	8.086	− 2.655	0.065
	<i>H. stipulacea</i> change	− 0.140	0.105	− 1.326	0.188



**Fig. 3** Herbivory rates, measured as daily change in biomass (mean  $\pm$  SD), for the native seagrass *S. filiforme* and *H. stipulacea* across different habitats. Experiment was replicated across 2 bays, Great Lameshur Bay (LB) and Saltpond Bay (SP)

were less clear and differences between species were less pronounced (Fig. 4, Table 2b). Overall consumption was far lower in the January 2017 experiment, roughly 25% of the July 2014 levels (based on consumption rate of *H. stipulacea* in Great Lameshur Bay which was quantified in both experiments). Consumption rates were again higher in the reef and halo habitats than seagrass beds for both species. In the reef habitat, where herbivory rates were greatest, loss of biomass was marginally greater for *T. testudinum* than *H. stipulacea* (see the parameter estimate for “species” alone in Table 2b as “reef” is the reference habitat) but the effect was small, did not persist in other habitats and was reversed in the *T. testudinum*-dominated seagrass bed.

### Chemical composition

For carbon, nitrogen, C:N ratio and crude protein *H. stipulacea* was markedly less nutritious than all native seagrass species (Fig. 5), though patterns varied among constituents measured. The levels of carbon, nitrogen and protein were substantially lower for *H. stipulacea* than any native species with nearly half the amount of nitrogen and protein as *T. testudinum* (Table 2c-h). Furthermore, the C:N ratio of *H. stipulacea* was ~30–50% higher than native seagrasses. Phosphorus (as phosphate) levels were highly variable and not significantly different between species. Phenol levels in *H. stipulacea* were intermediate compared to native species as they were lower than *S. filiforme* but higher than *H. wrightii*, and not significantly different from *T. testudinum*.

### Invertebrate community composition

A variety of invertebrate species recruited to litter bags, with individual samples having ~5 species on average. Crabs and shrimp were the most common invertebrates, followed by polychaete worms and snails (Fig. S1). Overall invertebrate biomass and species richness were extremely

variable with no differences between native, invasive and mixed seagrass beds (Fig. 6, Table 2i, j), but the multivariate species composition showed consistent differences in community composition between seagrass bed types, with *H. stipulacea*-dominated beds, in particular, being distinct from the other groups (Fig. 7; manyglm results: residual DF = 27, deviance = 139.9,  $p < 0.001$ ). These differences were likely driven by the presence of rare species which were generally found in either the native- or invasive-dominated beds (and potentially the mixed bed as well) but rarely in both (Fig. S1). Mixed seagrass communities showed an intermediate composition between each of the mono-specific beds and had the broadest range of species present.

### Nutrient availability

Algal growth assays showed strong nutrient limitation in habitats dominated by *H. stipulacea* but no limitation in habitats dominated by *T. testudinum* (Fig. 8, Table 2k). Under ambient conditions algal growth rates in the *T. testudinum* bed were double those seen in the *H. stipulacea* bed. This difference between bed types was completely removed with nutrient enrichment (significant interaction term with parameter estimates of the interaction term and the effect of *H. stipulacea* under ambient conditions of similar magnitude, but opposite sign) and there was no increase in growth rate in the *T. testudinum* bed. This indicates that there is lower nutrient availability in the *H. stipulacea*-dominated bed.

### Discussion

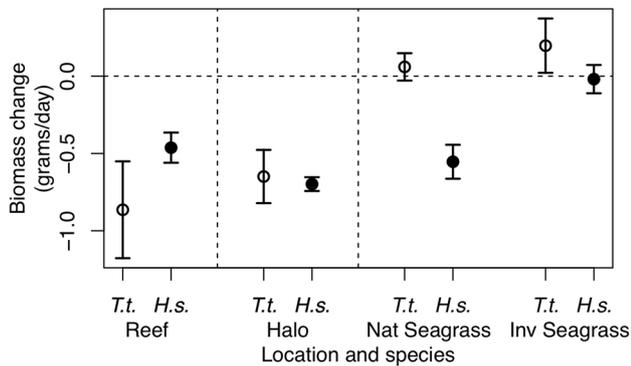
With the extent and number of invasions across the globe, it is not feasible to eradicate invasive species in every system. Thus to make effective management decisions, it is critical to explicitly evaluate the potential for spread as well as the likely impacts of an invader within an ecosystem (Vander Zanden and Olden 2008). In the case of *H. stipulacea*, while some native seagrass species, particularly *T. testudinum*, may be resilient to direct displacement, rapid expansion and replacement of other native species seems likely. Thus, the secondary question of equivalence of *H. stipulacea* with native seagrasses is central to understanding impact. On this issue we found that while *H. stipulacea* can act as a foundation species, providing habitat and trophic support to other species, it is not entirely equivalent to native species in most of the properties we were able to quantify. Consumption of *H. stipulacea* was generally lower than native seagrasses, its nutritional quality was lower, it was utilized by different invertebrate assemblages, and created different nutrient environments. As such, replacement of native seagrasses by *H. stipulacea* will shift, at least partially, a variety of top-down, bottom-up and environment modifying processes, which in

**Table 2** Results of fixed effects from univariate statistical models. Linear models were used in most analyses, but a mixed model was used for the herbivory experiment comparing *H. stipulacea* and *S. filiforme* to account for autocorrelation within bays. For each factor in models the particular levels described by parameter estimates are listed in parentheses

Analysis	Parameter	Estimate	Std. Error	Test statistic	<i>p</i> -value
<b>Herbivory</b>					
a) Compared with <i>S. filiforme</i>	Intercept ( <i>S. filiforme</i> in reef habitat)	-2.968	0.148	20.071	<0.001
	Species ( <i>H. stipulacea</i> )	0.672	0.190	-3.534	0.001
	Habitat (Halo)	0.430	0.190	-2.261	0.026
	Habitat (Seagrass)	2.727	0.190	-14.353	0.000
	Species × Habitat ( <i>H. stipulacea</i> and Halo)	0.428	0.269	-1.595	0.114
b) Compared with <i>T. testudinum</i>	Species × Habitat ( <i>H. stipulacea</i> and Seagrass)	-0.834	0.269	3.102	0.002
	Intercept ( <i>T. testudinum</i> in reef habitat)	-0.864	0.156	-5.541	0.000
	Species ( <i>H. stipulacea</i> )	0.402	0.227	1.773	0.081
	Habitat (Halo)	0.215	0.227	0.949	0.346
	Habitat ( <i>T. testudinum</i> bed)	0.924	0.227	4.079	0.000
	Habitat ( <i>H. stipulacea</i> bed)	1.062	0.234	4.539	0.000
	Species × Habitat ( <i>H. stipulacea</i> and Halo)	-0.451	0.325	-1.388	0.170
Chemical composition	Species × Habitat ( <i>H. stipulacea</i> and <i>T. testudinum</i> bed)	-1.015	0.325	-3.127	0.003
	Species × Habitat ( <i>H. stipulacea</i> and <i>H. stipulacea</i> bed)	-0.618	0.330	-1.875	0.065
	<b>c) % Carbon</b>				
c) % Carbon	Intercept ( <i>H. stipulacea</i> )	30.033	0.351	85.519	<0.001
	Species ( <i>H. wrightii</i> )	4.700	0.497	9.463	<0.001
	Species ( <i>S. filiforme</i> )	2.833	0.497	5.705	<0.001
	Species ( <i>T. testudinum</i> )	6.367	0.497	12.819	<0.001
d) % Nitrogen	Intercept ( <i>H. stipulacea</i> )	1.127	0.049	22.762	<0.001
	Species ( <i>H. wrightii</i> )	0.630	0.070	9.000	<0.001
	Species ( <i>S. filiforme</i> )	0.640	0.070	9.143	<0.001
	Species ( <i>T. testudinum</i> )	1.003	0.070	14.333	<0.001
e) Phosphorus	Intercept ( <i>H. stipulacea</i> )	586.667	70.119	8.367	<0.001
	Species ( <i>H. wrightii</i> )	-96.667	99.163	-0.975	0.358
	Species ( <i>S. filiforme</i> )	-63.333	99.163	-0.639	0.541
	Species ( <i>T. testudinum</i> )	30.000	99.163	0.303	0.770
f) C:N ratio	Intercept ( <i>H. stipulacea</i> )	26.680	0.467	57.103	<0.001
	Species ( <i>H. wrightii</i> )	-6.883	0.661	-10.417	<0.001
	Species ( <i>S. filiforme</i> )	-8.055	0.661	-12.190	<0.001
	Species ( <i>T. testudinum</i> )	-9.566	0.661	-14.477	<0.001
g) % Protein	Intercept ( <i>H. stipulacea</i> )	7.033	0.303	23.230	<0.001
	Species ( <i>H. wrightii</i> )	3.933	0.428	9.186	<0.001
	Species ( <i>S. filiforme</i> )	3.967	0.428	9.264	<0.001
	Species ( <i>T. testudinum</i> )	6.300	0.428	14.714	<0.001
h) Total phenols	Intercept ( <i>H. stipulacea</i> )	4.070	0.403	10.105	<0.001
	Species ( <i>H. wrightii</i> )	-1.680	0.570	-2.949	0.018
	Species ( <i>S. filiforme</i> )	8.507	0.570	14.934	<0.001
	Species ( <i>T. testudinum</i> )	0.697	0.570	1.223	0.256
i) Invertebrate biomass	Intercept (Native)	0.878	0.220	3.987	<0.001
	Seagrass bed (mixed)	-0.218	0.275	-0.791	0.436
	Seagrass bed ( <i>H. stipulacea</i> )	0.403	0.389	1.035	0.310
j) Invertebrate species richness	Intercept (Native)	5.100	0.625	8.163	<0.001
	Seagrass bed (mixed)	-0.400	0.884	-0.453	0.654
	Seagrass bed ( <i>H. stipulacea</i> )	-0.500	0.884	-0.566	0.576

**Table 2** (continued)

Analysis	Parameter	Estimate	Std. Error	Test statistic	p-value
k) Nutrient limitation	Intercept (Native seagrass bed and unenriched)	0.227	0.019	12.184	<0.001
	Habitat ( <i>H. stipulacea</i> bed)	-0.129	0.026	-4.891	<0.001
	Treatment (enriched)	-0.016	0.026	-0.599	0.553
	Habitat × Treatment ( <i>H. stipulacea</i> bed and enriched)	0.116	0.037	3.121	0.004



**Fig. 4** Herbivory rates, measured as daily change in biomass, for the native seagrass *T. testudinum* and the invasive *H. stipulacea* across different habitats including native-dominated (*T. testudinum*) and invasive-dominated (*H. stipulacea*) seagrass beds

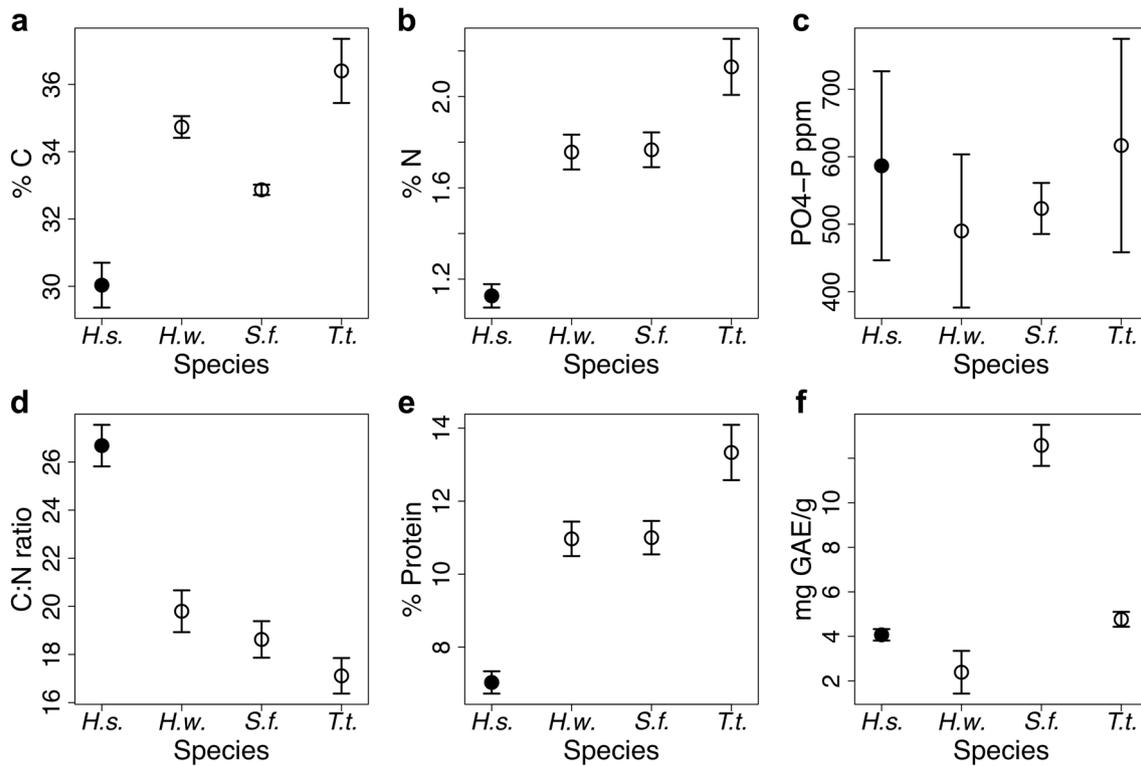
turn could drive further shifts in community structure and ecosystem functioning.

### Seagrass community shifts and expansion

It is clear that populations of *H. stipulacea* are expanding both in St. John and around the Caribbean (Willette et al. 2014), but this may not impact all native seagrasses species equivalently. While the seagrass monitoring data were not a direct measure of competition, they suggest that *H. stipulacea* is likely to displace at least some seagrass species. In particular, *S. filiforme* and *H. wrightii* seemed more susceptible to displacement, which aligns with patterns observed in other parts of the Caribbean (Steiner and Willette 2015; Scheibling et al. 2018). While we could not estimate an effect on *T. testudinum* from the monitoring data, other data, particularly from herbivory assays suggest *T. testudinum* may be more resilient to invasion than other species (but see Smulders et al. 2017). While *S. filiforme* was heavily consumed *T. testudinum* was not, suggesting some protection from herbivore mediated removal. At the same time *T. testudinum* is more physically robust than most other seagrasses in the community which may limit physical removal from events such as storms. In part, this aligns with expectations that the effects of particular invasions are highly contingent on characteristics of both the invader and

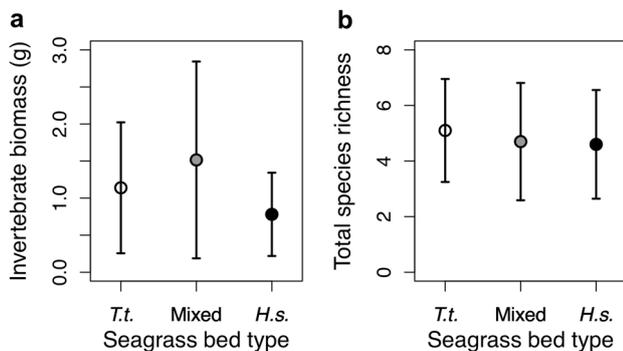
the native community (Levine et al. 2004; Muthukrishnan et al. 2018). This ecosystem may present a scenario, where *H. stipulacea* is both a “driver” and “passenger” (sensu MacDougall and Turkington 2005) of community shifts depending on the native species present. *Halophila stipulacea* may be able to readily displace some seagrass species (as a “driver” of change), while invasion of *T. testudinum* could require other external disturbances to create available space that *H. stipulacea* can recolonize (as a “passenger” with other disturbances). This could still eventually result in *H. stipulacea* dominance, but on a longer time scale. This may be facilitated by the rapid expansion rates of *H. stipulacea* (Smulders et al. 2017) and the large production of biomass in those patches requiring substantial nutrient resources, leading to the lower nutrient availability observed in invasive-dominated seagrass beds. This environmental shift could in turn limit growth or recovery of other seagrass species. To evaluate these dynamics further, direct assessments of competition between species and the ability of different seagrass species to establish and recover after disturbances (e.g., Willette et al. 2020) would be necessary.

A shift toward *H. stipulacea* as the dominant seagrass in the system could also lead to expansion or changes of overall seagrass habitat. In particular, the weaker top-down control of *H. stipulacea* relative to *S. filiforme* suggests a potential for expansion to new areas and particularly towards coral communities (Steiner and Willette 2015), where high consumption rates had previously maintained “reef halos” (Randall 1965; Ogden et al. 1973). The herbivory comparison with *T. testudinum* was more equivocal, but that experiment may have been confounded by seasonal variation as the consumption rate of *H. stipulacea* itself was 3–4 times higher in July (when evaluated with *S. filiforme*) than in January (when evaluated with *T. testudinum*) and other work has shown that sea turtles strongly prefer *T. testudinum* (Christianen et al. 2019). That overall reduction in herbivore activity may have limited our ability to identify differences between species. Nonetheless, reduced consumption may be a component of why *H. stipulacea* has intermixed with coral reefs in the Red Sea rather than remaining separated by a halo (Rotini et al. 2017). In the Caribbean Sea, because of the rapid rates of expansion and lack of coevolutionary experience, *H.*



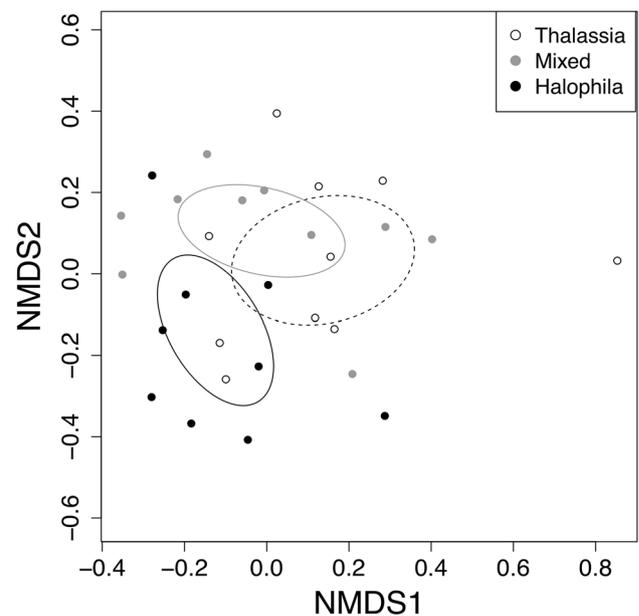
**Fig. 5** Measurements (mean  $\pm$  SD) of tissue nutrients **a** carbon, **b** nitrogen, **c** phosphorus (as phosphate), **d** C:N ratio, **e** total protein, and **f** total phenols across different seagrass species: *H. stipulacea*,

*H. wrightii*, *S. filiforme*, and *T. testudinum*. Filled circles indicate the invasive species (*H. stipulacea*), while open circles are native species

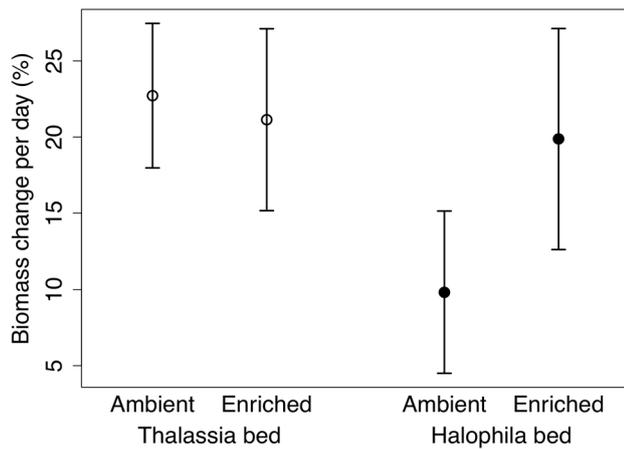


**Fig. 6** Comparison of **a** invertebrate biomass and **b** invertebrate species richness in litter bags deployed in seagrass beds dominated by *T. testudinum*, *H. stipulacea* or a mixed assemblage

*stipulacea*'s spread into reef habitat may not be as benign, but rather pose a significant threat to highly valued coral reefs that are already threatened by a variety of other stressors (Rogers et al. 2008). In addition, high growth rates (Willette and Ambrose 2009) and low consumption rates of *H. stipulacea* likely facilitate expansion into sandflats that were previously seagrass free (Steiner and Willette 2015) expanding the total extent of seagrass habitat.



**Fig. 7** Non-metric multidimensional scaling analysis of invertebrate community composition between seagrass bed types. Points are individual samples and ellipses reflect the 95% confidence interval for the group centroid. The open circles and dashed ellipse represent the *T. testudinum* bed, filled black circles and black ellipse indicate the *H. stipulacea* bed, and grey circles and ellipse indicate the mixed bed



**Fig. 8** Evaluation of nutrient availability between *T. testudinum* and *H. stipulacea*-dominated seagrass beds by comparison of algal growth rates in each habitat with and without nutrient enrichment. Nutrient limitation in the macroalgae, which can be seen from an increase in growth rate with enrichment, is used as a proxy for overall nutrient availability

### Community impacts of invasion

Expansion of *H. stipulacea* will likely drive further community consequences, most directly because seagrasses are key primary producers supporting the food web. The difference in nutrient and chemical composition between *H. stipulacea* and native seagrass species makes the invader lower quality forage for herbivores (Hemmi and Jormalainen 2002; Hessen et al. 2002) and as a result, a shift in seagrass composition could drastically impact the community via bottom-up effects (Tuchman et al. 2002; Hladysz et al. 2011). This effect could be partly ameliorated by overall increase in the extent of seagrass habitat and total available biomass, but it may be a limited set of species that could easily adapt to the shifted resource stoichiometry (Urabe and Waki 2009; Schoo et al. 2013). Because seagrasses are a key primary producer, expansion of *H. stipulacea* could drive population shifts in a variety of invertebrates, fishes, and sea turtles that utilize seagrasses as a component of their diet (Williams 1988; Kirsch et al. 2002; Alcoverro and Mariani 2004). In its native habitat *H. stipulacea* is a key foundation species and thus it has the ability to provide trophic support, but likely at lower levels than the native species it replaces in the Caribbean Sea. In addition, because of its lower quality (lower nitrogen and protein content, and higher C:N ratio), equivalent consumption will provide less resources to herbivores relative to native seagrasses. The high consumption rates of *S. filiforme* are also notable because the species is preferentially consumed despite phenol levels nearly three times as high as *H. stipulacea*, suggesting high levels of chemical defenses (Levin 1976; Boeckler et al. 2011). This suggests

herbivores strongly prefer high quality resources (Prado 2011) even at the cost of processing defensive compounds. Despite the mechanism, lower consumption and quality of *H. stipulacea* compared to native seagrasses would certainly change the rate of energy transfer between trophic levels, potentially limiting abundance or diversity of the food web as a whole (Power 1992).

As seagrasses create habitat for a range of other species, shifts toward invasive dominance could also have a variety of additional effects mediated via changes in the invertebrate community utilizing the seagrass beds. Though we only were able to evaluate a subset of the invertebrate community we observed qualitative differences between seagrass types. While the overall invertebrate biomass and diversity was similar between *H. stipulacea* and *T. testudinum* beds, the complement of species differed between beds of different seagrass species. Shifts in invertebrate communities could potentially influence rates of detrital processing and decomposition (Harrison 1989), nutrient availability (Peterson and Heck 1999), and other ecosystem fluxes (Spivak et al. 2009). Invertebrates themselves can also provide a food resource to fish or other predator species (Luczkovich et al. 2002). In addition, a shift in community composition toward greater dominance of common species and loss of rare species can lead to biotic homogenization (Olden 2006) which can have broader implications for ecosystem functioning (Hautier et al. 2018).

Censusing the invertebrate community via individuals that recruit into litter bags is an imperfect method for quantifying community differences, because placing biomass within bags removes the structural differences between seagrass types. However, the samples likely offer a conservative measure of community differences, because they still reflect individuals accumulated from the adjacent habitats which have a variety of differences. From a structural perspective *H. stipulacea* has a much shorter stature than *T. testudinum* influencing water flow and light penetration. These differences in overall physical structure can impact a broad range of species (Heck and Wetstone 1977; Orth et al. 1984). In addition, many invertebrates are microherbivores, and thus issues of forage quality may be important to them (Heck and Valentine 2006; Vonk et al. 2008). Similarly, epiphytic algae are an important resource to herbivores (Heck and Valentine 2006) and different epiphytes or other microbial symbionts (Rotini et al. 2017) present on invasive and native seagrasses may impact seagrass associated species. Reduced nutrient availability in invasive seagrass beds could also limit the growth of benthic or epiphytic algae or phytoplankton, which can be equally important as seagrasses in transferring energy to higher compartments of the seagrass associated foodweb (Moncreiff 2001).

## Evaluating invasion impacts and management options

Management of established invasions can require extensive effort and potential benefits need to be evaluated in the context of both the costs of management effort and the actual ecosystem consequences of the invasion. While invasive species may be able, at least in part, to perform many of the functions of native species (Ramus et al. 2017), it is both scientifically and ethically challenging to determine when an invasive species is similar or beneficial enough to take an accommodative management perspective and these decisions can be contentious (Sotka and Byers 2019; Thomsen et al. 2019; Byers and Sotka 2019). When dealing with complex systems and the embedded uncertainties, such as are seen with invasions (Besek 2019), the best strategy available is for explicit evaluation of risks and impacts considering the potential for both positive and negative effects to provide accurate predictions that stakeholders and managers can use to make informed decisions (Larson et al. 2011; Strayer 2012).

In the case of *H. stipulacea*, the invader is able to play the role of a foundation species, providing both habitat and food resources for other species, but it provides these services at levels that are not equivalent to native species. The differences are also subtle in some aspects (e.g., the associated invertebrate community was different in composition but not abundance or diversity, herbivory rates only differed in certain habitats), which attests to the need for holistic evaluation of invasion impacts, not only single metrics (Zavaleta et al. 2001; Vilà et al. 2010). In addition, Virgin Islands National Park has experienced significant expansion of *H. stipulacea* into areas where seagrasses had not previously established and the consequences of this shift remain uncertain (Rogers et al. 2014). Thus, management efforts that can maintain native populations would be valuable to protect broader ecosystem functioning, but the effort and cost involved in persistent management need to be considered. Because of the extent of the invasion in the region eradication may not be feasible, but protection of specific, high value locations is more realistic.

These results highlight the complex nature of the effects of invasive species and the need for more comprehensive approaches to evaluate their impacts (Hladyz et al. 2011). Invasive species, particularly when they are foundation species, will likely influence numerous aspects of the food web and ecosystem. For *H. stipulacea*, the net effects of invasion suggest some shift in ecosystem functioning, but it remains to be seen if major changes will occur if *H. stipulacea* more completely displaces native seagrasses or if behavioral shifts will allow other community members to adjust to the “new normal”. However, with the potential of these shifts there is a need for larger scale evaluations of

the impact of *H. stipulacea* invasion. Trying to understand large-scale impacts has been a perennial challenge when working with invasive species because of ethical and logistical challenges (Sol et al. 2008). This may require twinning small-scale work on specific mechanisms, as we present here, with broader observational studies comparing heavily invaded regions with uninvaded areas (Byers et al. 2002). One natural experiment would be to contrast the real-time transformation of the seagrass habitat in the U.S. Virgin Islands National Park to the seagrass beds of the Dry Tortugas National Park or Biscayne National Park along Florida that have not yet been invaded. Results from such efforts will not only inform managers about vulnerability and risks for continued spread of *H. stipulacea* through the Caribbean, but also offers insight into more basic questions about community structure and resilience.

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**Author contributions** RM, DW, and CAT designed the study. RM analyzed the data and wrote the initial draft of the manuscript. All authors were involved in conducting research and revising the manuscript.

**Data availability** All data utilized in the study as well as R scripts for analyses are archived in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.9p8cz8wcz>.

## Compliance with ethical standards

**Conflict of interest** The authors declare no conflicts of interest.

**Ethical approval** This research was conducted in accordance with all applicable national and institutional guidelines for sampling and experiments.

## References

- Adams MP, Hovey RK, Hipsey MR, Bruce LC, Marco G, Lowe RJ, Gruber RK, Leonardo R, Maxwell PS, Callaghan DP, Kendrick GA, O'Brien KR (2016) Feedback between sediment and light for seagrass: Where is it important? *Limnol Oceanogr* 61:1937–1955. <https://doi.org/10.1002/lno.10319>
- Albins MA, Hixon MA (2013) Worst case scenario: potential long-term effects of invasive predatory lionfish (*Pterois volitans*) on Atlantic and Caribbean coral-reef communities. *Environ Biol Fishes* 96:1151–1157. <https://doi.org/10.1007/s10641-011-9795-1>
- Alcoverro T, Mariani S (2004) Patterns of fish and sea urchin grazing on tropical Indo-Pacific seagrass beds. *Ecography (Cop)* 27:361–365. <https://doi.org/10.1111/j.0906-7590.2004.03736.x>
- Barbier EB, Hacker SD, Kennedy C, Koch EW, Stier AC, R. SB (2011) The value of estuarine and coastal ecosystem services. *Ecol Monogr* 81:169–193. doi: 10.1890/10-1510.1

- Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48. <https://doi.org/10.18637/jss.v067.i01>
- Baxter CV, Fausch KD, Murakami M, Chapman PL (2004) Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. *Ecology* 85:2656–2663. <https://doi.org/10.1890/04-138>
- Beck MW, Heck KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MP (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* 51:633–641. [https://doi.org/10.1641/0006-3568\(2001\)051\[0633:TICAMO\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0633:TICAMO]2.0.CO;2)
- Besek J (2019) Invasive uncertainties: environmental change and the politics of limited science. *Environ Sociol* 5(4):416–427. <https://doi.org/10.1080/23251042.2019.1624002>
- Blossey B, Skinner LC, Taylor J (2001) Impact and management of purple loosestrife (*Lythrum salicaria*) in North America. *Biodivers Conserv* 10:1787–1807. <https://doi.org/10.1023/A:1012065703604>
- Boeckler GA, Gershenzon J, Unsicker SB (2011) Phenolic glycosides of the Salicaceae and their role as anti-herbivore defenses. *Phytochemistry* 72:1497–1509. <https://doi.org/10.1016/j.phytochem.2011.01.038>
- Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory. *Trends Ecol Evol* 18:119–125
- Buckley YM, Catford J (2016) Does the biogeographic origin of species matter? Ecological effects of native and non-native species and the use of origin to guide management. *J Ecol* 104:4–17. <https://doi.org/10.1111/1365-2745.12501>
- Byers JE, Sotka EE (2019) Promoting invasive species to enhance multifunctionality in a native ecosystem still requires strong(er) scrutiny. *Biol Invasions* 21:277–280. <https://doi.org/10.1007/s10530-018-1851-8>
- Byers JE, Reichard S, Randall JM, Parker IM, Smith CS, Lonsdale WM, Atkinson IAE, Seastedt TR, Williamson M, Chornesky E, Hayes D (2002) Directing research to reduce the impacts of nonindigenous species. *Conserv Biol* 16:630–640. <https://doi.org/10.1046/j.1523-1739.2002.01057.x>
- Carreiro-Silva M, McClanahan TR, Kiene WE (2005) The role of inorganic nutrients and herbivory in controlling microbioerosion of carbonate substratum. *Coral Reefs* 24:214–221
- Christianen MJA, Smulders FOH, Engel MS, Nava MI, Willis S, Debrot AO, Palsbøll PJ, Vonk JA, Becking LE (2019) Megaherbivores may impact expansion of invasive seagrass in the Caribbean. *J Ecol* 107:45–57. <https://doi.org/10.1111/1365-2745.13021>
- Cornacchia L, van de Koppel J, van der Wal D, Wharton G, Puijalón S, Bouma TJ (2018) Landscapes of facilitation: how self-organized patchiness of aquatic macrophytes promotes diversity in streams. *Ecology* 99:832–847. <https://doi.org/10.1002/ecy.2177>
- Davis MA, Thompson K (2000) Eight ways to be a colonizer; two ways to be an invader: a proposed nomenclature scheme for invasion ecology. *Bull Ecol Soc Am* 81:226–230
- Davis MA, Chew MK, Hobbs RJ, Lugo AE, Ewel JJ, Vermeij GJ, Brown JH, Rosenzweig ML, Gardener MR, Carroll SP, Thompson K, Pickett STA, Stromberg JC, Del TP, Suding KN, Ehrenfeld JG, Philip Grime J, Mascaro J, Briggs JC (2011) Don't judge species on their origins. *Nature* 474:153–154
- Dijkstra JA, Harris LG, Mello K, Litterer A, Wells C, Ware C (2017) Invasive seaweeds transform habitat structure and increase biodiversity of associated species. *J Ecol* 105:1668–1678. <https://doi.org/10.1111/1365-2745.12775>
- Ellison AM, Bank MS, Clinton BD, Colburn EA, Elliott K, Ford CR, Foster DR, Kloeppel BD, Knoepp JD, Lovett GM, Mohan J, Orwig DA, Rodenhouse NL, Sobczak WV, Stinson KA, Stone JK, Swan CM, Thompson J, Von Holle B, Webster JR (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Front Ecol Environ* 3:479–486. [https://doi.org/10.1890/1540-9295\(2005\)003\[0479:LOFSCF\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2)
- Ferreira V, Encalada AC, Graça MAS (2012) Effects of litter diversity on decomposition and biological colonization of submerged litter in temperate and tropical streams. *Freshw Sci* 31:945–962. <https://doi.org/10.1899/11-062.1>
- Fong CR, Bittick SJ, Fong P (2018) Simultaneous synergist, antagonistic and additive interactions between multiple local stressors all degrade algal turf communities on coral reefs. *J Ecol* 106:1390–1400. <https://doi.org/10.1111/1365-2745.12914>
- Gallardo B, Clavero M, Sánchez MI, Vilà M (2015) Global ecological impacts of invasive species in aquatic ecosystems. *Glob Chang Biol* 22:151–163. <https://doi.org/10.1111/gcb.13004>
- Grutters BMC, Pollux BJA, Verberk WCEP, Bakker ES (2015) Native and non-native plants provide similar refuge to invertebrate prey, but less than artificial plants. *PLoS ONE* 10:e0124455
- Gurevitch J, Padilla DK (2004) Are invasive species a major cause of extinctions? *Trends Ecol Evol* 19:470–474. <https://doi.org/10.1016/j.tree.2004.07.005>
- Harrison PG (1989) Detrital processing in seagrass systems: a review of factors affecting decay rates, remineralization and detritivory. *Aquat Bot* 35:263–288. [https://doi.org/10.1016/0304-3770\(89\)90002-8](https://doi.org/10.1016/0304-3770(89)90002-8)
- Hautier Y, Isbell F, Borer ET, Seabloom EW, Harpole WS, Lind EM, MacDougall AS, Stevens CJ, Adler PB, Alberti J, Bakker JD, Brudvig LA, Buckley YM, Cadotte M, Caldeira MC, Chaneton EJ, Chu C, Daleo P, Dickman CR, Dwyer JM, Eskelinen A, Fay PA, Firm J, Hagenah N, Hillebrand H, Iribarne O, Kirkman KP, Knops JMH, La Pierre KJ, McCulley RL, Morgan JW, Pärtel M, Pascual J, Price JN, Prober SM, Risch AC, Sankaran M, Schuetz M, Standish RJ, Virtanen R, Wardle GM, Yahdjian L, Hector A (2018) Local loss and spatial homogenization of plant diversity reduce ecosystem multifunctionality. *Nat Ecol Evol* 2:50–56. <https://doi.org/10.1038/s41559-017-0395-0>
- Hay ME, Fenical W (1988) Marine plant-herbivore interactions: the ecology of chemical defense. *Annu Rev Ecol Syst* 19:111–145. <https://doi.org/10.1146/annurev.es.19.110188.000551>
- Heck KL, Valentine JF (2006) Plant-herbivore interactions in seagrass meadows. *J Exp Mar Bio Ecol* 330:420–436. <https://doi.org/10.1016/j.jembe.2005.12.044>
- Heck KL, Wetstone GS (1977) Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. *J Biogeogr* 4:135–142. <https://doi.org/10.2307/3038158>
- Heck KL, Carruthers TJB, Duarte CM, Hughes AR, Kendrick G, Orth RJ, Williams SW (2008) Trophic transfers from seagrass meadows subsidize diverse marine and terrestrial consumers. *Ecosystems* 11:1198–1210. <https://doi.org/10.1007/s10021-008-9155-y>
- Heffernan JB (2008) Wetlands as an alternative stable state in desert streams. *Ecology* 89:1261–1271. <https://doi.org/10.1890/07-0915.1>
- Hejda M, Pyšek P, Jarošík V (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. *J Ecol* 97:393–403. <https://doi.org/10.1111/j.1365-2745.2009.01480.x>
- Hemmi A, Jormalainen V (2002) Nutrient enhancement increases performance of a marine herbivore via quality of its food alga. *Ecology* 83:1052–1064. [https://doi.org/10.1890/0012-9658\(2002\)083\[1052:NEIPOA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[1052:NEIPOA]2.0.CO;2)
- Hessen DO, Færøvig PJ, Andersen T (2002) Light, nutrients, and P:C ratios in algae: grazer performance related to food quality and quantity. *Ecology* 83:1886–1898. [https://doi.org/10.1890/0012-9658\(2002\)083\[1886:LNAPCR\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[1886:LNAPCR]2.0.CO;2)
- Hladyz S, Åbjörnsson K, Giller PS, Woodward G (2011) Impacts of an aggressive riparian invader on community structure

- and ecosystem functioning in stream food webs. *J Appl Ecol* 48:443–452. <https://doi.org/10.1111/j.1365-2664.2010.01924.x>
- Hobbs RJ, Higgs E, Harris JA (2009) Novel ecosystems: implications for conservation and restoration. *Trends Ecol Evol* 24:599–605. <https://doi.org/10.1016/j.tree.2009.05.012>
- Kamer K, Fong P, Kennison R, Schiff K (2004) Nutrient limitation of the macroalga *Enteromorpha intestinalis* collected along a resource gradient in a highly eutrophic estuary. *Estuaries* 27:201–208
- Katsanevakis S, Wallentinus I, Zenetos A, Leppäkoski E, Çinar ME, Öztürk B, Grabowski M, Golani D, Cardoso AC (2014) Impacts of invasive alien marine species on ecosystem services and biodiversity: a pan-European review. *Aquat Invasions* 9:391–423
- Kirsch KD, Valentine JF, Heck KL (2002) Parrotfish grazing on turtlegrass *Thalassia testudinum*. *Mar Ecol Prog Ser* 227:71–85
- Kuznetsova A, Brockhoff P, Christensen R (2017) lmerTest package: tests in linear mixed effects models. *J Stat Software, Artic* 82:1–26. <https://doi.org/10.18637/jss.v082.i13>
- Larson DL, Phillips-Mao L, Quiram G, Sharpe L, Stark R, Sugita S, Weiler A (2011) A framework for sustainable invasive species management: environmental, social, and economic objectives. *J Environ Manage* 92:14–22. <https://doi.org/10.1016/j.jenvman.2010.08.025>
- Levin DA (1976) The chemical defenses of plants to pathogens and herbivores. *Annu Rev Ecol Syst* 7:121–159
- Levine JM, Adler PB, Yelenik SG (2004) A meta-analysis of biotic resistance to exotic plant invasions. *Ecol Lett* 7:975–989. <https://doi.org/10.1111/j.1461-0248.2004.00657.x>
- Luczakovich JJ, Ward GP, Johnson JC, Christian RR, Baird D, Neckles H, Rizzo WM (2002) Determining the trophic guilds of fishes and macroinvertebrates in a seagrass food web. *Estuaries* 25:1143–1163. <https://doi.org/10.1007/BF02692212>
- MacDougall AS, Turkington R (2005) Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* 86:42–55. <https://doi.org/10.1890/04-0669>
- Moncreiff CA (2001) Trophic importance of epiphytic algae in subtropical seagrass beds: evidence from multiple stable isotope analyses. *Mar Ecol Prog Ser* 215:93–106
- Moore AFP, Duffy JE (2016) Foundation species identity and trophic complexity affect experimental seagrass communities. *Mar Ecol Prog Ser* 556:105–121
- Muthukrishnan R, Lloyd-Smith JO, Fong P (2016) Mechanisms of resilience: empirically quantified positive feedbacks produce alternate stable states dynamics in a model of a tropical reef. *J Ecol* 104:1662–1672. <https://doi.org/10.1111/1365-2745.12631>
- Muthukrishnan R, Davis AS, Jordan NR, Forester JD (2018) Invasion complexity at large spatial scales is an emergent property of interactions among landscape characteristics and invader traits. *PLoS ONE* 13:e0195892. <https://doi.org/10.1371/journal.pone.0195892>
- Nelson SB, Coon JJ, Duchardt CJ, Fischer JD, Halsey SJ, Kranz AJ, Parker CM, Schneider SC, Swartz TM, Miller JR (2017) Patterns and mechanisms of invasive plant impacts on North American birds: a systematic review. *Biol Invasions* 19:1547–1563. <https://doi.org/10.1007/s10530-017-1377-5>
- Ogden J, Brown R, Salesky N (1973) Grazing by the echinoid *Diadema antillarum philippi*: formation of halos around west indian patch reefs. *Science* 182:715–717. <https://doi.org/10.1126/science.182.4113.715>
- Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solyomos P, Steven MHH, Szoecs E, Wagner H (2019) vegan: Community Ecology Package. R package version 2.5-6. <https://CRAN.R-project.org/package=vegan>
- Olden JD (2006) Biotic homogenization: a new research agenda for conservation biogeography. *J Biogeogr* 33:2027–2039. <https://doi.org/10.1111/j.1365-2699.2006.01572.x>
- Oliver I, Beattie AJ (1996) Invertebrate Morphospecies as surrogates for species: a case study. *Conserv Biol* 10:99–109. <https://doi.org/10.1046/j.1523-1739.1996.10010099.x>
- Orth RJ, Heck KL, van Montfrans J (1984) Faunal communities in seagrass beds: A review of the influence of plant structure and prey characteristics on predator-prey relationships. *Estuaries* 7:339–350. <https://doi.org/10.2307/1351618>
- Parsons DM, MacDonald I, Buckthought D, Middleton C (2018) Do nursery habitats provide shelter from flow for juvenile fish? *PLoS ONE* 13:e0186889
- Peterson BJ, Heck KL (1999) The potential for suspension feeding bivalves to increase seagrass productivity. *J Exp Mar Bio Ecol* 240:37–52. [https://doi.org/10.1016/S0022-0981\(99\)00040-4](https://doi.org/10.1016/S0022-0981(99)00040-4)
- Power ME (1992) Top-down and bottom-up forces in food webs: do plants have primacy. *Ecology* 73:733–746. <https://doi.org/10.2307/1940153>
- Prado P (2011) Seagrass selection by omnivorous and herbivorous consumers: determining factors. *Mar Ecol Prog Ser* 429:45–55
- Pyšek P, Jarošík V, Hulme PE, Pergl J, Hejda M, Schaffner U, Vilà M (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Glob Chang Biol* 18:1725–1737. <https://doi.org/10.1111/j.1365-2486.2011.02636.x>
- R Core Team (2018) R: A language and environment for statistical computing.
- 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
- Randall JE (1965) Grazing effect on sea grasses by Herbivorous Reef fishes in the West Indies. *Ecology* 46:255–260
- Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. *Divers Distrib* 6:93–107. <https://doi.org/10.1046/j.1472-4642.2000.00083.x>
- Rodriguez LF (2006) Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. *Biol Invasions* 8:927–939. <https://doi.org/10.1007/s10530-005-5103-3>
- Rogers CS, Miller J, Muller EM, Edmunds P, Nemeth RS, Beets JP, Friedlander AM, Smith TB, Boulon R, Jeffrey CFG, Menza C, Caldwell C, Idrisi N, Kojis B, Monaco ME, Spitzack A, Gladfelter EH, Ogden JC, Hillis-Starr Z, Lundgren I, Schill WB, Kuffner IB, Richardson LL, Devine BE, Voss JD (2008) Ecology of coral reefs in the US Virgin Islands. In: Riegl BM, Dodge RE (eds) *Coral reefs of the USA*. Springer, Netherlands, Dordrecht, pp 303–373
- Rogers CS, Willette DA, Miller J (2014) Rapidly spreading seagrass invades the Caribbean with unknown ecological consequences. *Front Ecol Environ* 12:546–547. <https://doi.org/10.1890/14.WB.016>
- Rohr JR, Mahan CG, Kim KC (2009) Response of arthropod biodiversity to foundation species declines: the case of the eastern hemlock. *For Ecol Manage* 258:1503–1510. <https://doi.org/10.1016/j.foreco.2009.07.002>
- Rotini A, Mejia AY, Costa R, Migliore L, Winters G (2017) Ecophysiological plasticity and bacteriome shift in the seagrass *Halophila stipulacea* along a depth gradient in the northern Red Sea. *Front Plant Sci* 7:2015
- Salisbury A, Al-Beidh S, Armitage J, Bird S, Bostock H, Platoni A, Tatchell M, Thompson K, Perry J (2017) Enhancing gardens as habitats for plant-associated invertebrates: should we plant native or exotic species? *Biodivers Conserv* 26:2657–2673. <https://doi.org/10.1007/s10531-017-1377-x>

- Sanders NJ, Gotelli NJ, Heller NE, Gordon DM (2003) Community disassembly by an invasive species. *Proc Natl Acad Sci* 100:2474–2477
- Scheibling RE, Patriquin DG, Filbee-Dexter K (2018) Distribution and abundance of the invasive seagrass *Halophila stipulacea* and associated benthic macrofauna in Carriacou, Grenadines, Eastern Caribbean. *Aquat Bot* 144:1–8. <https://doi.org/10.1016/j.aquabot.2017.10.003>
- Schlaepfer MA, Sax DF, Olden JD (2011) The potential conservation value of non-native species. *Conserv Biol* 25:428–437. <https://doi.org/10.1111/j.1523-1739.2010.01646.x>
- Schoo KL, Malzahn AM, Krause E, Boersma M (2013) Increased carbon dioxide availability alters phytoplankton stoichiometry and affects carbon cycling and growth of a marine planktonic herbivore. *Mar Biol* 160:2145–2155. <https://doi.org/10.1007/s00227-012-2121-4>
- Schooler SS, McEvoy PB, Coombs EM (2006) Negative per capita effects of purple loosestrife and reed canary grass on plant diversity of wetland communities. *Divers Distrib* 12:351–363. <https://doi.org/10.1111/j.1366-9516.2006.00227.x>
- Simberloff D (2014) Biological invasions: What's worth fighting and what can be won? *Ecol Eng* 65:112–121. <https://doi.org/10.1016/j.ecoleng.2013.08.004>
- Smulders FOH, Vonk JA, Engel MS, Christianen MJA (2017) Expansion and fragment settlement of the non-native seagrass *Halophila stipulacea* in a Caribbean bay. *Mar Biol Res* 13:967–974. <https://doi.org/10.1080/17451000.2017.1333620>
- Sol D, Vilà M, Kühn I (2008) The comparative analysis of historical alien introductions. *Biol Invasions* 10:1119–1129. <https://doi.org/10.1007/s10530-007-9189-7>
- Sotka EE, Byers JE (2019) Not so fast: promoting invasive species to enhance multifunctionality in a native ecosystem requires strong(er) scrutiny. *Biol Invasions* 21:19–25. <https://doi.org/10.1007/s10530-018-1822-0>
- Spivak AC, Canuel EA, Duffy JE, Richardson JP (2009) Nutrient enrichment and food web composition affect ecosystem metabolism in an experimental seagrass habitat. *PLoS ONE* 4:e7473
- Steiner SCC, Willette DA (2015) Dimming sand halos in Dominica and the expansion of the invasive seagrass *Halophila stipulacea*. *Reef Encount* 30:43–45
- Stohlgren TJ, Rejmánek M (2014) No universal scale-dependent impacts of invasive species on native plant species richness. *Biol Lett* 10:1–12
- Strayer DL (2012) Eight questions about invasions and ecosystem functioning. *Ecol Lett* 15:1199–1210. <https://doi.org/10.1111/j.1461-0248.2012.01817.x>
- Thomsen MS, Wernberg T, Altieri A, Tuya F, Gulbransen D, McGlathery KJ, Holmer M, Silliman BR (2010) Habitat cascades: the conceptual context and global relevance of facilitation cascades via habitat formation and modification. *Integr Comp Biol* 50:158–175
- Thomsen MS, Ramus AP, Long ZT, Silliman BR (2019) A seaweed increases ecosystem multifunctionality when invading bare mudflats. *Biol Invasions* 21:27–36. <https://doi.org/10.1007/s10530-018-1823-z>
- Tuchman NC, Wetzel RG, Rier ST, Wahtera KA, Teeri JA (2002) Elevated atmospheric CO<sub>2</sub> lowers leaf litter nutritional quality for stream ecosystem food webs. *Glob Chang Biol* 8:163–170. <https://doi.org/10.1046/j.1365-2486.2002.00460.x>
- Urabe J, Waki N (2009) Mitigation of adverse effects of rising CO<sub>2</sub> on a planktonic herbivore by mixed algal diets. *Glob Chang Biol* 15:523–531. <https://doi.org/10.1111/j.1365-2486.2008.01720.x>
- van Tussenbroek BI, van Katwijk MM, Bouma TJ, van der Heide T, Govers LL, Leuven RSEW (2016) Non-native seagrass *Halophila stipulacea* forms dense mats under eutrophic conditions in the Caribbean. *J Sea Res* 115:1–5. <https://doi.org/10.1016/j.seares.2016.05.005>
- Vander Zanden MJ, Olden JD (2008) A management framework for preventing the secondary spread of aquatic invasive species. *Can J Fish Aquat Sci* 65:1512–1522. <https://doi.org/10.1139/F08-099>
- Viana IG, Siriwardane-de Zoysa R, Willette DA, Gillis LG (2019) Exploring how non-native seagrass species could provide essential ecosystem services: a perspective on the highly invasive seagrass *Halophila stipulacea* in the Caribbean Sea. *Biol Invasions* 21:1461–1472. <https://doi.org/10.1007/s10530-019-01924-y>
- Vilà M, Basnou C, Pyšek P, Josefsson M, Genovesi P, Gollasch S, Nentwig W, Olenin S, Roques A, Roy D, Hulme PE, Partners D, (2010) How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Front Ecol Environ* 8:135–144. <https://doi.org/10.1890/080083>
- Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol Lett* 14:702–708. <https://doi.org/10.1111/j.1461-0248.2011.01628.x>
- Vonk JA, Christianen MJA, Stapel J (2008) Redefining the trophic importance of seagrasses for fauna in tropical Indo-Pacific meadows. *Estuar Coast Shelf Sci* 79:653–660. <https://doi.org/10.1016/j.ecss.2008.06.002>
- Wang Y, Naumann U, Wright ST, Warton DI (2012) mvabund— an R package for model-based analysis of multivariate abundance data. *Methods Ecol Evol* 3:471–474. <https://doi.org/10.1111/j.2041-210X.2012.00190.x>
- Whitfield AK (2017) The role of seagrass meadows, mangrove forests, salt marshes and reed beds as nursery areas and food sources for fishes in estuaries. *Rev Fish Biol Fish* 27:75–110. <https://doi.org/10.1007/s11160-016-9454-x>
- Willette DA, Ambrose RF (2009) The distribution and expansion of the invasive seagrass *Halophila stipulacea* in Dominica, West Indies, with a preliminary report from St. Lucia. *Aquat Bot* 91:137–142. <https://doi.org/10.1016/j.aquabot.2009.04.001>
- Willette DA, Ambrose RF (2012) Effects of the invasive seagrass *Halophila stipulacea* on the native seagrass, *Syringodium filiforme*, and associated fish and epibiota communities in the Eastern Caribbean. *Aquat Bot* 103:74–82. <https://doi.org/10.1016/j.aquabot.2012.06.007>
- Willette DA, Chalifour J, Debrot AOD, Engel MS, Miller J, Oxenford HA, Short FT, Steiner SCC, Védie F (2014) Continued expansion of the trans-Atlantic invasive marine angiosperm *Halophila stipulacea* in the Eastern Caribbean. *Aquat Bot* 112:98–102. <https://doi.org/10.1016/j.aquabot.2013.10.001>
- Willette DA, Chiquillo KL, Cross C, Fong P, Kelley T, Toline CA, Zweng R, Muthukrishnan R (2020) Growth and recovery after small-scale disturbance of a rapidly-expanding invasive seagrass in St. John, US Virgin Islands. *J Exp Mar Bio Ecol* 523:151265. <https://doi.org/10.1016/j.jembe.2019.151265>
- Williams SL (1988) *Thalassia testudinum* productivity and grazing by green turtles in a highly disturbed seagrass bed. *Mar Biol* 98:447–455. <https://doi.org/10.1007/BF00391121>
- Williams SL (1990) Experimental studies of caribbean seagrass bed development. *Ecol Monogr* 60:449–469
- Zavaleta ES, Hobbs RJ, Mooney HA (2001) Viewing invasive species removal in a whole-ecosystem context. *Trends Ecol Evol* 16:454–459. [https://doi.org/10.1016/S0169-5347\(01\)02194-2](https://doi.org/10.1016/S0169-5347(01)02194-2)
- Ziegler S (1999) Nutrient cycling in the water column of a subtropical seagrass meadow. *Mar Ecol Prog Ser* 188:51–62