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Seagrass coastal protection services reduced by invasive species expansion and megaherbivore grazing

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Handling Editor: A. Randall Hughes**Abstract**

1. Seagrasses provide an important ecosystem service by creating a stable erosion-resistant seabed that contributes to effective coastal protection. Variable morphologies and life-history strategies, however, are likely to impact the sediment stabilization capacity of different seagrass species. We question how opportunistic invasive species and increasing grazing by megaherbivores may alter sediment stabilization services provided by established seagrass meadows, using the Caribbean as a case study.
2. Utilizing two portable field-flumes that simulate unidirectional and oscillatory flow regimes, we compared the sediment stabilization capacity of natural seagrass meadows in situ under current- and wave-dominated regimes. Monospecific patches of a native (*Thalassia testudinum*) and an invasive (*Halophila stipulacea*) seagrass species were compared, along with the effect of three levels of megaherbivore grazing on *T. testudinum*: ungrazed, lightly grazed and intensively grazed.
3. For both hydrodynamic regimes, the long-leaved, dense meadows of the climax species, *T. testudinum* provided the highest stabilization. However, the loss of above-ground biomass by intensive grazing reduced the capacity of the native seagrass to stabilize the surface sediment. Caribbean seagrass meadows are presently threatened by the rapid spread of the invasive opportunistic seagrass, *H. stipulacea*. The dense meadows of *H. stipulacea* were found to accumulate fine sediment, and thereby, appear to be effective in reducing bottom shear stress during calm periods. This fine sediment within the invasive meadows, however, is

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easily resuspended by hydrodynamic forces, and the low below-ground biomass of *H. stipulacea* make it susceptible to uprooting during storm events, potentially leaving large regions vulnerable to erosion. Overall, this present study highlights that intensive megaherbivore grazing and opportunistic invasive species threaten the coastal protection services provided by mildly grazed native species.

4. *Synthesis.* Seagrass meadows of dense, long-leaved species stabilize the sediment surface and maintain the seabed integrity, thereby contributing to coastal protection. These services are threatened by intensive megaherbivore grazing, which reduces the stability of the surface sediment, and opportunistic invasive species, which are susceptible to uprooting in storms and thereby can leave the seabed vulnerable to erosion.

KEYWORDS

coastal protection, conservation, ecosystem services, exotic species, marine ecology, marine vegetation, storm resilience, tropical ecology

1 | INTRODUCTION

Seagrass meadows are well-known for the vital ecosystem services that they provide in coastal environments. As primary producers, they make up the base of the food web, being utilized as a primary food source by reef fish, urchins and turtles (Duarte, 1989; Nagelkerken, 2009), while also providing structural complexity that can be used as habitat (Gillis et al., 2014; Orth et al., 2006). In addition, seagrass meadows provide coastal protection services (Christianen et al., 2013; James et al., 2019; Ondiviela et al., 2014; Paul, 2018), by attenuating waves (Fonseca & Fisher, 1986; Hansen & Reidenbach, 2012; Lei & Nepf, 2019), by reducing tidal currents (Gambi, Nowell, & Jumars, 1990; Widdows, Pope, Brinsley, Asmus, & Asmus, 2008) and by protecting the seabed from erosion (Gacia & Duarte, 2001; Koch & Gust, 1999; Potouroglou et al., 2017). This protective effect can be so large that seagrass may even prevent the need of sand-nourishments to preserve beaches (James et al., 2019).

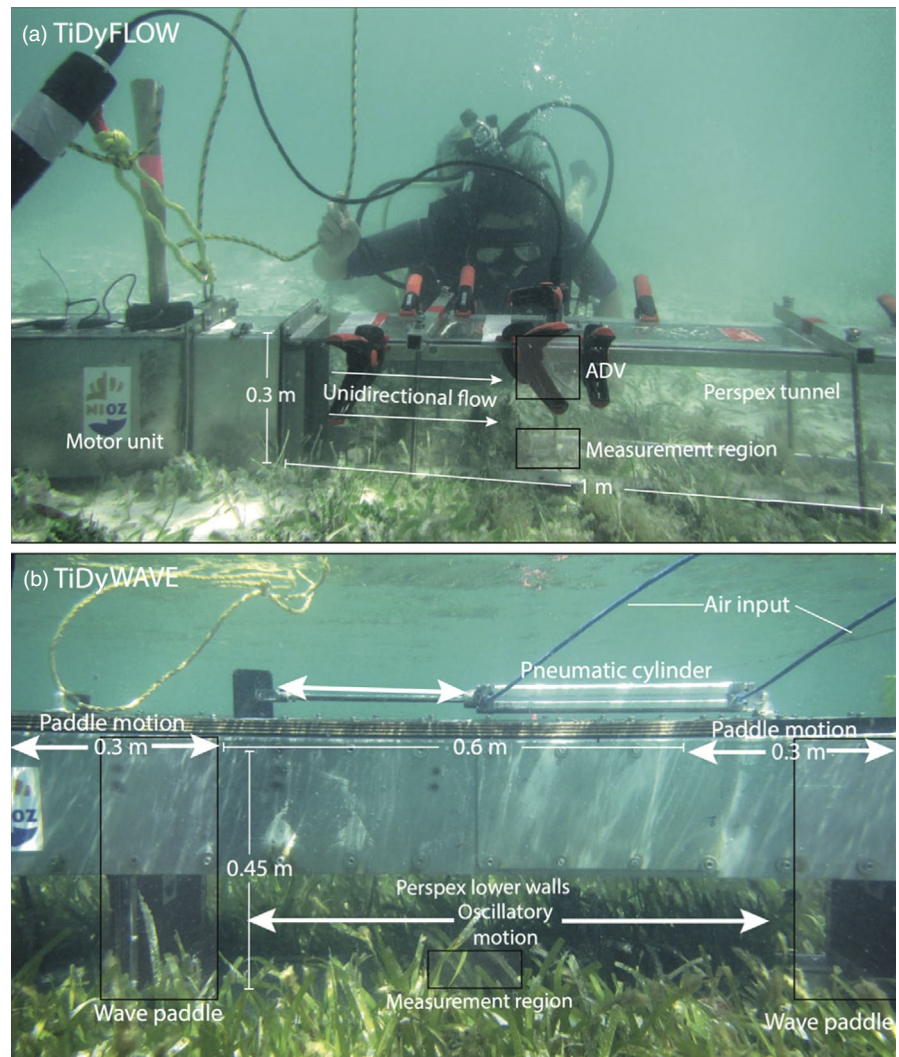
The flexible leaves of seagrass sway back and forth as waves propagate over them, with the drag forces exerted on the seagrass leaves causing a reduction in wave energy (Bouma et al., 2005; Bradley & Houser, 2009; Fonseca & Cahalan, 1992; Lei & Nepf, 2019). This process can result in a 20% reduction in wave height in shallow water (Hansen & Reidenbach, 2012). Within the seagrass canopy itself, flows can be 70%–90% lower than that of adjacent unvegetated areas (Gambi et al., 1990; Hansen & Reidenbach, 2012; Koch, Ackerman, Verduin, & van Keulen, 2006; Koch & Gust, 1999). The direct influence that seagrasses have on reducing the water flow within and around their meadows, provides a coastal protection service by preventing sediment resuspension (Gacia & Duarte, 2001), and thus mitigating erosion (James et al., 2019; Paul, 2018; Potouroglou et al., 2017). The ability of seagrasses to provide coastal protection services is expected to be largely dependent on both the species-specific and the grazer-affected morphology of the seagrass. With over 60–70 seagrass species worldwide, there is a large diversity of morphologies (strap-, paddle-, feather-like) and

life-history strategies (Kilminster et al., 2015). This morphological diversity is likely to result in varying levels of coastal protection provided by seagrasses (Fonseca, 1989; Mellors, Marsh, Carruthers, & Waycott, 2002).

Declining seagrass area in combination with a reduction of apex predators, has led megaherbivores (e.g. green turtles *Chelonia mydas*) to intensively graze zones of seagrass in some tropical regions (Christianen et al., 2014). Intensive grazing changes the seagrass morphology, and thus may affect the coastal protection services of seagrass meadows. Indeed, Christianen et al. (2013) showed that the coastal protection services of short, intensively grazed canopies of *Halodule univervis* were reduced compared to ungrazed seagrass; however, the roots and rhizomes continued to provide some sediment stabilization by reducing the erodibility of the seabed. A general understanding of the role of seagrass morphology, including the effect of species-specific differences and grazing induced biomass changes, on the sediment-stabilizing services provided by seagrass meadows remains lacking. Such knowledge is, however, critical given that species-oriented nature conservation strategies may cause increasing megaherbivore grazing pressure (Christianen et al., 2014), and biological invasions cause shifts in the species structure of marine communities to more opportunistic (*r*-selected) species (Olinger et al., 2017; Williams, 2007).

Invasive species are threatening the diversity and natural functioning of seagrass ecosystems in many regions of the world, with approximately 56 non-native species being introduced within seagrass meadows before 2007 (Williams, 2007). One of the most dominant invasive seagrass species is *Halophila stipulacea*, which originates from the Red Sea, but invaded the Mediterranean (Lipkin, 1975) and then subsequently the Caribbean region (Ruiz & Ballantine, 2004). *Halophila stipulacea* is an opportunistic seagrass (Erftemeijer & Shuail, 2012; Kilminster et al., 2015) that can quickly colonize disturbed areas (Smulders, Vonk, Engel, & Christianen, 2017). It has spread rapidly throughout the Caribbean (Willette et al., 2014) where it forms dense monospecific stands and competes with native

FIGURE 1 The TiDyFLOW flume (a) consists of a motor unit with two propellers that generate a unidirectional flow through the clear Perspex tunnel that is embedded into the sediment. The speed of the propellers is regulated to control the flow speed, with an ADV positioned in the centre of the tunnel, which records the flow velocity. Sediment movement is monitored beneath the ADV to determine the threshold flow velocity at which the sediment begins to move. The TiDyWAVE flume (b) mimics the oscillatory flow created by an unbreaking wave. Wooden wave paddles on either end of the flume move back and forth by the pneumatic cylinder observed on the top of the flume. The speed of the movement is controlled by regulating the airflow into the pneumatic cylinder. The time at which the boards moved back and forth in one cycle was calculated to be the oscillatory velocity. Clear Perspex surrounds the base of the flume allowing for the sediment movement within the flume to be observed [Colour figure can be viewed at wileyonlinelibrary.com]



species like *Thalassia testudinum* and *Syringodium filiforme*. This invasive species not only threatens the biodiversity of coastal ecosystems (Olinger et al., 2017), but is rarely grazed upon by turtles, thus its spread is likely to have large consequences for ecosystem functioning (Christianen et al., 2018). Furthermore, due to its short canopy and shallow root system, the replacement of native seagrass species by *H. stipulacea* may impact the coastal protection services provided by seagrass in tropical bays, however, this remains to be tested.

Understanding the ability of different types of marine vegetation in providing coastal protection services is vital at this time when erosion is being exacerbated by increasing coastal infrastructure, sea-level rise and increasing storm intensity (Church et al., 2013; Jevrejeva, Jackson, Riva, Grinsted, & Moore, 2016; McGranahan, Balk, & Anderson, 2007; Saunders & Lea, 2008). Hence, we test how (a) intensifying megaherbivore grazing pressure and (b) species shifts (due to invasions) alter the extent to which seagrass meadows provide erosion protection. To address this question, we directly measured the sediment stabilization capacity of contrasting seagrass patches in situ by deploying two portable field flumes that mimicked unidirectional- and oscillatory-flow (Figure 1). We compared three

levels of megaherbivore grazing (ungrazed, lightly grazed and intensively grazed) on the native climax seagrass, *T. testudinum*, in addition to the invasive opportunistic seagrass *H. stipulacea*, and a bare unvegetated patch. As the flume measurements were conducted in situ, the sediment dynamics of the naturally formed system could be measured, and an absolute measure of the sediment stability in the field is obtained. The seagrass patch characteristics of vegetation density, canopy bendability and biomass allocation were measured to further describe the sediment stabilization ability of the different species. It was hypothesized that patches of the long-leaved ungrazed native turtle grass *T. testudinum*, will provide more effective erosion protection than patches of short-leaved species, like the invasive *H. stipulacea* and intensively grazed seagrasses.

2 | MATERIALS AND METHODS

2.1 | Site description

This study was conducted within Lac Bay, Bonaire, Caribbean Netherlands (12.108177, -68.226289). Lac Bay is a shallow lagoon

(<6 m deep) located at the windward eastern coast of Bonaire (Figure 2). Extensive seagrass meadows composed of the native seagrass species *T. testudinum* have historically dominated the bay. However, more recently the invasive seagrass *H. stipulacea* has expanded rapidly throughout the deeper parts of the bay since its first sighting in 2010 (Debrot et al., 2019; Willette et al., 2014) and is starting to encroach on the shallower parts (Smulders et al., 2017). Lac Bay is a Ramsar Site (wetland designated to be of international importance) and has an extensive mangrove forest bordering the landward side of the lagoon. A large turtle population has developed, which intensively grazes upon the native seagrass, creating areas of ungrazed, lightly and intensively grazed seagrass patches (Christianen et al., 2018). Calcifying macroalgae from the *Halimeda* family are interspersed amongst the seagrass and are an important contributor to the calcareous sediment within the bay, along with the fringing coral reef. A fringing coral reef on the eastern side protects the bay creating a sheltered lagoon, with a tidal range of <0.3 m. Rainfall is low (<560 mm/year) and storms are infrequent within the Bonaire region, with only six tropical storms and hurricanes occurring between 1944 and 2010 (van Dijken, 2011).

2.2 | Sediment stabilization ability of contrasting seagrass patch types

The sediment stabilization ability, measured as the critical erosion threshold, of the calcareous sediment within different subtidal seagrass patch types was measured in situ with two portable field-flumes developed at the Royal Netherlands Institute for Sea Research (NIOZ): TiDyFLOW is a unidirectional flow flume and TiDyWAVE is an oscillatory flow flume that mimics waves. The field flumes were placed within Lac Bay, Bonaire, over the five most dominant patch types (see photos Figure 2): bare (no vegetation), intensively grazed *T. testudinum* (canopy < 50 mm), lightly grazed *T. testudinum*, ungrazed *T. testudinum* (canopy > 180 mm height) and patches of the invasive *H. stipulacea*, which is rarely grazed by mega-herbivores (Christianen et al., 2018). Three to four replicate patches of each seagrass type were measured; each time moving the flumes to a new undisturbed position and conducting duplicate flume runs on each position. All but *H. stipulacea* were available in the first study area, which ranged between 1 and 1.3 m depth (Figure 2). Because *H. stipulacea* has a heterogeneous distribution within the bay, it had to be measured further away within a second study area, which was slightly deeper at 1.5–2 m depth (Figure 2). To test if there was an 'area' difference, a neighbouring

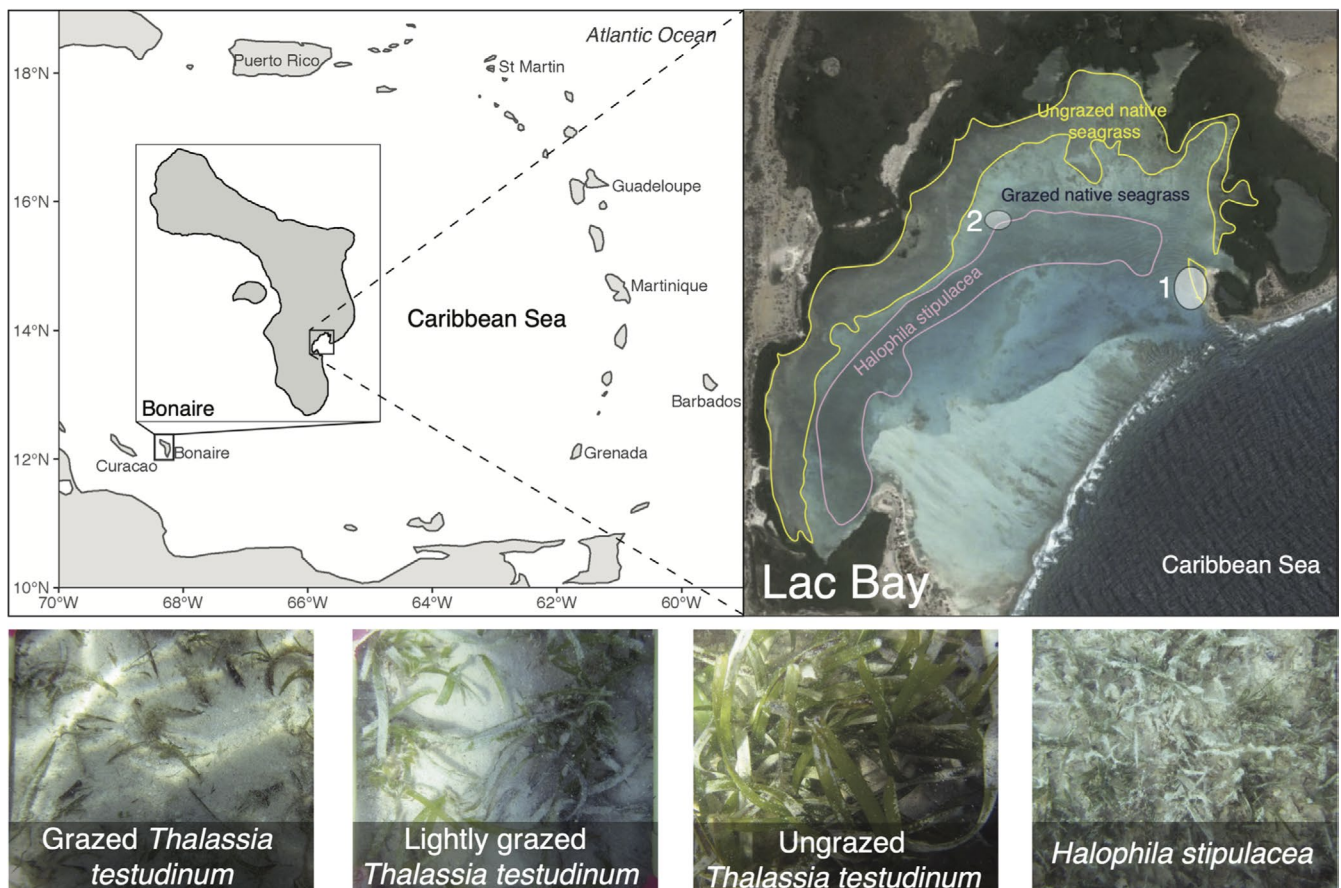


FIGURE 2 Map of the two study areas within Lac Bay, Bonaire (white circles), with the approximate distribution of the ungrazed (yellow) and grazed native seagrass, and the area dominated by invasive *Halophila stipulacea* (pink) within Lac Bay (distribution obtained from Christianen et al., 2018). The majority of the measurements were conducted in study area one, with the invasive *H. stipulacea* being measured in study area two along with an additional three replicates of grazed *Thalassia testudinum*. Photographs above show the four different seagrass patch types that were measured [Colour figure can be viewed at wileyonlinelibrary.com]

intensively grazed *T. testudinum* patch was also measured in the second study area. Due to logistical limitations, only the oscillatory flume could be used in the second area.

The TiDyFLOW flume (Figure 1a) uses two motor-driven propellers to generate unidirectional flow up to speeds of 1.0 m/s through a 1-metre-long clear Perspex tunnel (James et al., 2019). The flow velocity within the field flume was continuously measured with an ADV (Nortek AS[®] Vectrino Field Probe) that was suspended 0.25 m above the seagrass canopy within the flume tunnel. Divers closely observed the sediment surface within the flume tunnel, and the critical erosion threshold was the velocity at which sediment grains situated beneath the ADV began to move along the bed surface. As bed-load transport depends on flow velocity to the power of 3, the difference in flow velocity between stochastic movement of some grains and continuous movement of many grains remains small. Therefore, human observations are sufficiently precise to determine critical erosion thresholds. Two divers conducted the sediment observations and training was conducted before the measurements to ensure the observations were standardized.

The TiDyWAVE oscillatory channel flume (Figure 1b) was controlled by a pneumatic cylinder that pushed two wooden boards (wave paddles) at either end of the flume back and forth in a synchronized motion. Although the physics are not exactly the same, the movement of the two wave paddles generates an oscillating flow at the sediment surface that mimics the oscillatory flow at the seabed when a wave passes over. The speed of the movement of the wave paddles was controlled by regulating the airflow into the cylinder. The velocity of the wave paddles was used as a measure for the root mean square (rms) oscillatory flow velocity, with the period at which the boards moved between the outermost positions being timed to give the rms oscillatory velocity in m/s. The sediment surface was closely observed by divers, and the critical erosion threshold under oscillatory flow conditions was considered to be the speed at which the sediment grains in the centre of the flume began to move.

Smaller sediment particles will move easier and at lower bottom shear stress values than larger particles (Shields, 1936), therefore, the sediment grain size distribution within each patch type was assessed to account for sediment variations between patch types. To help with the comparison between the two study areas (Figure 2), the sediment grain size distribution was also measured within a bare patch in study area 2. Sediment samples of the surface sediment were collected in 50 ml sampling containers from each measured position directly after the flume measurements. The sediment samples were freeze-dried and sieved through a 1-mm sieve, sediment larger than 1 mm was weighed, while the remaining sediment grain size distribution was measured by laser diffraction on a Malvern Mastersizer 2000 (McCave, Bryant, Cook, & Coughanowr, 1986).

2.3 | Seagrass meadow characteristics: Vegetation density, leaf bendability and biomass allocation

At each flume measurement position, the canopy height was measured, and photos were taken within a 0.25 m × 0.25 m quadrat to

estimate seagrass cover. These measurements were utilized to estimate seagrass volume (m³), with the per cent benthic cover of the seagrass multiplied by the canopy height. Seagrass volume was considered a comparable measure of the vegetation density across the different vegetation patches given the contrasting morphologies.

A seagrass trait that promotes the stabilization of sediment is leaf bendability, with the leaves of seagrass bending over the sediment surface and deflecting the flow away from the sediment surface (Gambi et al., 1990). Thus, bending protects the sediment surface from erosion (Peralta, Van Duren, Morris, & Bouma, 2008) while at the same time reducing the drag experienced by the seagrass leaves (Bouma et al., 2005). Individual shoots of the seagrass *T. testudinum* (grazed and ungrazed) and *H. stipulacea* were collected with their roots attached from Lac Bay (<1.3 m deep) and transported to the Netherlands wrapped in moist paper towels (total travel time was 20 hr). The seagrass shoots were placed in a heated seawater holding tank set to 25°C and bubbled continuously with air. Lights were set to a 12:12 hr light:dark cycle and the seagrasses were left for 24 hr as pre-treatment before measurements. The bendability of ungrazed *T. testudinum*, grazed *T. testudinum* and *H. stipulacea* was measured within a week of collection. The roots of the seagrass shoots were removed directly before the measurements were conducted. The seagrass shoots (without roots) were placed within a racetrack flume at NIOZ (Yerseke, The Netherlands), which produces a controlled unidirectional flow. Seagrass shoots were attached with a 3-mm wide cable tie to a small platform so they stood upright. One shoot at a time was placed within the centre of the flume with the broadest part of the leaf positioned adjacent to the flow, to allow for the natural bending direction of the seagrass. The flow within the flume was increased at 0.1 m/s increments, from 0 to 0.5 m/s, and a digital photograph was taken of the seagrass shoots at each flow speed. Using ImageJ 1.50i (Schneider, Rasband, & Eliceiri, 2012), a straight line was drawn from the base of the shoot to the most distal point of the leaves, and the angle of this line was recorded as the bending angle of the seagrass shoot. Bending angles are presented relative to the angle of the shoot at 0 m/s. These measurements were repeated three to five times for each seagrass species/type, each time with a new healthy shoot.

Biomass allocation to above- and below-ground structures can be used to identify the robustness of the seagrass patches to storm events (Cruz-Palacios & Van Tussenbroek, 2005; van Tussenbroek, Barba Santos, van Dijk, Sanabria Alcaraz, & Téllez Calderón, 2008), and thereby their ability to provide long-term sediment stabilization services. Five replicate cores of 0.15-m diameter and length were taken from within the ungrazed and intensively grazed *T. testudinum* patches and 0.1-m diameter and length within the *H. stipulacea* seagrass patches. As lightly grazed *T. testudinum* patches were a mix of grazed and ungrazed *T. testudinum*, biomass measurements within this patch type were deemed unnecessary, and therefore damage to the seagrass meadow from taking cores could be minimized. Sediment was washed from the biomass, and the biomass was separated into above-ground biomass (leaves and sheath), and below-ground biomass (roots and rhizomes). The biomass was dried in a 60°C drying oven and weighed.

2.4 | Statistical analyses

To firstly test if there were significant differences in the critical erosion threshold and median grain size between the seagrass patch types, one-way ANOVAs and Tukey HSD pair-wise comparisons were conducted with R version 3.6.1 (R Core Team, 2017) for each water motion type (unidirectional and oscillatory). A linear regression was subsequently used to identify the effect of the seagrass volume and grain size on the critical erosion threshold in the unidirectional and oscillatory flow regimes. Due to the oscillatory flow measurements being conducted within the two study areas (Figure 2), so that *H. stipulacea* patches could be measured, area was also included as a factor in the linear regression for the oscillatory flow measurements. Residual scatter plots were examined to ensure homoscedasticity and a Shapiro–Wilk test was conducted to test normality, with the data passing these assumptions. 95% confidence intervals (CI) were calculated for all data and are presented throughout the results text.

Biomass and leaf bendability were not included in the regression analyses due to their strong correlation with seagrass volume and because the biomass samples were not taken directly within the flume measurement positions. These measurements were therefore used to describe the observed relationships.

3 | RESULTS

3.1 | Vegetation effects on critical erosion threshold

The critical erosion threshold varied significantly between the different seagrass patch types in both the unidirectional flow

regime (one-way ANOVA: $F_{3,9} = 40.16$, $p < 0.01$, Supporting Information S1a) and the oscillatory flow regime (one-way ANOVA: $F_{5,13} = 11.07$, $p < 0.01$, Supporting Information S1b). In bare areas with no seagrass cover, the median grain size was $295.84 \pm 4.00 \mu\text{m}$ ($n = 3$; Figure 4), with 41% of the grains measuring between 250 and 500 μm . This bare sediment began moving at an average unidirectional flow speed of $0.11 \pm 0.02 \text{ m/s}$ (95% CI, $n = 3$; Figure 3a), and at an rms oscillatory flow velocity of $0.11 \pm 0.02 \text{ m/s}$ (95% CI, $n = 3$; Figure 3b). Contrastingly, in areas where ungrazed *T. testudinum* is present, the volume of seagrass is the highest at $0.17 \pm 0.03 \text{ m}^3$ ($n = 7$), and a strong unidirectional flow of $0.50 \pm 0.08 \text{ m/s}$ ($n = 4$; Figure 3a) or an rms oscillatory flow velocity of $0.17 \pm 0.03 \text{ m/s}$ ($n = 3$; Figure 3b) were required to move the sediment beneath the ungrazed canopy. A post-hoc Tukey test showed that the critical erosion threshold was significantly greater within the ungrazed *T. testudinum* patches compared to bare areas, under both a unidirectional flow regime ($\Delta = 0.39$, $p < 0.01$, Supporting Information S1a) and an oscillatory flow regime ($\Delta = 0.06$, $p = 0.01$, Supporting Information S1b). The sediment grain size did not significantly differ from that of bare areas, with a median grain size of $355.57 \pm 48.97 \mu\text{m}$ ($n = 3$; Figure 4). Ungrazed *T. testudinum* had the longest leaves, with an average canopy height of $0.20 \pm 0.02 \text{ m}$ tall ($n = 7$; Figure 5a), and a benthic area coverage of $82.86 \pm 5.60\%$ ($n = 7$; Figure 5c). These long leaves bent over immediately in a unidirectional flow, and by a flow velocity of 0.40 m/s , the leaf of *T. testudinum* reached a maximum bending angle of $64.43 \pm 25.74^\circ$ ($n = 3$; Figure 5d). The dense cover of *T. testudinum* translated into a below-ground biomass of $298.34 \pm 89.24 \text{ g}_{\text{dwt}}/\text{m}^2$ ($n = 5$) and an above-ground biomass (leaves and sheath) of $420.18 \pm 126.11 \text{ g}_{\text{dwt}}/\text{m}^2$ ($n = 5$; Figure 5b).

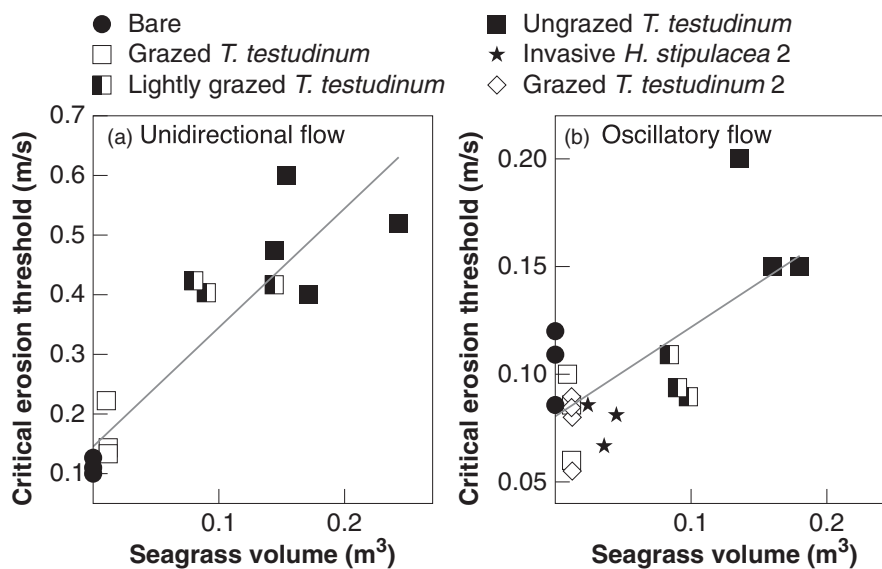


FIGURE 3 The critical erosion threshold (m/s) versus seagrass volume (area cover of seagrass \times canopy height) under unidirectional (a) and oscillatory flow (b) conditions produced by portable field flumes. The five studied patch types are represented by different symbols, in (b) there are three additional measurements of grazed *Thalassia testudinum* conducted in area 2 (open diamonds) to coincide with the invasive *Halophila stipulacea* (black stars) measurements. The fitted line demonstrates the relationship between seagrass volume and the critical erosion threshold (unidirectional: $p_{(\text{SG volume})} < 0.001$, $R^2_{(\text{adj})} = 0.833$; oscillatory: $p_{(\text{SG volume})} < 0.01$, $R^2_{(\text{adj})} = 0.64$; Supporting Information S1c and S1d). Note the different y-axis scales

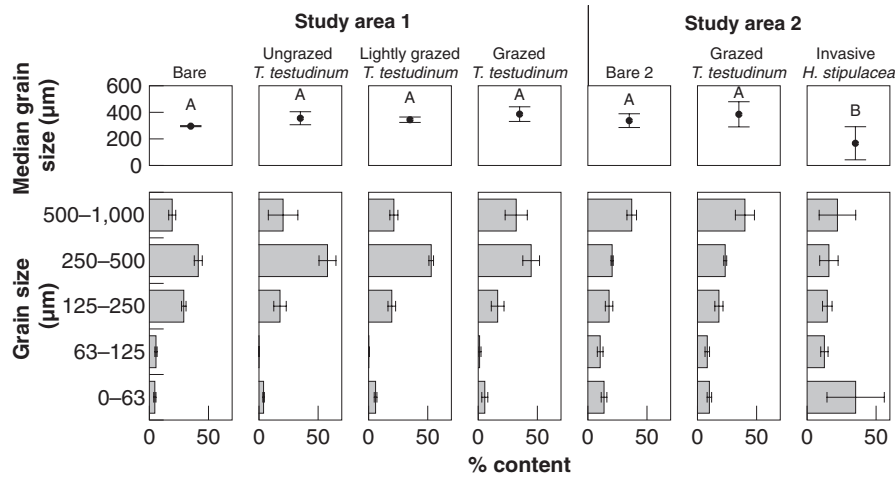
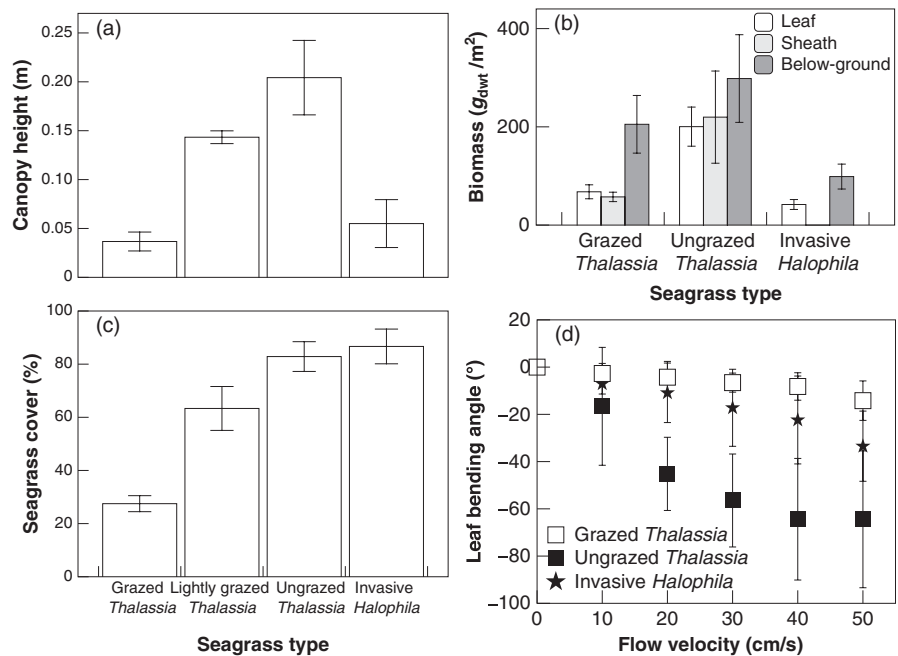


FIGURE 4 The median grain size and grain size distribution of the sediment within the two study areas and each seagrass patch type where the critical erosion threshold measurements were conducted. Most seagrass patch types existed within the same area (study area 1, see Figure 2), however, the invasive *Halophila stipulacea* and an additional grazed *Thalassia testudinum* were measured in study area 2. To help with the comparison of the two study areas, the grain size distribution of bare sediment within study area 2 was also measured. Bars and points represent mean values \pm 95% CI ($n = 3$). Different capital letters above points indicate a significant difference tested with Tukey HSD pair-wise comparisons (Supporting Information S1e), $p < 0.05$ are considered statistically significant

FIGURE 5 The canopy height (a), leaf (white bars), sheath (light grey bars) and below-ground (dark grey bars) biomass (b) and percentage seagrass cover (c) is displayed for the dominant seagrass patches present in Lac Bay, Bonaire (*Thalassia testudinum*—grazed and ungrazed, and *Halophila stipulacea*). The angles at which the leaves of the seagrasses bend under increasing unidirectional flow velocities within a racetrack flume is depicted in (d). Bars and points represent means \pm 95% CI ($n = 3-7$)



3.2 | Influence of megaherbivore grazing on sediment stabilization by seagrass

Intensive megaherbivore grazing of *T. testudinum* in some areas reduced the volume of seagrass to $0.01 \pm 0.01 \text{ m}^3$ ($n = 10$) and the canopy height of *T. testudinum* by 80% to $0.04 \pm 0.01 \text{ m}$ ($n = 10$; Figure 5a). This corresponded with a 70% reduction in the above-ground biomass to $125.17 \pm 16.69 \text{ g}_{\text{dwt}}/\text{m}^2$ ($n = 5$) and a 31% reduction in below-ground biomass to $205.19 \pm 58.70 \text{ g}_{\text{dwt}}/\text{m}^2$ ($n = 5$; Figure 5b) when compared to ungrazed areas of *T. testudinum*. The intensive grazing of *T. testudinum* decreased its influence on the critical

erosion threshold significantly in both flow regimes (Tukey test: $\Delta_{\text{unidirectional}} = 0.33$, $p < 0.01$; $\Delta_{\text{oscillatory}} = 0.09$, $p < 0.01$, Supporting Information S1a and S1b), so that the critical erosion threshold within the intensively grazed patches did not significantly vary from that of bare sediment. The critical erosion threshold within the grazed *T. testudinum* patches under the oscillatory flow regime did not significantly differ between the two study areas (Figure 2), and the sediment began moving at $0.08 \pm 0.02 \text{ m/s}$ ($n = 6$; Figure 3b) in both study areas. The median sediment grain size in grazed patches did not significantly differ from that of the ungrazed *T. testudinum* and bare patches (Figure 4). Between the two study areas, there was

almost double the proportion of silt grains (<63 μm) within area 2 ($10.07 \pm 1.90\%$; $n = 5$) compared with area 1 ($5.55 \pm 2.54\%$; $n = 3$), however, there was no significant difference in the median grain size in both areas (Figure 4). The bending angle of grazed *T. testudinum* was restricted by its shortness, and grazed leaves bent by only $14.20 \pm 8.35^\circ$ ($n = 3$) at the strongest flow of 0.5 m/s (Figure 5d).

Lightly grazed *T. testudinum* was a mix of grazed and ungrazed leaves, resulting in a seagrass volume 42% less than in completely ungrazed areas ($0.10 \pm 0.02 \text{ m}^3$; $n = 6$). The lightly grazed *T. testudinum* still provided protection to the sediment layer under a unidirectional flow regime, with a flow speed of $0.41 \pm 0.01 \text{ m/s}$ ($n = 3$; Figure 3a) required to move the sediment beneath the canopy, which was significantly greater than the sediment in bare patches (Tukey test: $\Delta = 0.30$, $p < 0.01$, Supporting Information S1a). However, under a wave regime, the critical erosion threshold did not significantly differ to that of bare areas (0.10 ± 0.01 , $n = 3$; Figure 3b) and was significantly less than the ungrazed *T. testudinum* patches (Tukey test: $\Delta = 0.07$, $p < 0.01$, Supporting Information S1b).

3.3 | Effect of invasive *H. stipulacea* on sediment stabilization

Halophila stipulacea had a high benthic cover of $86.67 \pm 6.53\%$ (Figure 5c). However, the short canopy height ($0.04 \pm 0.01 \text{ m}$, $n = 3$; Figure 5a) meant that the calculated seagrass volume was only $0.04 \pm 0.01 \text{ m}^3$ for areas inhabited by *H. stipulacea* ($n = 3$). *H. stipulacea* only occurred within the deeper second study area (Figure 2). The median grain size between the bare patches in the two opposing study areas did not significantly differ, however, the bare sediment within study area 2 had a greater proportion of fine grains (<125 μm) compared to the bare sediment within study area 1 (Figure 4). The sediment within patches of invasive seagrass *H. stipulacea*, was however, significantly distinct to the sediment within all other seagrass patch types (one-way ANOVA; $F_{6,17} = 6.43$, $p < 0.01$; Supporting Information S1e). The median grain size within the *H. stipulacea* patches was the lowest observed at $167.10 \pm 124.59 \mu\text{m}$ ($n = 3$), and the dominant proportion of the sediment was very fine calcareous grains (<63 μm , Figure 4). Tukey pairwise comparisons showed that the median grain size within *H. stipulacea* patches was significantly finer than the sediment within the neighbouring grazed *T. testudinum* that was also in the second study area ($\Delta = -217.93$, $p < 0.01$). The mean critical erosion threshold within the *H. stipulacea* patches under an oscillatory flow was $0.08 \pm 0.01 \text{ m/s}$ ($n = 3$; Figure 3b). The low canopy height of *H. stipulacea* contributed to it only having a mean above-ground biomass of $41.92 \pm 10.11 \text{ g/m}^2$ ($n = 5$), with a higher below-ground biomass of $98.77 \pm 25.36 \text{ g/m}^2$ ($n = 5$; Figure 5b). The short leaf of invasive *H. stipulacea* bent up to $33.48 \pm 14.86^\circ$ ($n = 5$) at flow speeds of 0.5 m/s (Figure 5d).

3.4 | Importance of meadow characteristics

The volume of seagrass within the different patch types exhibited a significant positive relationship with the critical erosion threshold in

both the unidirectional flow (Linear regression: $\beta = 7.55$, $t_{df=9} = 2.71$, $p = 0.02$; Figure 3a) and the oscillatory flow regime (Linear regression: $\beta = -2.14$, $t_{df=14} = -2.37$, $p = 0.03$; Figure 3b). However, within the oscillatory flow regime, there was a significant interaction between the seagrass volume and sediment grain size (Linear regression: $\beta = 0.01$, $t_{df=14} = 2.80$, $p = 0.01$). The study area did not significantly affect the critical erosion threshold in the oscillatory flow measurements.

4 | DISCUSSION

The capacity of tropical seagrasses to stabilize the sediment surface and the influence of megaherbivore grazing on this sediment stabilization was directly measured in situ, using two portable field flumes. Seagrass meadow morphology strongly affected the sediment stabilization services, with seagrass patches that have a high seagrass volume, such as the tall and dense canopies of ungrazed *T. testudinum*, effectively protecting the sandy sediment surface from erosion in both unidirectional and oscillatory flow regimes. By reducing the seagrass canopy volume, megaherbivore grazing had a strong negative effect on the erosion-protection ecosystem service of the native *T. testudinum* meadows and increased the likelihood of erosion of the sediment surface. The sediment within the short canopy of *H. stipulacea* was also easily eroded, with only slow flows required to cause sediment resuspension within the invasive patches. The higher proportion of fine sediment within the *H. stipulacea* patches, however, has to be considered when evaluating the sediment stabilization capacity of this invasive seagrass.

4.1 | Vegetation properties affect critical erosion threshold under flow and waves

In a unidirectional flow environment, the long, bendable, strap-like leaves of *T. testudinum* create a tightly packed barrier that deflects the main flow over the canopy rather than along the sediment surface (Koch et al., 2006; Koch & Gust, 1999). This long, strap-like leaf morphology was also demonstrated to be advantageous in providing effective sediment stabilization by Widdows et al. (2008), who showed that in high flow conditions, sediment stability was increased 10-fold within dense beds of *Zostera marina* compared to unvegetated sediments. Contrastingly, the short canopy of grazed *T. testudinum* scarcely bends, and as a result, sediment within the intensively grazed patches begins to move at similar flow velocities as in unvegetated areas.

The ability of dense ungrazed seagrass meadows to stabilize the surface sediment in oscillatory flow conditions still persists, but its effectiveness is reduced over twofold compared to unidirectional flow conditions. The loss of only a small amount of the canopy to light grazing reduced the sediment protection ability of *T. testudinum* to an extent that the seagrass had no significant effect on the critical erosion threshold. Strong unidirectional flow can create a skimming effect, which reduces the mixing between the bulk water and the

water inside the seagrass canopy (Koch & Gust, 1999), and thus reduces bottom shear. Contrastingly, oscillatory motion creates a more turbulent environment. Seagrass leaves sway back and forth with the oscillatory motion, leading to increased flow penetration and thereby allowing the flow to exert greater drag and lift forces on the seabed (Koch & Gust, 1999; Lowe, Koseff, & Monismith, 2005; Luhar, Coutu, Infantes, Fox, & Nepf, 2010). This turbulence and greater penetration of flow into the seagrass canopy results in smaller boundary layers at the seabed (Luhar et al., 2010; Tinoco & Coco, 2018), and increases the likelihood of sediment resuspension. In addition, stiff structures (i.e. seagrass shoots) increase turbulence inside the boundary layer (Tinoco & Coco, 2018), which can lead to enhanced erosion when flow reduction by leaves is inhibited due to, for example, grazing.

4.2 | Megaherbivore grazing lowers critical erosion threshold

The significant loss of above-ground biomass from megaherbivore grazing, lessens the amount of protection given by the seagrass to the sediment surface layer, and thus the erosion protection. A great effort has been put into the conservation of large herbivores, and is resulting in a recovery of green turtle populations (Chaloupka et al., 2008). This effort, unfortunately, has largely not extended to the conservation of the native seagrass populations that they are dependent upon, which are generally in decline (Orth et al., 2006). The high number of turtles residing within Lac Bay has led to 78% of the seagrass area being grazed (Christianen et al., 2018), significantly reducing the biomass of the native seagrass species *T. testudinum*.

Even though the above-ground biomass is reduced by grazing, which creates a more unstable surface sediment layer, the extensive root network of *T. testudinum* should continue to cement the deeper layers of sediment together, reducing its erodibility and helping to maintain the overall seabed (Christianen et al., 2013). The root network of *T. testudinum* is robust and is resistant to extreme hydrodynamic conditions (Cabaço, Santos, & Duarte, 2008; van Tussenbroek et al., 2008). This resilience to uprooting during storms thereby allows *T. testudinum* to continue to provide erosion protection over a prolonged period. However, a high megaherbivore grazing pressure eventually impacts the below-ground biomass of seagrass, as the plants have to reallocate energy to photosynthetic tissue rather than roots (Dahl et al., 2016; Hemminga, 1998). A reduction in the root biomass of *T. testudinum* following grazing was observed in this present study as well as by Christianen et al. (2014) and has the potential to create a 'runaway feedback' (Suykerbuyk et al., 2016). Further reductions in the below-ground seagrass biomass could compromise the long-term stability of the sediment bed, and thereby, discourage the growth of native seagrass species. In addition, the voracity of the spread of *H. stipulacea* is hampering the self-regeneration of the native seagrass species, which threatens the natural ecosystem functioning of Caribbean seagrass meadows. Overall, there is urgent need to match the conservation of large herbivores with an equally

strong conservation of their preferred grazing habitats of native seagrass (Christianen et al., 2018).

4.3 | Effects of invasive *H. stipulacea* on coastal protection services

Preferential grazing of native seagrass species by turtles within the deeper areas of the bay (<2 m), creates large areas of cropped, sparse vegetation, which has subsequently become overgrown by the invasive *H. stipulacea* (Christianen et al., 2018). The sediment within the invasive seagrass patches was composed of a significantly higher proportion of fine grains compared to all other seagrass patches studied. More fine sediment grains are expected to accumulate in deeper regions compared with the shallows due to the reduction in wave forces reaching the seabed (Swift & Niedoroda, 1985). It is however noted that this cannot be the only reason for *H. stipulacea* having finer sediments, as the sediment within the *H. stipulacea* patch was even finer than the neighbouring grazed *T. testudinum* and bare patches that were present in the deeper site (study area 2).

The effect of the significantly smaller grain size in the *H. stipulacea* meadows must be considered in relation to its erosion protection of the seabed. Smaller unconsolidated sediment particles will move easier and at lower bottom shear stress values than larger particles (Shields, 1936). In our experiments, the oscillatory flow velocity at which the (smaller) calcareous grains within the invasive *H. stipulacea* patches were put in motion, did not significantly differ from the velocity observed for the larger grains in grazed *T. testudinum* (Figure 3b). As both populations are subject to similar physical conditions, it is not surprising to find that the sediment grains present in the meadows start moving at a similar current velocity. A seagrass meadow would not be able to collect finer grains, such as is observed in *H. stipulacea*, if these were resuspended and carried away during normal physical conditions. The critical erosion threshold of an rms oscillatory flow of around 0.08 m/s must therefore correspond to conditions that are sufficiently rare within the deeper regions of Lac Bay for the meadows to collect sediment of a grain size that is stable under conditions below this threshold.

As the erosion threshold and volume of seagrass is similar in the *H. stipulacea* and grazed *T. testudinum* patches within study area 2, the difference in grain size between these two patch types is intriguing. The high-density canopy of *H. stipulacea*, which is close to the seabed, must effectively reduce the shear stress inside its canopy up to oscillatory flow velocities of 0.08 m/s, thereby preventing sediment resuspension and allowing for the accumulation of fine grains. In the same deeper region, the sparse shoot density of grazed *T. testudinum* does little to reduce the bed shear stress, and the sediment grain size distribution does not significantly differ to that of bare patches.

On occasions when the oscillatory flow at the seabed is >0.08 m/s in areas where *H. stipulacea* is present, such as during storm events, the presence of *H. stipulacea* constitutes a vulnerability for the system. *H. stipulacea* is an opportunistic species, and although it is able to rapidly colonize bare areas (Hernández-Delgado et al., 2020), the

low below-ground biomass of *H. stipulacea* makes it vulnerable to uprooting (Malm, 2006). Large meadows of *H. stipulacea* were uprooted in 10-m deep waters within Oranjestad Bay, St Eustatius (Caribbean) after category 5 Hurricane Irma in 2017 (Pers. obser. 2017, Supporting Information S2). Contrastingly, meadows of *T. testudinum* on the neighbouring island of St Martin, were unaffected even though they were in the direct path of the same hurricane. The replacement of *T. testudinum* by *H. stipulacea*, which is susceptible to uprooting during strong hydrodynamic events, could potentially leave vast areas of the seabed bare and exposed, hence vulnerable to erosion for periods of time after severe storms.

4.4 | Storm resilience of seagrass ecosystems

We postulate that the storm resilience of a seagrass ecosystem can be determined by the erosion resilience and uprooting resilience of the seagrass meadow (Figure 6). In this way, ungrazed *T. testudinum* meadows increase the storm resilience of the tropical seagrass ecosystem, by stabilizing the sediment surface under strong oscillatory flow at the seabed (i.e. between 0.15 and 0.2 m/s), and through the extensive root network that ensures the meadow and seabed remains intact even during strong storm events (van Tussenbroek et al., 2008; Figure 6). Intensive megaherbivore grazing has a strong negative effect on the storm resilience during storms through the loss of above-ground biomass, and thereby, reduction in sediment stabilization. The robust root network of the climax seagrass, however, helps to maintain the seabed

integrity even when grazed (Figure 6). Intensive grazing also facilitates the spread of opportunistic seagrass species that can quickly colonize the bare sediment (Christianen et al., 2018). Seagrasses with more opportunistic life strategies allocate less energy into the development of their below-ground biomass, and are therefore, more vulnerable to uprooting in storms (Preen, Lee Long, & Coles, 1995; van Tussenbroek et al., 2008). This susceptibility to uprooting reduces the overall storm resilience of the seagrass ecosystem, and potentially accelerates the spread of *H. stipulacea* by dispersing vegetative propagules (Smulders et al., 2017).

4.5 | Mechanistic study of sediment dynamics

Observational studies examining the effect of seagrass meadows and grazing on sediment stability highlight the variability of the sediment dynamics between sites. Intertidal seagrass meadows of *T. hemprichii* experienced significant erosion after the above-ground biomass was clipped to mimic grazing (Dahl et al., 2016; Githaiga, Frouws, Kairo, & Huxham, 2019). Contrastingly, Johnson, Gulick, Bolten, and Bjorndal (2019) reported no significant difference in the sediment level between grazed and ungrazed plots of *T. testudinum* over a 3-month experiment. The opposing observations between sites are likely to be caused by variations in the hydrodynamic regime, depth, seagrass morphology, sediment characteristics and sediment supply. Because the sediment dynamics of a site depend upon a range of local processes, it is difficult to directly compare observations between sites.

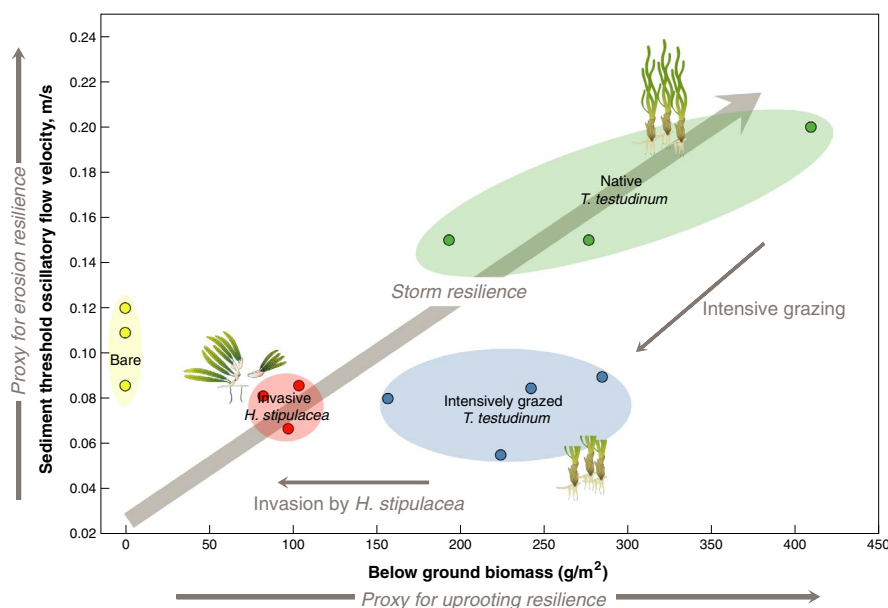


FIGURE 6 The resilience of the ecosystem to storms can be demonstrated by the below-ground biomass of the seagrass (a proxy for uprooting resilience) and the critical erosion threshold under oscillatory flow (a proxy for erosion resilience). High below-ground biomass and effective sediment stabilization by ungrazed *Thalassia testudinum* (green circles) provides an ecosystem resilient to storm conditions. Heavy grazing of *T. testudinum* (blue circles) reduces the sediment stability. Invasion by *Halophila stipulacea* (red circles) results in a sediment surface vulnerable to erosion, while the low below-ground biomass of the invasive species makes it vulnerable to uprooting, potentially leading to bare areas after storms. Bare (yellow) areas have no vegetated biomass to protect the sediment, leaving these areas vulnerable to erosion during storms. Solid circles represent raw data, while larger shaded areas indicate the groupings of the different seagrass patch types. Seagrass illustrations obtained from IAN images (Collier 2019; Saxby 2019) [Colour figure can be viewed at wileyonlinelibrary.com]

A sheltered site with a steady sediment supply is unlikely to erode, even if the seagrass canopy is lost. In contrast, sites experiencing stronger hydrodynamic forces, such as in the intertidal zone, are highly likely to display a strong erosional response when the seagrass canopy is removed. Using field flumes, we provide mechanistic insight into the erosion protection provided by seagrass meadows. Although the absolute erosion threshold values are likely to differ between seagrass meadows depending upon the local sediment grain size, the mechanistic trends that are revealed remain the same, irrespective of local conditions. That is, (a) seagrass meadows provide less erosion protection under an oscillatory flow regime compared to a unidirectional flow regime and (b) the level of erosion protection is positively correlated to the volume (density and canopy height) of the seagrass canopy. By understanding the mechanisms of a key process of the ecosystem functioning, we can improve the development of ecosystem models, and thereby, make more robust predictions for the future of coastal ecosystems in this changing world.

4.6 | Ecosystem services under threat?

When examining the mechanisms that affect the erosion protection capacity of seagrass meadows, it is evident that the effectiveness of the erosion protection declines within a disturbed and degraded system. This decline in the provision of ecosystem services has been observed in other ecosystems too. The accumulation of peat is negatively impacted by reduced growth of *Sphagnum* species in peatlands (Dieleman, Branfireun, Mclaughlin, & Lindo, 2015), and hydrology processes are affected by the loss of soil crusts in dryland communities (Ferreberg, Reed, Belnap, & Schlesinger, 2015). Furthermore, community shifts towards more fast-growing opportunistic species disrupts the natural functioning of the ecosystem and may significantly impact the ecosystem services provided. We see this in the alteration in the erosion protection services provided by the invasive opportunistic *H. stipulacea*, but this is also in line with other ecosystems. Nutrifaction in grassland communities leads to species-shifts in both the plant community and also the associated pollinators (Habel et al., 2016), while shifts towards a turfing-algae dominated reef systems in the coastal environment impacts the abundance and composition of mussels (Sorte et al., 2017) and reef fish species (Bellwood, Hoey, Ackerman, & Depczynski, 2006). Ultimately, a shift in the biological community could cause a shift in the ecosystem services provided by that community. Further investigation is required to quantify the extent that ecosystem services are affected within different ecosystem types with global change, and the consequences that changing ecosystem services have on the associated communities.

The strong seabed stabilization by native climax seagrass species provides a vital coastal protection service throughout the Caribbean, by reducing erosion and maintaining a stable beach foreshore, even under storm conditions. Intensive grazing and opportunistic invasive species are not only threatening the abundance of native seagrass species but are also threatening the important coastal protection services that are provided by the native climax species.

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AUTHORS' CONTRIBUTIONS

T.J.B., R.K.J. and M.J.A.C. conceived and designed the study; R.K.J., M.J.A.C., M.M.v.K., J.C.d.S., E.S.B. and T.J.B. performed the data collection; R.K.J. conducted the data analysis; R.K.J., M.J.A.C., M.M.v.K., P.M.J.H. and T.J.B. wrote the manuscript with contribution from all authors; P.M.J.H. and T.J.B. supervised the project and provided critical feedback.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.hmgqnk9d2> (James et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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