




















# Herbivore effects increase with latitude across the extent of a foundational seagrass

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Climate change is altering the functioning of foundational ecosystems. While the direct effects of warming are expected to influence individual species, the indirect effects of warming on species interactions remain poorly understood. In marine systems, as tropical herbivores undergo poleward range expansion, they may change food web structure and alter the functioning of key habitats. While this process ('tropicalization') has been documented within declining kelp forests, we have a limited understanding of how this process might unfold across other systems. Here we use a network of sites spanning 23° of latitude to explore the effects of increased herbivory (simulated via leaf clipping) on the structure of a foundational marine plant (turtlegrass). By working across its geographic range, we also show how gradients in light, temperature and nutrients modified plant responses. We found that turtlegrass near its northern boundary was increasingly affected (reduced productivity) by herbivory and that this response was driven by latitudinal gradients in light (low insolation at high latitudes). By contrast, low-latitude meadows tolerated herbivory due to high insolation which enhanced plant carbohydrates. We show that as herbivores undergo range expansion, turtlegrass meadows at their northern limit display reduced resilience and may be under threat of ecological collapse.

Climate change is rapidly altering the functioning and distribution of Earth's biota. While previous studies have addressed the direct effects of climate on organismal functioning, few have considered the potential indirect effects of altered biotic interactions<sup>1</sup>. For instance,

temperature-induced expansions in the geographic ranges of key species can create transient and novel communities with potentially unanticipated or dramatic effects on ecosystem structure<sup>2</sup>. As warming promotes shifts in species' distributions, the establishment of new

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biotic associations (predator–prey/plant–herbivore interactions) can outweigh the direct effects of climate warming, as displayed in both terrestrial and freshwater environments<sup>3</sup>. Such phenomena have also been widely documented in marine environments, where oceanic currents can routinely facilitate the dispersal of tropical species to subtropical and temperate regions<sup>4</sup>, profoundly altering community structure and ecological processes<sup>5</sup>.

Some of the most illustrative marine examples stem from reports of tropicalization in temperate kelp forests, where warmer temperatures facilitate the range expansion of mobile herbivores, resulting in increased grazing on communities previously isolated from such effects. For instance, in response to a marine heatwave event, western Australia experienced a 100-km-range contraction and 43% loss of temperate kelp<sup>6</sup>. These effects persisted long after the heatwave subsided, likely due to an influx of tropical herbivorous fishes that increased grazing pressure and suppressed kelp recovery<sup>7–9</sup>. Similar events have been noted along the eastern coast of Australia and along the Japanese archipelago<sup>4,10</sup>. In most cases, warm poleward currents assisted in driving rapid range expansion and increased grazing pressure by herbivorous fishes<sup>11</sup>. As grazing can exert strong top-down control<sup>12–14</sup>, the consequences of herbivore range shifts may outweigh the direct effects of warming on the ecological performance of foundational species.

While algal- and kelp-dominated systems serve as prime examples of tropicalization, there are other important marine habitats that might be affected by similar processes<sup>15</sup>. Seagrasses are foundational marine plants that provide key ecological services such as primary production, nutrient cycling and habitat provisioning for economically and culturally important species<sup>16</sup>. Across the tropical to subtropical boundaries of the western North Atlantic, turtlegrass (*Thalassia testudinum*) is a dominant seagrass that spans nearly 30° of latitude and broadly structures the marine seascape. However, at the northern range boundary of this species, many meadows are experiencing an influx of grazers, as warming has been linked to increases in tropical fishes across the northern Gulf of Mexico<sup>17</sup>, most notably, a 22-fold increase in the emerald parrotfish, *Nicholsina usta*, which consumes seagrass at nearly five times the rate of native grazers<sup>18</sup>. Other megaherbivores, such as green sea turtles and manatees, have also increased in abundance across these waters<sup>19,20</sup>, likely also driven by successful conservation efforts<sup>21</sup>. While many tropical meadows can tolerate moderate levels of herbivory<sup>22</sup>, locally intense grazing (particularly across higher subtropical latitudes) may lead to dramatic declines in seagrass cover and drastically alter meadow functioning<sup>23,24</sup>.

In addition to temperature, other environmental factors such as light and nutrient availability can influence plant–herbivore interactions across latitude and geography<sup>25–27</sup>. For instance, plants at increasingly higher latitudes must contend with reduced photoperiods, which constrains photosynthetic carbon gain required to replace lost tissue. Previous work has shown that high-latitude, subtropical plants may require a higher proportion of incident light relative to their low-latitude, tropical counterparts<sup>28</sup>, and thus limited insolation (combined with increased grazing) could drive ‘tropicalization-induced’ declines in the functioning of subtropical plant communities. Nutrient availability can also (1) modify ecological responses to grazing by regulating overall rates of plant growth, as shown for terrestrial<sup>29</sup> and marine systems<sup>30,31</sup>, and (2) influence palatability by increasing leaf nitrogen content<sup>32</sup>. While these varying environmental forcings can have a large influence on plant functioning and overall resilience<sup>33</sup>, they have rarely been considered within previous frameworks of tropicalization<sup>3</sup>.

Coordinated experiments, especially those using standardized methods, have the power to provide mechanistic insight towards the dynamics of ecological processes that operate over large environmental gradients<sup>34–36</sup>. In this Article, we used a network of 650 experimental plots distributed across 13 seagrass meadows in the western North Atlantic to explore the effects of increased herbivory on a marine

ecosystem under the emerging threat of tropicalization. We were particularly interested in high-latitude turtlegrass meadows at the northern edge of this species’ range, and our approach was a comparative analysis of herbivore effects (and the drivers of its variation) across tropical–subtropical waters. We specifically asked (1) What are the effects of increased herbivory on the health and ecological functioning of turtlegrass across its geographic extent? (2) Are these effects more prominent at the higher latitudes near northern range boundaries? and (3) Does variation in light, temperature and/or nutrient availability modify herbivore effects and overall meadow resilience? To answer these questions, we conducted a synchronous, year-long manipulative field experiment at turtlegrass sites distributed from Panama (9° N) to Bermuda (32° N) (Fig. 1a). At each site, we factorially manipulated grazing intensity and nutrient availability. Grazing was manipulated using two techniques (1) the exclusion of large natural grazers (turtles and large herbivorous fishes) using mesh caging and (2) the simulation of increased grazing by clipping the leaf canopy to varying degrees, severe grazing (full-clip) and moderate grazing (half-clip) (Fig. 1 and Extended Data Fig. 1). Nutrient availability was manipulated by fertilizer amendments. We also measured other cross-latitude metrics of fish grazing by counting the frequency of grazing marks on turtlegrass leaves. Sites were established in early spring, and the response variables of seagrass structure (shoot density, leaf width) and function (leaf productivity) were recorded twice, once at the end of the summer growing season (~4 months post-establishment) and then again at the end of the following winter season (~12 months post-establishment). Belowground carbohydrate reserves were also measured following the winter season to gain a better overall perspective on plant health/status<sup>37</sup>. To understand the mechanisms driving variable plant responses across our network, light and temperature, along with background levels of ambient nutrient availability, were measured and included as covariates in our analysis. Separate linear mixed-effects models (see Methods for full description) were used to first examine how latitude influenced responses to grazing and then how gradients in light and temperature potentially accounted for variable responses across the network. We hypothesized that (1) high-latitude turtlegrass meadows would be increasingly susceptible to our simulated grazing treatments compared to low-latitude meadows, (2) these differences in grazing responses would primarily be driven by variation in light and temperature and (3) increased nutrient availability would further alter plant responses to grazing by providing essential nutrients for growth.

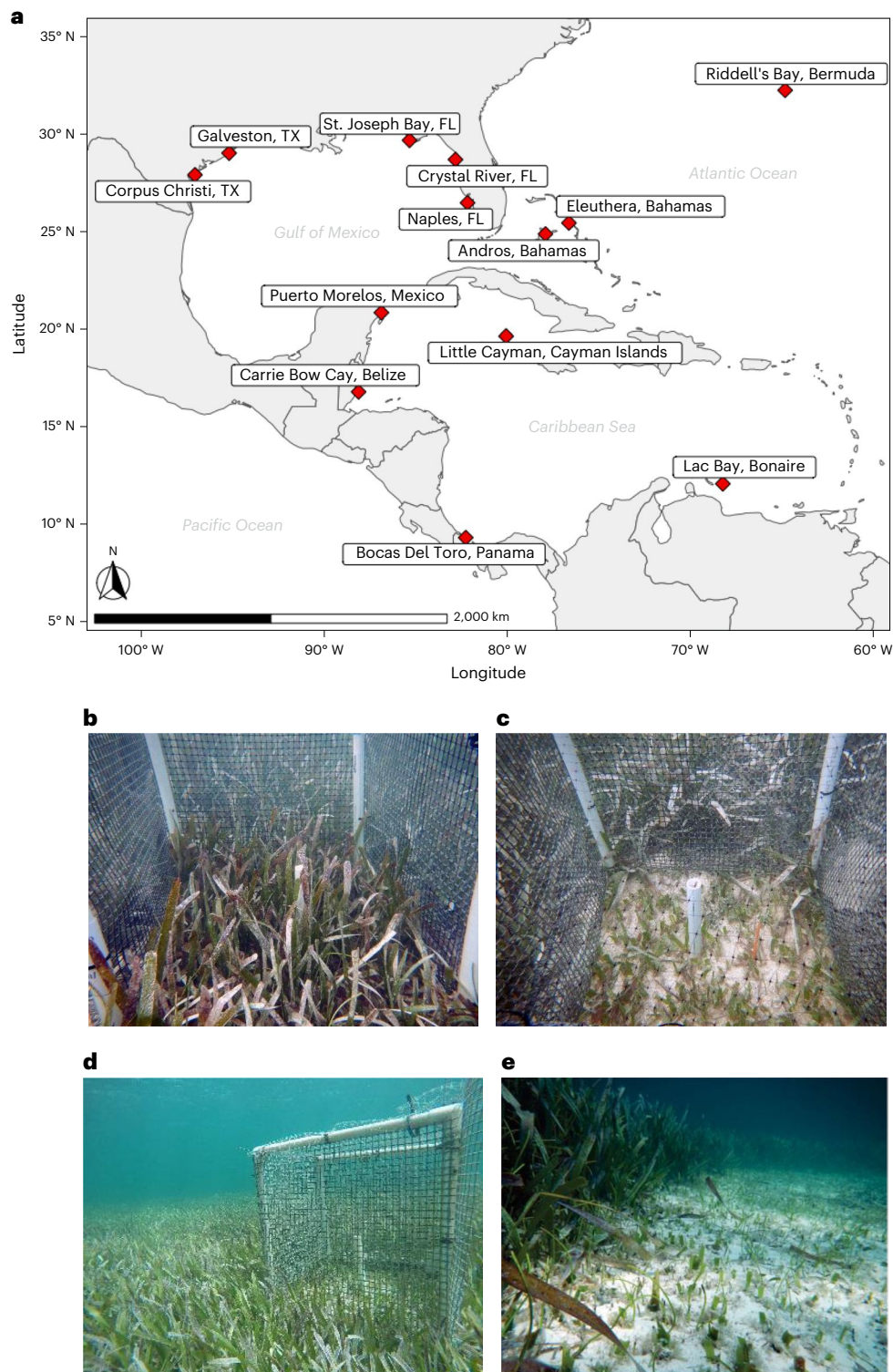
## Results

### The effects of grazing on seagrass vary across latitude

Across both summer and winter seasons, seagrass productivity (leaf growth) declined with latitude ( $P < 0.05$ ) and was reduced by simulated grazing (full-clip,  $P < 0.0001$ ) (Figs. 2a and 3 and Supplementary Table 1). Moderate grazing (half-clip) reduced productivity but to a lesser extent. While the effects of latitude and simulated grazing were significant across both seasons, effect sizes were smaller during the winter (Fig. 3).

The effects of simulated grazing were also greater at the higher latitudes (latitude  $\times$  full-clip,  $P = 0.019$ ; Fig. 2a and Supplementary Table 1). During the summer, severe grazing (full-clip) had a larger negative effect on leaf productivity at high latitudes compared to low latitudes. In the winter, this trend was surprisingly reversed, but the effect size was small (Fig. 3, Extended Data Fig. 2 and Supplementary Table 1). For more moderate grazing, latitude  $\times$  half-clip interactions for productivity were not significant in either season.

Shoot density did not vary by latitude but declined with simulated grazing (full-clip,  $P < 0.0001$  and  $P = 0.028$  in summer and winter, respectively; Supplementary Table 2). Similar to productivity, the effects of severe grazing on shoot density varied by latitude, with larger grazing-related declines in shoot density at the higher latitudes (latitude  $\times$  full-clip interaction,  $P < 0.0001$  and  $P = 0.0137$ , summer and



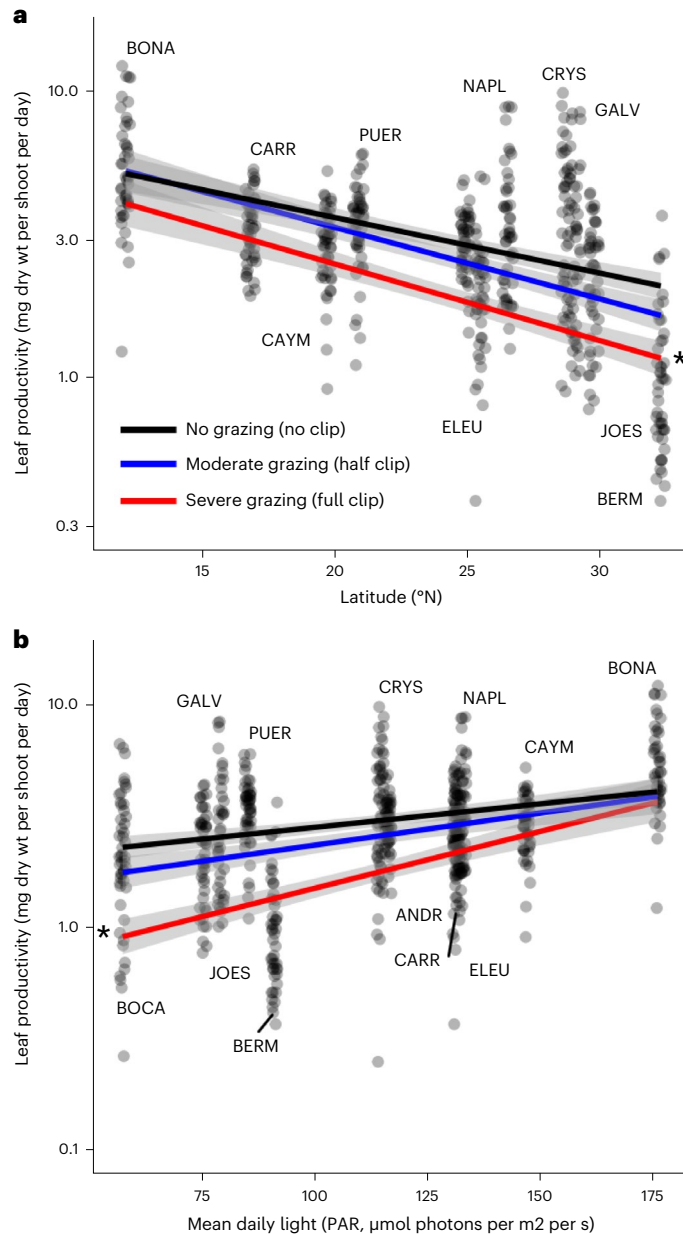
**Fig. 1** | Map of study area and representative photos of simulated grazing. **a**, Map of study region and locations of individual sites. **b,c**, Comparison between unclipped (**b**) and clipped (**c**) plots. All clipped plots were caged and re-clipped

every 2 weeks. **d**, A caged clipped plot. **e**, Photograph of natural turtle grazing in Mexico, from Hernandez and Tussenbroek (2014). See Extended Data Fig. 1 for a graphical display of all treatments.

winter, respectively; Supplementary Table 2). Half-clip treatments did not reduce shoot density, and there were no latitude  $\times$  half-clip interactions.

Plant morphology (leaf width) was altered by both latitude and simulated grazing. High-latitude sites had thinner leaves ( $P < 0.001$  both seasons; Supplementary Table 3), and grazing also reduced

leaf width (full-clip,  $P < 0.0001$  both seasons). Half-clip treatments reduced leaf width ( $P < 0.05$ ) yet by a lower magnitude. There was no significant interaction between latitude and grazing in the summer; however, there was a significant interaction during the winter (latitude  $\times$  full-clip,  $P < 0.0001$ ), when the effect of grazing was higher at low latitudes.



**Fig. 2 | Grazing effects on seagrass productivity across latitude and light gradients. a, b,** Effects of simulated grazing across latitude ( $^{\circ}$ N) (a) and light (PAR,  $\mu\text{mol photons per m}^2 \text{ per s}$ ) (b) after the summer growing season. Jittered points are the raw data and represent individual plots ( $n = 50$  plots per site). Lines represent linear fits with 95% confidence intervals for the severe grazing (red), moderate grazing (blue) and no grazing (black) treatments. Interaction terms were significant for the severe grazing treatments (indicated with an asterisk): latitude  $\times$  full clip,  $P = 0.0185$  (a); light  $\times$  full clip,  $P < 0.0001$  (b); linear mixed-effects models, two-sided tests. Sites: BOCA, Panama; BONA, Bonaire; CARR, Belize; CAYM, Cayman Islands; PUER, Mexico; ANDR, Bahamas-Andros; ELEU, Bahamas-Eleuthera; NAPL, Florida-Naples; CRY, Florida-Crystal River; GALV, Texas-Galveston; JOES, Florida-St. Joseph Bay; BERM, Bermuda. Note, BOCA was excluded from the latitude model in a (Methods).

Plant reserves (measured at the end of the winter season as total non-structural carbohydrates (TNCs)) declined nonlinearly with latitude ( $P = 0.0312$ ), and the effects of grazing on TNC also depended on latitude (latitude  $\times$  full-clip,  $P = 0.0269$ ; Fig. 4a and Supplementary Table 4). High-latitude sites displayed low TNC reserves, and simulated grazing marginally reduced these reserves. However, at the low latitudes, where TNC reserves were higher, simulated grazing had a larger

effect. Thus, tropical sites tolerated sustained grazing by (1) drawing down ample carbohydrate reserves and (2) consequently displaying minimal declines in productivity under simulated grazing (Fig. 4b).

### Seagrass responses to grazing are coupled to light gradients

Mean seasonal light availability (photosynthetically active radiation or PAR) reduced the effects of simulated grazing on seagrass productivity (light  $\times$  full-clip,  $P < 0.0001$ ; Figs. 2b and 5 and Supplementary Table 5) but only during the summer when light gradients across the network were strongest (Extended Data Fig. 3; Methods). Thus, productivity at the tropical 'high-light' sites was relatively unaffected by grazing compared to the subtropical 'low-light' sites, echoing the latitudinal trends (Fig. 5). This light  $\times$  grazing interaction was still significant ( $P = 0.018$ ; Supplementary Table 6) in a revised model that excluded one outlier site (Panama, BOCA) that had extremely low PAR values (Extended Data Table 1); thus, this trend was representative across the broader network and not solely driven by a single site. During the winter, light  $\times$  grazing interactions were not significant. Simulated grazing effects on both shoot density and leaf width were also modified by light availability (light  $\times$  full-clip,  $P < 0.05$ ; Supplementary Tables 7 and 8), such that 'high-light' sites were relatively unaffected compared to 'low-light' sites, consistent with trends in productivity. Carbohydrate reserves (which were only measured in the winter; Methods) increased with annual light levels across the network ( $P = 0.0171$ ; Supplementary Table 9), and the effects of clipping on TNC were greatest at sites with higher light availability (light  $\times$  full-clip,  $P = 0.0037$ ). Thus, sites with ample TNC tended to rely more on these reserves to tolerate grazing compared to sites with depleted TNC.

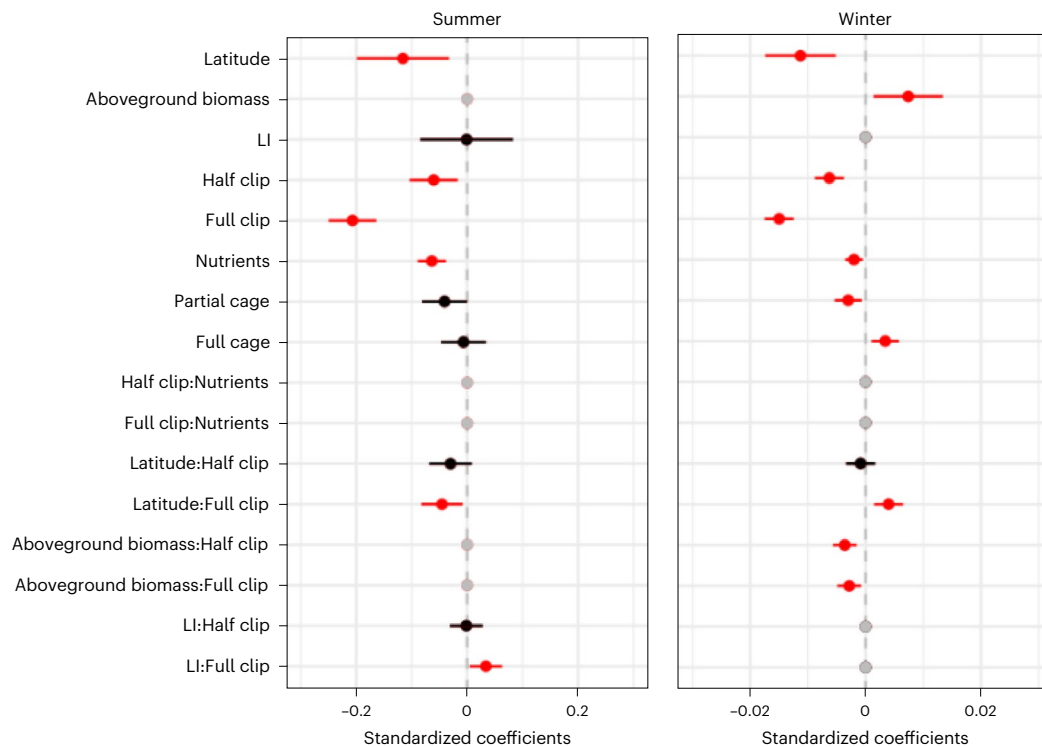
### Grazing effects are weakly related to temperature

Mean water temperatures were comparable across all sites during the summer season (Extended Data Figs. 3 and 4) and had no influence on seagrass productivity (Fig. 5 and Supplementary Table 5). During the winter, temperatures declined at higher latitudes, and cooler sites displayed lower productivity ( $P = 0.03$ ; Supplementary Table 6). There was a significant interaction between temperature and simulated grazing, as the effects of clipping on productivity were higher at warmer sites (temperature  $\times$  full-clip,  $P = 0.003$  and  $P = 0.023$ , summer and winter, respectively), although the effect sizes were relatively small (Fig. 5). Temperature also had no effect on shoot density, nor were there any significant interactions between temperature and simulated grazing for shoot density (Supplementary Table 7).

Leaf width was influenced by temperature but only during the winter season, when leaves were thinner at sites with cooler temperatures (Supplementary Table 8). The effects of simulated grazing on leaf width were also strongest at warmer temperatures (temperature  $\times$  full-clip,  $P = 0.006$  and  $P < 0.0001$ , summer and winter, respectively; Supplementary Table 8), with a larger effect during the winter season.

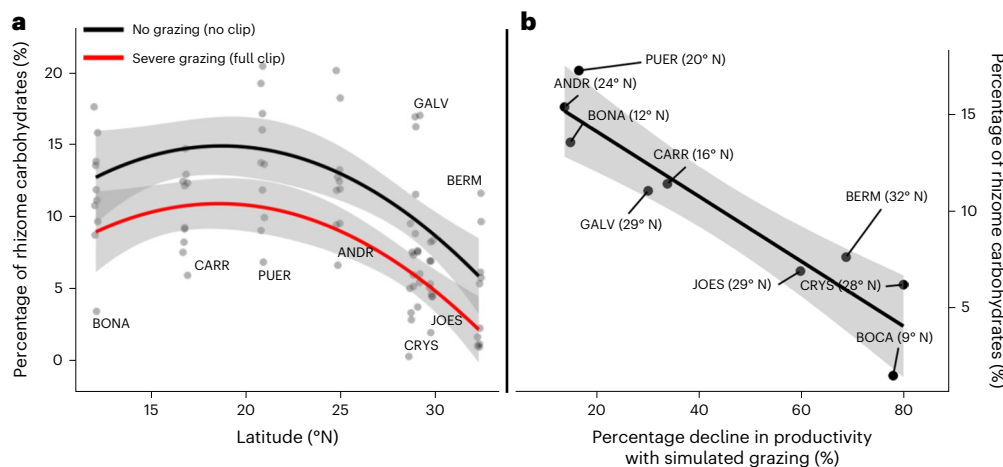
### Nutrients increase grazing effects on seagrass productivity

Ambient nutrient availability at each site was assessed by examining the background nutrient content of leaf tissue in our control plots using a limitation index<sup>38</sup> (LI), which assesses the degree to which seagrasses are limited by either nitrogen or phosphorus. In brief, this index is calculated as the absolute deviation of leaf N:P values from a balanced 30:1 ratio (see Methods for full description); thus, large LI values indicate low nutrient availability. For productivity, sites with high ambient nutrient availability (low LI) were more negatively affected by grazing than nutrient-limited sites (LI  $\times$  full-clip,  $P = 0.03$ ; Fig. 3 and Supplementary Table 1). This effect was valid after controlling for cross-network variation in light and temperature (Fig. 5 and Supplementary Table 5). In the winter, when effect sizes were smaller, LI  $\times$  full-clip interactions were not significant, nor were any LI  $\times$  half-clip interactions in either season. We also experimentally added nutrients to select plots at each



**Fig. 3 | Standardized coefficients from the 'latitude' model of seagrass productivity.** Standardized coefficients from the 'latitude' model of leaf productivity after the summer (left) and winter (right) seasons. Note distinct scales on the x-axis, and thus slope coefficients were an order of magnitude lower in the winter. Centre points represent standardized coefficient estimates from model 1, and lines represent 95% confidence intervals (linear mixed-effects

models, two-sided tests). Significant predictors ( $P < 0.05$ ) are displayed in red. Non-significant predictors included in the model are displayed in black. Grey points indicate predictors that were eliminated during AIC model selection procedures. See Supplementary Table 1 for full statistical results; see Methods for description of LI.

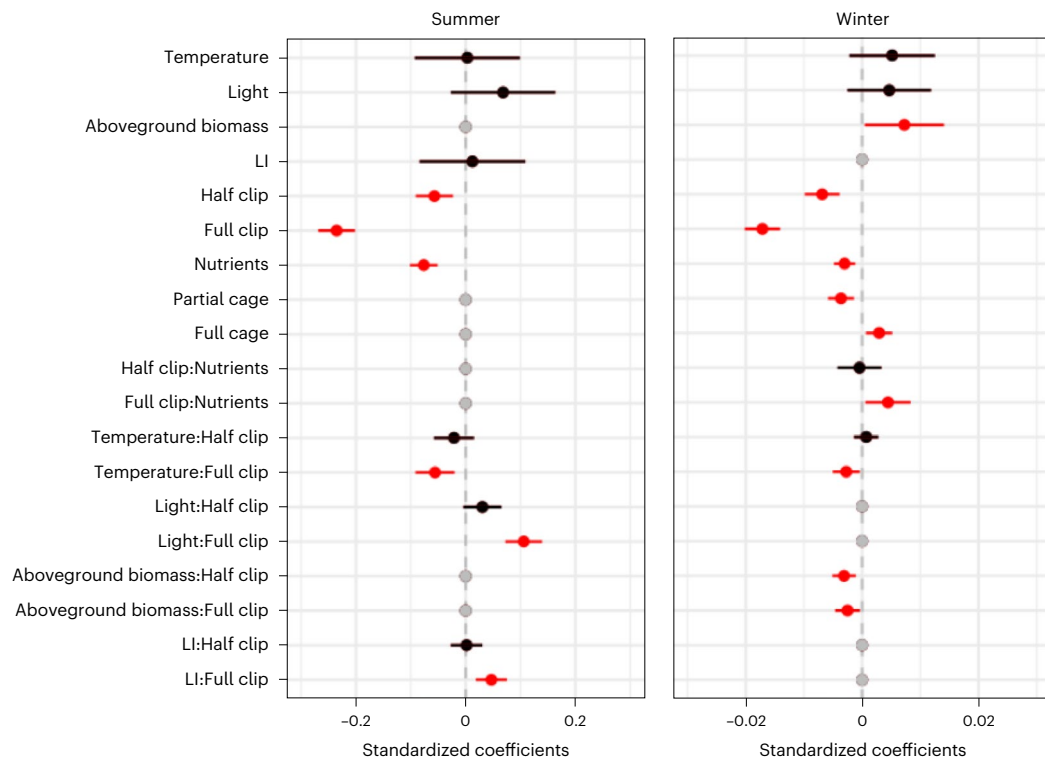


**Fig. 4 | Grazing effects on rhizome non-structural carbohydrates.** a, Effects of simulated grazing on total rhizome non-structural carbohydrates across latitude ( $^{\circ}$ N) after the winter season. Jittered points are the raw data and represent individual plots ( $n = 10$  plots per site). Lines represent second-order polynomial fits with 95% confidence intervals of the severe grazing (red) and no grazing (black) treatments. Interaction term between latitude and grazing was significant (latitude  $\times$  full clip,  $P = 0.027$ ; linear mixed-effects model, two-sided tests).

b, Relationship between site-level percentage change in leaf productivity with severe clipping and mean rhizome carbohydrates of the control plots ( $n = 9$  sites). Line represents a linear model fit with 95% confidence intervals ( $P = 0.0003$ ). Sites: BONA, Bonaire; CARR, Belize; PUER, Mexico; ANDR, Bahamas-Andros; CRYST, Florida-Crystal River; GALV, Texas-Galveston; JOES, Florida-St. Joseph Bay; BERM, Bermuda; BOCA, Panama.

site using Osmocote fertilizer (Extended Data Fig. 1). Added nutrients reduced seagrass productivity (nutrients,  $P < 0.0001$  and  $P = 0.01$  in summer and winter, respectively; Supplementary Table 1); however, there were no interactions between experimental nutrient addition and simulated grazing.

Ambient nutrient availability (LI) had no effect on shoot density or leaf width. However, within each site, experimental Osmocote addition did reduce shoot density and leaf width (nutrients,  $P < 0.01$  in both seasons; Supplementary Tables 2 and 3). Furthermore, LI  $\times$  grazing and nutrient  $\times$  grazing interactions were only significant for leaf width in



**Fig. 5 | Standardized coefficients from the 'light/temperature' model of seagrass productivity.** Standardized coefficients from the 'light/temperature' model of leaf productivity after the summer (left) and winter (right) seasons. Note distinct scales on the x axis, and thus slope coefficients were an order of magnitude lower in the winter. Centre points represent standardized coefficient estimates from model 2, and lines represent 95% confidence intervals (linear

mixed-effects models, two-sided tests). Significant predictors ( $P < 0.05$ ) are displayed in red. Non-significant predictors included in the model are displayed in black. Grey points indicate predictors that were eliminated during AIC model selection procedures. See Supplementary Table 5 for full statistical results; see Methods for description of LI.

the winter (Supplementary Table 3), whereby nutrients reduced the effects of clipping. Ambient nutrient availability (LI) also influenced TNC ( $P = 0.005$ ; Supplementary Table 4), as more nutrient-limited sites had higher carbohydrate reserves and the effects of grazing on TNC also increased with nutrient limitation (LI  $\times$  full-clip,  $P = 0.003$ ; Supplementary Table 4).

### Gradients in natural herbivory across the network

In addition to simulated grazing, our experimental design also allowed us to assess the magnitude of natural grazing across the network by (1) comparing our full cage plots with procedural controls (Extended Data Fig. 1) and (2) observing the frequency of leaf grazing marks (grazing pressure; Methods) within the uncaged control plots. Overall, reductions in natural grazing (caging) did not consistently lead to increases in any plant metric (productivity, shoot density or leaf width), nor were there any significant interactions between caging and latitude (Supplementary Tables 1–3). However, many of the leaves within our control plots (uncaged, unclipped, unfertilized) did display grazing bite marks, and the frequency of these bite marks declined with latitude (Extended Data Fig. 5). In comparing our two techniques of manipulating herbivory, plant responses to simulated grazing (particularly the severe, full-clip treatments) were stronger than responses to reductions in natural grazing (caging) (Figs. 3 and 5 and Supplementary Tables 1–3).

### Discussion

Our coordinated field experiments show that the negative effects of simulated herbivory (primarily severe overgrazing) increase with latitude across the tropical–subtropical range of a foundational seagrass in the western North Atlantic. We further reveal that these trends are

mechanistically linked to latitudinal gradients in daily photoperiod and ambient insolation, which broadly govern plant carbohydrate storage and overall resilience. Accordingly, these results are consistent with other reports documenting that the resilience of marine ecosystems may be compromised near geographic range boundaries, with implications for future responses to climate-driven disturbances<sup>39,40</sup>. Our work suggests that as tropical herbivores respond to ocean warming (and large megaherbivores to successful conservation efforts), their impacts on subtropical seagrass meadows will be increasingly severe, with consequences for the ecological functioning of these systems.

Our study further highlights that increasing herbivory may lead to seagrass meadow decline across broader scales, building upon and unifying individual case studies that show local meadow collapse across the high latitudes. For example, successful conservation initiatives have led to increases in green sea turtle (*Chelonia mydas*) populations and subsequent overgrazing along the Bermuda platform, with strong effects on canopy cover, production and carbohydrate storage<sup>23</sup>. Long-term monitoring (since 2006) has documented seagrass declines on the platform, along with the associated collapse of several meadows<sup>41</sup>. Meadows in the northern Gulf of Mexico show similar responses to severe grazing, with some showing prolonged signs of stress and limited recovery<sup>42</sup>. Our observed declines in two other seagrass metrics, shoot density and leaf width across the subtropical latitudes, further support the impacts of simulated grazing and the reduced resilience of meadows at their northern range limit. During our experiments, three network sites experienced similar declines in seagrass cover due to overgrazing by turtles (Bermuda and Eleuthera, Bahamas) and sea urchins (St. Joseph Bay, Florida). While extensive meadow overgrazing is not the main driver of seagrass decline at all locations, our manipulative study suggests that these individual case studies may preface other

overgrazing-driven turtlegrass declines in the lower light conditions of high-latitude, subtropical meadows.

Our network also reveals that low-latitude meadows are generally more resilient to simulated grazing (mostly severe overgrazing) and that this differential response is driven by increased insolation which promotes plant carbohydrate storage (Fig. 4 and Supplementary Table 9). Thus, across low latitudes, many meadows can utilize ample reserves to replace leaf biomass and consequently display minor shifts in leaf productivity in response to grazing. While carbohydrate reserves did decline at all sites, it is likely that high-latitude meadows are particularly constrained as reserve levels were already low and further decreased to near zero at some sites (Bermuda) with continued grazing (Extended Data Fig. 6). Our Panama site 'BOCA' was an outlier, as it represents a low-latitude, tropical site with compromised carbohydrate reserves and large grazer-driven declines in leaf productivity (Extended Data Figs. 7 and 8). We attribute this to extremely low light availability (Extended Data Table 1), driven by high water column turbidity from freshwater/nutrient inputs and dredging activities within the region<sup>43,44</sup>. After accounting for light availability (measured in situ with loggers), simulated grazing effects at the Panama site aligned with the broader trends across the network (Fig. 2b).

Temperature effects were limited to the winter season, as subtropical sites displayed cooler temperatures (Extended Data Figs. 3 and 4) and reduced leaf productivity and leaf width (Supplementary Tables 6 and 8). These trends are supported by other studies documenting temperature regulation of plant metabolism, growth and morphology<sup>45</sup>. Interactions between temperature and simulated grazing were also significant, as the effect of clipping increased at sites with warmer winter temperatures (which were positioned at low latitudes). This contrasts with the influence of light, which reduced the effects of clipping at the low latitudes (Fig. 2b). Thus, while tropical sites received more insolation during the summer growing season (which mitigated grazing), they also experienced warmer winter temperatures which marginally increased grazing effects during this season. Comparatively, light gradients during the summer had a greater influence on grazing responses (standardized slope coefficient = 0.105) than temperature gradients during the winter (standardized slope coefficient = -0.003). Hence, while seagrass productivity in the winter will increase across subtropical meadows with future warming, the compounding effects of low light and increased grazing pressure will likely outweigh any future temperature effects. Our findings also contrast with some predictions that range-expanding herbivores might have greater impacts during the winter season when light levels are generally lower<sup>15</sup>. Here we find the strongest responses toward the end of the summer growing season, when water temperatures are still moderately high and control plant metabolism/growth. Thus, during the winter, cooler waters may tend to suppress plant metabolism/growth and minimize responses to grazing.

Natural grazing pressure (assessed by the presence/absence of seagrass bite marks) varied across our network and displayed latitudinal trends (Extended Data Fig. 5). Grazing pressure declined with latitude, and these trends were strongest for the crescent-shaped bite marks characteristic of parrotfish grazing<sup>46</sup>. Fish grazing was significantly (and positively) related to the relative abundance of grazers observed in visual surveys at each site, a pattern that is explored in greater depth in another study (O.K.R., C.J.M., W.L.W., C.J.P., A.H.A. et al., manuscript in preparation). These findings are supported by other studies, which document latitudinal trends in seagrass grazing<sup>5,26</sup> and grazing on reefs<sup>47</sup>, suggesting that increased ocean temperatures across the higher latitudes may elevate plant herbivory<sup>48</sup>. However, we note that our caging treatments (which reduced ambient grazing at each site) had relatively minor influence on seagrass characteristics. Other meta-analyses have similarly found weak caging effects across latitudes, potentially due to the match between plant production and consumption (high-latitude plants grow slowly, yet also suffer less herbivory)<sup>26</sup>. While we document latitudinal trends in grazing marks, these

generally represent the activity of smaller meso-herbivores which also may not cleanly translate into strong caging effects. Our severe clipping treatment had the greatest impact, as it replicated more intense grazing by mega-herbivores such as turtles which proportionally remove more plant biomass and may be increasing their distributional range due to a combination of ocean warming and successful conservation efforts. The effects of moderate clipping did not strongly vary across latitude; thus, our primary findings of latitudinal trends only apply to severe overgrazing. Given that we applied standardized clipping intensities across latitude (whereby seagrass productivity naturally varies), we tested tropicalization scenarios by which plant consumption can commonly exceed the production of high-latitude regions<sup>26</sup>.

Experimental nutrient addition reduced leaf productivity, shoot density and leaf width (Supplementary Tables 1–3). These findings echo previous assessments of seagrass–nutrient interactions<sup>49</sup> and may be driven by shading from algal overgrowth<sup>50</sup> or from increased grazing by small mesoherbivores<sup>51,52</sup>. Interactions between fertilization and simulated grazing were uncommon; thus, we find little evidence that localized nutrient enrichment mitigates the effects of grazing by provisioning key elements (nitrogen and phosphorus)<sup>31</sup>. The role of nutrients was secondarily examined by quantifying the influence of regional variation in ambient nutrient availability (LI) across all sites, which covered a larger range of values compared to our within-site fertilization (Extended Data Fig. 9) and thus had a greater effect. We find that across the network, nutrient availability decreases rhizome carbohydrates (TNC) and promotes sensitivity to severe grazing. Conversely, seagrasses at low-nutrient sites had higher TNC reserves and displayed an increased tolerance to severe grazing even after controlling for variation in light (Supplementary Table 9). The direct influence of nutrients on TNC has been previously documented in terrestrial plants and may result from a process of 'reserve accumulation', whereby nutrient limitation constrains the production of new biomass and excess carbohydrates are shunted towards storage tissues<sup>53,54</sup>. Our documented nutrient–carbohydrate relationships are also in agreement with previous surveys which show inverse relationships between turtlegrass nutrient content and TNC across multiple meadows in Florida, USA<sup>55</sup>. Manipulative experiments have further confirmed that as nutrient-limited seagrasses are fertilized, carbohydrate reserves decline<sup>56</sup>. Combined, we suggest that elevated light levels and low-nutrient availability jointly serve to promote seagrass resilience by bolstering TNC reserves that can be mobilized to replace leaves lost to grazing. As such, rhizome carbohydrates could serve as a useful ecological indicator for meadows facing tropicalization or other related disturbances. We suggest that future work describing the relationship between rhizome carbohydrates and overall meadow resilience are warranted.

Our study focused on turtlegrass, which represents the dominant, slow-growing, climax species in the tropical–subtropical western North Atlantic. Questions remain about how other faster-growing, early successional species may respond to increased grazing across latitudes. Overgrazing work in Bermuda (which formerly had meadows of mixed composition) has shown that other smaller-bodied seagrasses (*Syringodium filiforme* and *Halodule* sp.) are equally susceptible to grazing and, similar to turtlegrass, decline in cover with sustained grazing<sup>41</sup>. It is plausible that the mechanisms for grazing tolerance (carbohydrate reserves; Fig. 4b) also operate for smaller-bodied species, which might comparatively have fewer reserves (based on rhizome diameter) than turtlegrass. However, other studies outside the western North Atlantic have shown that faster-growing species are more tolerant of grazing and become competitively dominant under grazing regimes<sup>57,58</sup>.

The role of chemical defenses also remains an open question within the context of our study, which (1) may be partially responsible for driving latitudinal grazing gradients (as for seaweeds<sup>59</sup>) and (2) could have been influenced by our simulated grazing treatments. Work with the temperate seagrass, *Zostera marina*, has revealed that

plant defenses vary nonlinearly with latitude and may be driven by resource availability, with a higher investment in grazing resistance traits (phenolic compounds, fibre content) at mid-latitude sites with higher nutrient availability<sup>60</sup>. Other studies with turtlegrass have found that the induction of chemical defenses with previous grazing can be variable and elicit species-specific effects on palatability<sup>61,62</sup>. Using a networked approach, future studies that evaluate the extent and magnitude of inducible chemical defenses on turtlegrass palatability across large spatial scales would be highly valuable.

Weighing the balance between the direct and indirect effects of climate change will be critical for understanding and predicting the future trajectories of foundational ecosystems. While direct effects are undoubtedly important, the alternate forces of shifting biological interactions and food web dynamics may serve to obscure, or even amplify, previously documented responses. As oceans warm and tropical species migrate poleward (or increase in abundance due to successful conservation initiatives), they can alter the functioning of marine systems, particularly in the case of overgrazing by marine herbivores<sup>10,63,64</sup>. Our results show that tropical seagrasses positioned near their northern range boundary are increasingly affected by simulated grazing due to lower insolation and compromised carbohydrate reserves. Thus, tropicalization-driven increases in herbivory across these latitudes may dramatically alter the ecological functioning and structure of these valuable systems, as documented for temperate kelp<sup>10</sup>. Seagrass meadows are declining globally<sup>65</sup>, and historical datasets suggest that these trends may be most pronounced for the Tropical Atlantic<sup>66</sup>, which already faces a number of co-occurring stressors (poor water quality, coastal development, urbanization). As meadows along subtropical waters currently have limited capacity to respond to overgrazing, management strategies targeted towards improving overall water quality (reductions in coastal nutrient loading that directly increase light and indirectly raise carbohydrate reserves) may serve to increase seagrass resilience in the face of climate change.

## Methods

### Experimental network

Replicated arrays of caged and uncaged plots were established in turtlegrass beds (*T. testudinum*) at 13 sites across the western North Atlantic (Fig. 1), spanning nearly the entire geographic range of this species (9° N–32° N) and representing tropical–subtropical gradients in temperature and photoperiod. Each site was selected by adhering to a standardized set of criteria: (1) depth (<3 m), (2) plant community composition (turtlegrass, >50% relative abundance), (3) meadow dimensions (minimum 25 m × 25 m) and (4) low wave energy/storm exposure.

### Experimental design

At each site, 50 plots (0.25 m<sup>2</sup>) were established in a grid with a minimum separation of 2 m between adjacent plots. Herbivory (natural and simulated via leaf clipping) and nutrient availability (fertilizer additions) were factorially manipulated and randomly assigned to each plot (Extended Data Fig. 1). Cages (0.5 m × 0.5 m × 0.5 m) were constructed of aquaculture-grade plastic mesh with 1 cm openings supported by a cubic frame made of 3/4-inch polyvinyl chloride (PVC) pipe. Caging treatments consisted of three levels: open plots (PVC frame, allowing natural herbivory), partially caged controls (PVC frame with three mesh sides and a top, allowing natural herbivory and serving as a control for full cages) and full cages (PVC frame with four mesh sides and a top). Simulated herbivory treatments consisted of three levels (severe grazing, moderate grazing, no grazing) and were implemented by manually clipping the seagrass canopy with shears at ~2-week intervals within fully caged plots. The canopy was cut to a height of 2 cm above the sediment surface in the severe grazing treatment ('full clip'), simulating intense herbivory by large megafauna (for example, turtles). For turtlegrass, leaves emerge from a basal meristem

which is protected via burial in the sediment, and thus our severe clipping technique did not remove or damage the basal meristem. Half of the standing canopy was cut in the moderate grazing treatment ('half clip'), simulating more moderate grazing by smaller mesoherbivores (for example, fishes). This allowed us to simulate natural grazing more effectively as plant responses are known to vary by herbivore type<sup>13</sup>. In areas of natural turtle grazing in the western North Atlantic (Bonaire; Mexico; Bahamas; Florida, USA; Bermuda), seagrass meadows are often repeatedly cropped down to the sediment<sup>23,42</sup> (Fig. 1e) for a period of up to 13 months<sup>67</sup> (similar to our experimental duration). Despite this technique being widely used in other grazing studies to simulate herbivory<sup>30,31,42,68</sup>, we acknowledge that some plant responses (for example, inducible defenses) may differ between natural and simulated herbivory.

Herbivory treatments were fully crossed with manipulations of nutrient availability, nitrogen (N) and phosphorus (P), which consisted of two levels (fertilized and unfertilized). Fertilized plots received 300 g of slow-release Osmocote fertilizer (Everris NPK 14–14–14) suspended in a fiberglass mesh bag in the centre of the plot 5 cm above the sediment. These bags were replaced approximately every 4 weeks to ensure consistent delivery. Exhausted bags were retrieved, briefly rinsed with freshwater and oven-dried to a constant weight. Loading rates were calculated for each plot based on fertilizer mass loss, fertilizer NP content and deployment duration. Daily loading rates across all plots and sites averaged 0.36 g N and 0.23 g P per plot per day, similar to studies documenting the effects of coastal eutrophication<sup>51,69</sup>. Linear mixed models revealed that fertilization significantly increased plant nutrient content (Supplementary Table 10).

Sites were established in spring of 2018 (April to May, depending upon site) and maintained for approximately 1 year. In total, 10 treatments were established at each site with  $n = 5$  replicates per treatment (Extended Data Fig. 1). Light was recorded every 6 min by underwater PAR loggers (Odyssey Dataflow Systems) positioned at the top of the seagrass canopy, and temperature was recorded at the same time intervals by HOBO loggers (UA-002064). Cages and loggers were maintained and cleaned approximately every 14 days by divers (using stiff brushes) to minimize fouling and shading.

### Seagrass responses

Seagrass responses (productivity, shoot density and leaf width) were measured twice during the experiment, once at the end of the summer growing season (September 2018 to October 2018) and again at the end of the winter season (April 2019 to May 2019). For simplicity, these two periods will be referenced as 'summer' and 'winter', respectively. At the end of each period, leaf productivity was measured on four to six haphazardly selected shoots per plot by marking each with a needle inserted at the basal/lower portion of the leaves, near the top of the leaf sheath. This left a visible mark on all leaves that could be used to monitor new growth. Turtlegrass displays two to six leaves per shoot which grow upward from a basal meristem. The innermost leaves are the youngest and display the most active growth, while the outermost leaves are older and display little to no growth. After marking, the selected shoots were tagged and collected after 7–10 days. Growth was assessed per shoot (mg per shoot per day) by measuring and weighing new leaf material produced below the needle marks, similar to previous studies<sup>70,71</sup>. Leaves on collected shoots were also measured for width (mm). Ambient rates of seagrass grazing were assessed by recording the presence/absence of characteristic grazing marks<sup>46,72,73</sup> on the collected productivity shoots from the plots open to herbivore access (uncaged and partial cage treatments). Grazing marks were further classified by grazer type (fish, turtle or urchin), similar to other studies<sup>74</sup>. The average proportion of shoots grazed at each site was then calculated. Shoot density (number per m<sup>2</sup>) was measured by placing two replicate 15-cm-diameter rings in each plot and counting all shoots contained within. At the end of the experiment (immediately after the winter



sampling) all plots were also collected for biomass with a 15 cm steel corer. Cores from each plot were placed in mesh bags, transported to the lab on ice and gently rinsed in freshwater. Seagrass biomass was separated into aboveground and belowground biomass, dried at 60 °C to a constant weight and ground to a powder with a mortar and pestle. Leaf carbon and nitrogen content was measured with an elemental analyser, and leaf P content was measured through dry-oxidation/acid-hydrolysis extraction, followed by colorimetric analysis<sup>75</sup>. The TNC content of belowground biomass (rhizomes only) was analysed by the University of California, Davis Analytical Lab, following standard protocols<sup>76</sup>.

### Ambient nutrient availability

Ambient nutrient availability was assessed via the mean seagrass LI of the control plots at each site, which assesses the degree to which seagrasses are nutrient limited (by either N or P). LI is calculated as the absolute deviation of leaf N:P from the balanced 30:1 ratio ( $LI = |30 - N:P|$ )<sup>38,77</sup>, and thus large LI values indicate plants are further removed from this balanced ratio and are increasingly nutrient limited. Conversely, low LI values indicate plants that are closer to this balanced ratio and are less nutrient limited. This metric is more useful than simple metrics of plant nutrients (%N, %P, C:N, C:P) as it can be applied across large spatial scales where seagrasses may be either N or P limited<sup>75</sup>. For example, turtlegrass meadows along the Gulf shores have previously been shown as being nitrogen limited<sup>78,79</sup>, whereas meadows in Florida Bay were phosphorus limited<sup>80</sup>. Even within a region, meadows can shift from being P limited to N limited along nearshore–offshore gradients<sup>69,75</sup>. In our dataset, the LI index is negatively correlated to %N ( $P = 0.004$ ) and %P ( $P = 0.001$ ) and positively correlated to C:N ( $P = 0.0005$ ) and C:P ( $P < 0.0001$ ) (Supplementary Table 11), and thus as either N or P declines in plant tissues, LI increases. Furthermore, our fertilization treatment which increased plant %N and %P significantly reduced LI (Supplementary Table 10). These plant-based metrics of nutrient availability are also more informative than intermittent, ‘spot’ measurements of water column nutrient concentrations, which can be highly variable. Benthic vegetation integrates nutrient signals across longer time periods and serves as a more accurate estimate of nutrient availability<sup>75,81</sup>.

### Statistical analyses

Our objectives were to understand how grazing effects varied across large spatial scales and whether key environmental factors (for example, light, temperature, nutrient availability) regulated plant responses. Linear mixed-effects models were used to test whether our manipulated treatments (fixed effects: simulated grazing, caging and nutrients), site-specific environmental covariates (detailed below) or their interaction influenced seagrass metrics (productivity, density, morphology, carbohydrate reserves). Site was included as a random effect in all models. Covariates included latitude, temperature, light, ambient nutrient availability and canopy structure. Light, temperature and ambient nutrient availability were all included as they can jointly regulate seagrass productivity<sup>45</sup> and varied across our network (Extended Data Table 1 and Extended Data Figs. 3 and 9). Mean aboveground leaf biomass of the control plots was also included as a covariate to account for site-specific variation in seagrass canopy structure. All covariates were checked for collinearity using a Pearson’s rank correlation matrix, and highly correlated variables ( $r > 0.5$ ) were not simultaneously included as predictors in the same model. Latitude was correlated to both light and temperature ( $r = 0.8$ ; Supplementary Table 12), and thus two separate models were constructed, one including latitude and the other including light and temperature (see equations below). After model construction, a secondary check for multicollinearity was conducted by checking variance inflation factors for all predictors. In all cases, variance inflation factors were  $\leq 3$ , indicating low multicollinearity<sup>82</sup>. Covariates were centred and standardized, and some seagrass metrics were either  $\log_{10}$  or square-root transformed to improve normality in the distribution of

the residuals. The following are the mixed-effects models that we ran for each of the seagrass responses ( $y$  = leaf productivity, shoot density or leaf width), with multiplication symbols ( $\times$ ) referring to interaction terms and (1|site) referring to the random effect of site.

Model 1 (latitude):  $y$  - latitude + aboveground\_biomass + limitation\_index + clipping + cage + nutrients + clipping  $\times$  nutrients + latitude  $\times$  clipping + light  $\times$  clipping + aboveground\_biomass  $\times$  clipping + limitation\_index  $\times$  clipping + (1|site)

Model 2 (light and temperature):  $y$  - light + temperature + aboveground\_biomass + limitation\_index + clipping + cage + nutrients + clipping  $\times$  nutrients + temperature  $\times$  clipping + light  $\times$  clipping + aboveground\_biomass  $\times$  clipping + limitation\_index  $\times$  clipping + (1|site)

As we assessed seagrass responses twice during the experiment, separate models were constructed for each season. The light and temperature predictors in model 2 were adjusted accordingly. For example, site-level mean light in the summer model was calculated across the summer growing season, from the beginning of the experiment until the first sampling event (April/May 2018 to September/October 2018), and site-level mean light in the winter model was calculated across the winter season, from the first sampling event to the end of the experiment (September/October 2018 to April/May 2019). We note that significant latitudinal light gradients were only detected during the summer season. This is likely because light levels were more variable than expected during the winter due to (1) low tides at some high-latitude sites (Florida-Naples (NAPL)) which increased light levels, and (2) early season algal blooms at some low-latitude sites (Mexico (PUER) and Bonaire (BONA)) which reduced light levels.

Due to weather, we were unable to sample Texas-Corpus Christi (CORP) in 2018, and thus this site was not included in the summer models. Furthermore, Panama (BOCA) was an outlier in terms of both light and leaf productivity, which were extremely low given its latitudinal position (Extended Data Table 1). This was likely because the site was within an enclosed embayment frequently subjected to freshwater-driven turbidity events from the surrounding watershed, which led to extremely low light levels<sup>44</sup>. We therefore excluded Panama from models 1 and 3 to better understand broader latitudinal gradients in seagrass response across the network. However, we do include Panama in models 2 and 4, which account for the low light levels measured at the site.

We measured total rhizome non-structural carbohydrates (TNC) at the experiment end as an additional indicator of plant health/status<sup>37</sup>; however, we were only able to analyse a limited number of samples, so we constructed a separate carbohydrate model which only tested the effects of grazing at nine of our sites. Latitude for this model was fit as a second-order polynomial to account for nonlinearity, and annual means for light and temperature were used as TNC reserves reflect long-term storage<sup>37</sup>.

Model 3 (latitude): TNC - poly(latitude,2) + aboveground\_biomass + limitation\_index + clipping + poly(latitude,2)  $\times$  clipping + aboveground\_biomass  $\times$  clipping + limitation\_index  $\times$  clipping + (1|site)

Model 4 (light and temperature): TNC - light + temperature + aboveground\_biomass + limitation\_index + clipping + temperature  $\times$  clipping + light  $\times$  clipping + aboveground\_biomass  $\times$  clipping + limitation\_index  $\times$  clipping + (1|site)

We constructed our models based on our experimental design and initial hypotheses of the effects of grazing, nutrients, latitude, light and temperature on seagrass responses. A nutrient  $\times$  clipping interaction term was included in models 1 and 2 to test whether nutrient loading influenced plant responses to clipping. We tested the hypothesis that

herbivory response increases with latitude by incorporating a latitude  $\times$  clipping interaction term in models 1 and 3. We also tested the hypothesis that increased light reduced herbivory response by incorporating light  $\times$  clipping interactions terms in models 2 and 4. To control for cross-network variation in seagrass canopy structure and ambient nutrient availability, aboveground biomass and LI were included as predictors in all models, along with their interactions with clipping. Caging artefacts were assessed by the presence of a significant ‘partial cage’ coefficient in the models. No artefacts were detected for leaf productivity; however, we did detect some caging artefacts for shoot density (winter season only) and leaf width (summer and winter seasons). During the experiment, certain sites were periodically subjected to turbidity events from sargassum blooms (Mexico and Bonaire), while one other site experienced heavy barnacle fouling on the cages (Naples). We re-analysed our dataset by removing sites with significant ( $P < 0.05$ ) caging artefacts, and the primary conclusions of our original analysis remain unchanged; simulated clipping had a larger effect at high latitude sites with lower light levels (Supplementary Table 13). Partial least squares regression was also conducted on a sub-set of our data to confirm/validate the main results from our mixed models. This is a multivariate approach that uses a combination of latent variables (constructed from several predictors) to maximize the explained variance in a response variable. Full models with all site-level predictors (latitude, light, temperature, LI and aboveground biomass) were constructed for our main response variables: productivity (summer only), shoot density (summer only), leaf width (summer only) and non-structural carbohydrates (winter only). Cross validation was used to reconstruct the models with an optimal number of dimensions, and the resultant predictor coefficients were extracted and normalized. Bar plots (Supplementary Figs. 5–8) display the ranked coefficients and confirm primary conclusions from the mixed models; clipping had a greater effect at the higher latitudes with lower light levels.

All analyses were run using R (v.4.0.3). Models were fit with the lme function in the nlme R package (v.3.1) (ref. 83). Models were validated by visually assessing plots of the residuals versus the fitted values of each component model. Some models displayed heteroskedastic residuals, which were corrected by structuring the residual variance by network site with the varIdent function in nlme. After fitting, the above full models were then pruned via a backwards stepwise selection procedure (stepAIC), which sequentially removed model terms and compared the reduced models to the original full model using Akaike information criterion (AIC). Reduced models with the lowest AIC score were selected as the final model. Partial least squares regression was performed using the package pls (v.2.7.0) (ref. 84). Last, we assessed latitudinal gradients in light, temperature and grazing marks (Extended Data Figs. 3 and 5) using generalized additive models in the mgcv package (v.1.9) (ref. 85).

### Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

### Data availability

All data used in this study are available at the FigShare repository (<https://doi.org/10.6084/m9.figshare.24649641.v1>).

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## Author contributions

J.E.C., O.K.R., A.H.A., J.G.D., K.L.H. and V.J.P. designed the research; J.E.C., O.K.R., A.H.A., J.G.D., K.L.H., V.J.P., A.R.A., S.C.B., E.B., L.C., M.J.A.C., G.D., K.D., J.W.F., T.K.F., B.M.G., R.G., J.A.G., R.G.-V., V.J.J., O.A.A.K., S.T.L., C.W.M., I.G.M.L., A.M.M., V.A.M., S.A.M., C.M.-M., D.A.O'B., O.R.O'S., C.J.P., C.P., L.K.R., A.R., L.M.R.B., A.S., Y.S., K.S., F.O.H.S., U.S., J.E.T., B.V.T. and W.L.W. performed the research; J.E.C. analysed the data with contributions from C.J.M. and O.K.R.; and J.E.C. wrote the paper with contributions from all authors.

## Competing interests

The authors declare no competing interests.

## Additional information

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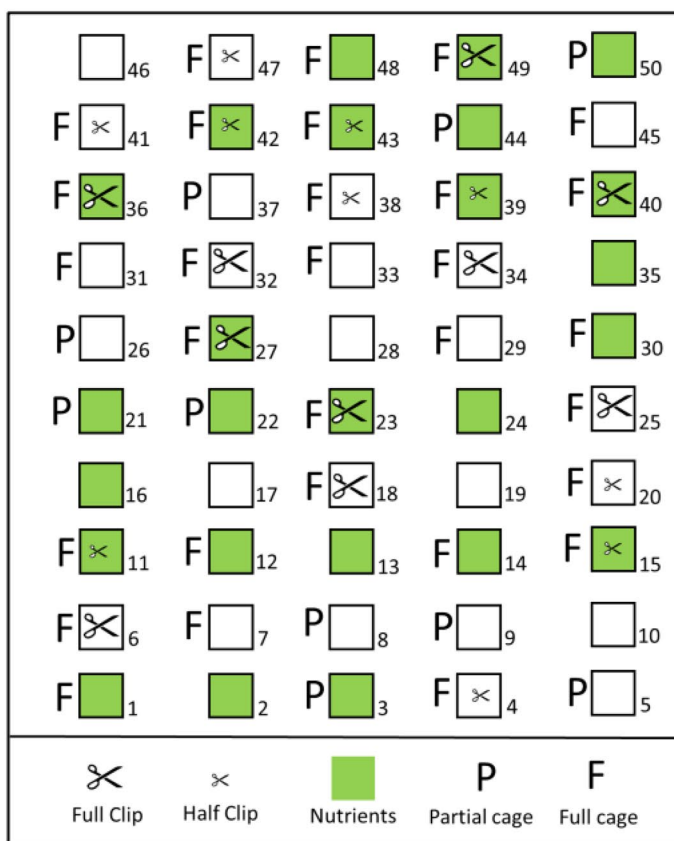
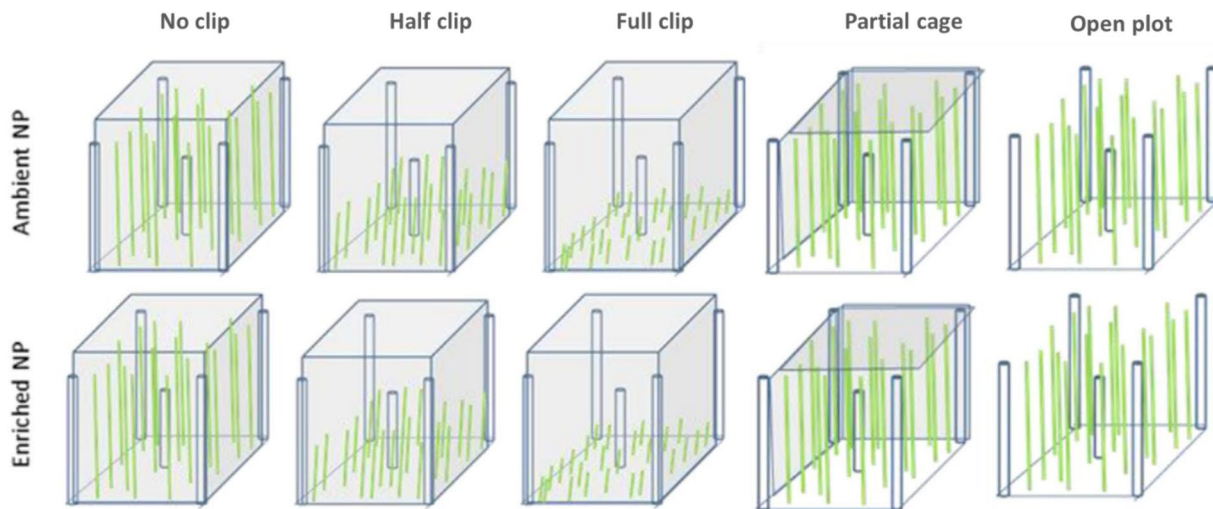
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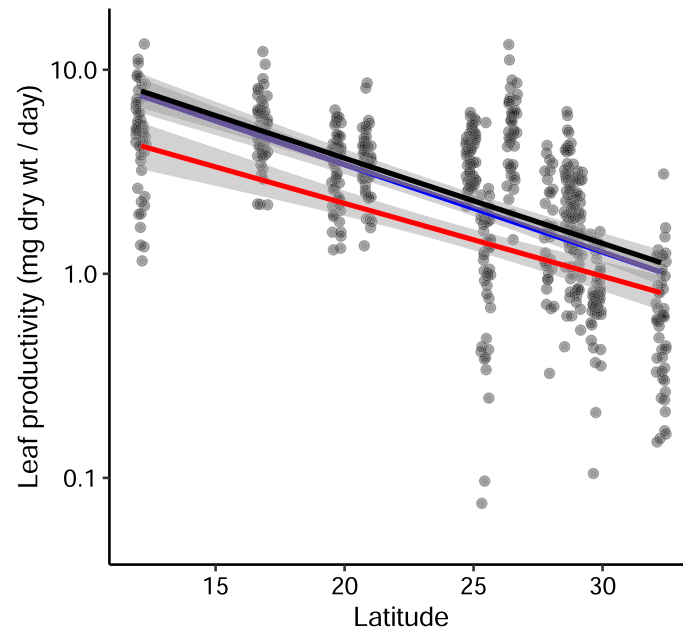
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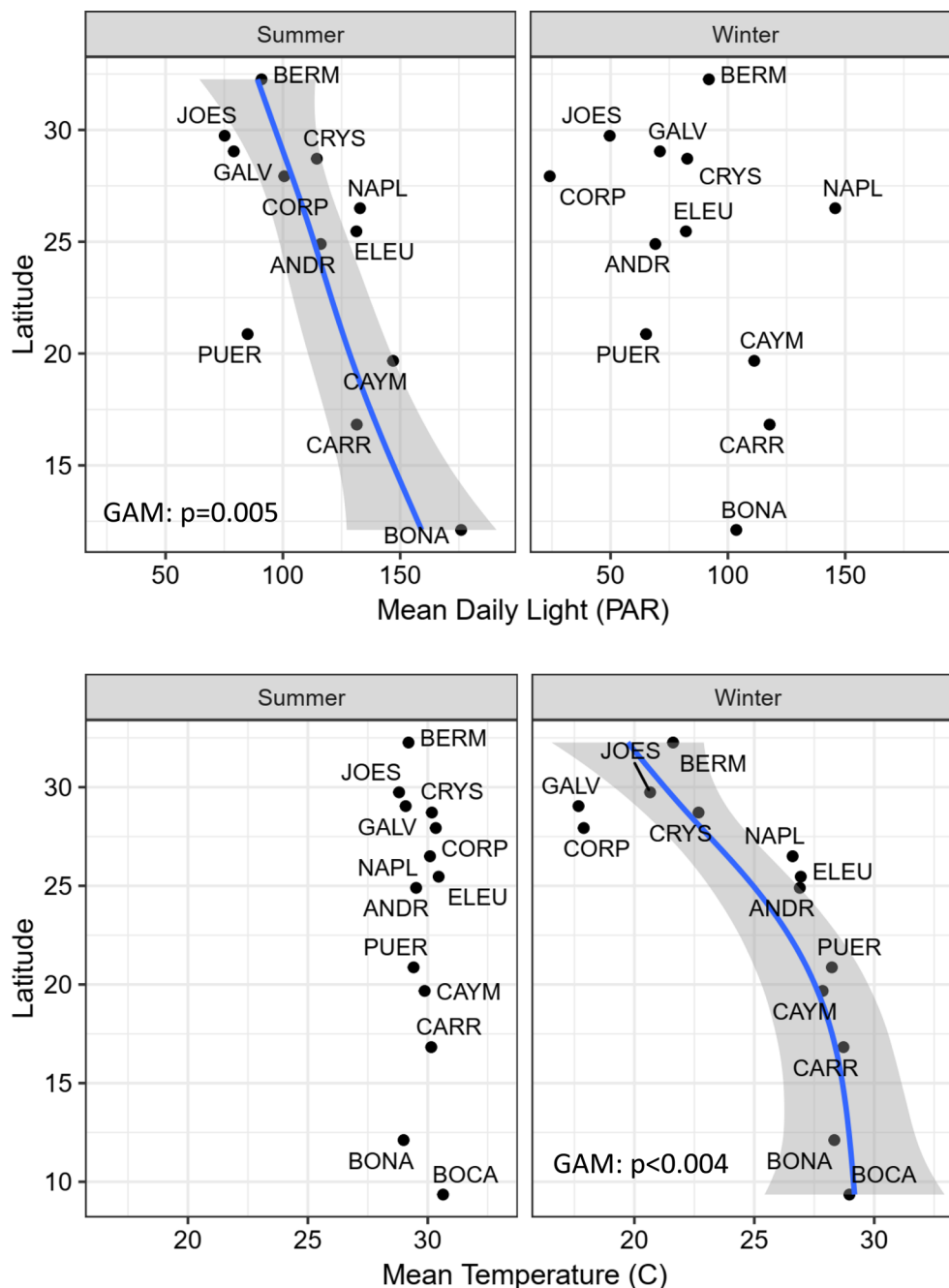


**Extended Data Fig. 1 | Graphical representation of treatments established at each site.** Plots (0.25m<sup>2</sup>) were established at each site manipulating (1) herbivory intensity (via leaf clipping) and (2) nutrient availability (via Osmocote nutrient bags attached center plot), for a total of 10 treatments (n = 5/site). Mesh cages were established around the clipped treatments to control variation in natural

grazing. Partial cages and open plots were also established, but these treatments did not receive leaf clipping. Lower panel displays the gridded plot arrangement at each site. Photographs display plot/ cage placement (upper) and Osmocote fertilizer bag (lower).



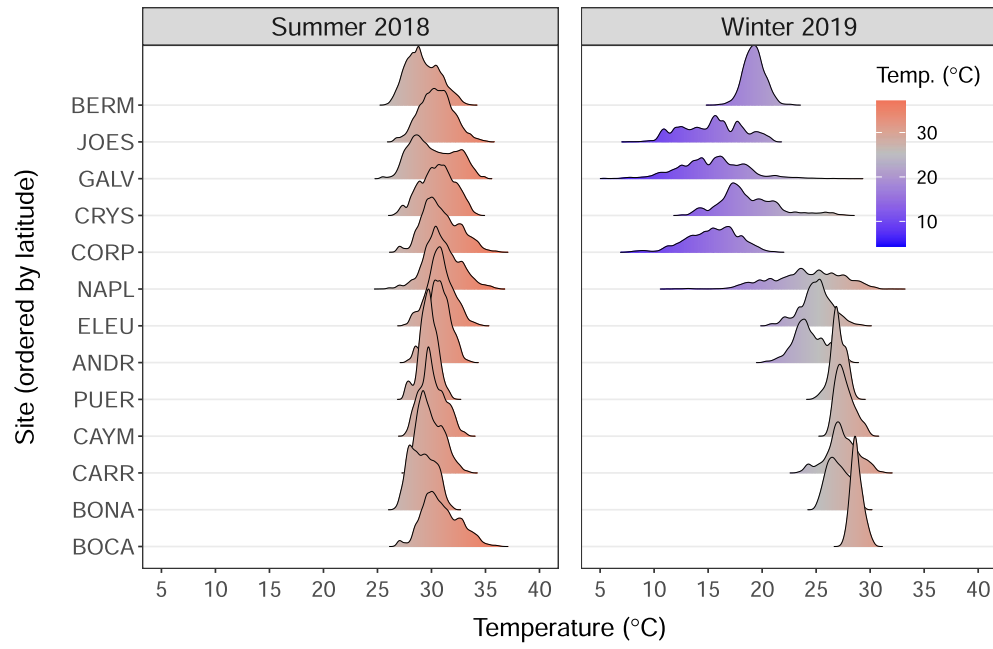
**Extended Data Fig. 2 | Winter effects of grazing on leaf productivity across latitude.** Lines represent linear fits plus 95% confidence intervals for the severe grazing (red), moderate grazing (blue) and no grazing (black) treatments. Points represent individual plots and are jittered for clarity (n = 50 plots/site).



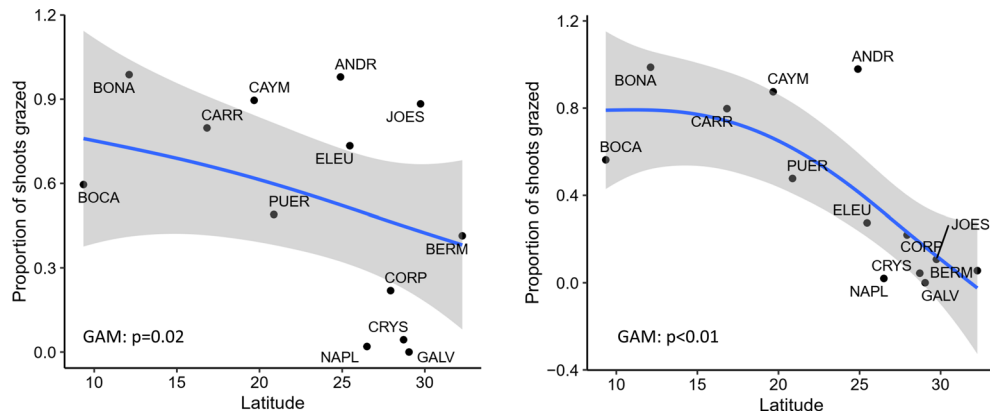
**Extended Data Fig. 3 | Light and temperature trends across latitude.** Site means for light (daily photosynthetically active radiation,  $\mu\text{mol photons m}^{-2}\text{s}^{-1}$ ) and temperature across latitude ( $^{\circ}\text{N}$ ). Data have been divided into two seasons based on sampling timeline. 'Summer' represents measurements recorded from approximately Apr 2018 - Sept 2018, and 'Winter' represents measurements recorded from approximately Sept 2018 - Apr 2019. Trend lines represent fits of generalized additive models (GAMs) and grey shading displays 95% confidence

intervals. Significant tests were two-sided. Sites are labeled: Lac Bay, Bonaire (BONA), Carrie Bow Cay, Belize (CARR), Little Cayman, Cayman Islands (CAYM), Puerto Morelos, Mexico (PUER), Andros, Bahamas (ANDR), Eleuthera, Bahamas (ELEU), Naples, Florida (NAPL), Crystal River, Florida (CRYS), Galveston, Texas (GALV), St. Joseph Bay, Florida (JOES), Riddell's Bay, Bermuda (BERM). Note that BOCA was an outlier for light levels and was excluded from the analysis (see Methods) to understand trends across the broader network.



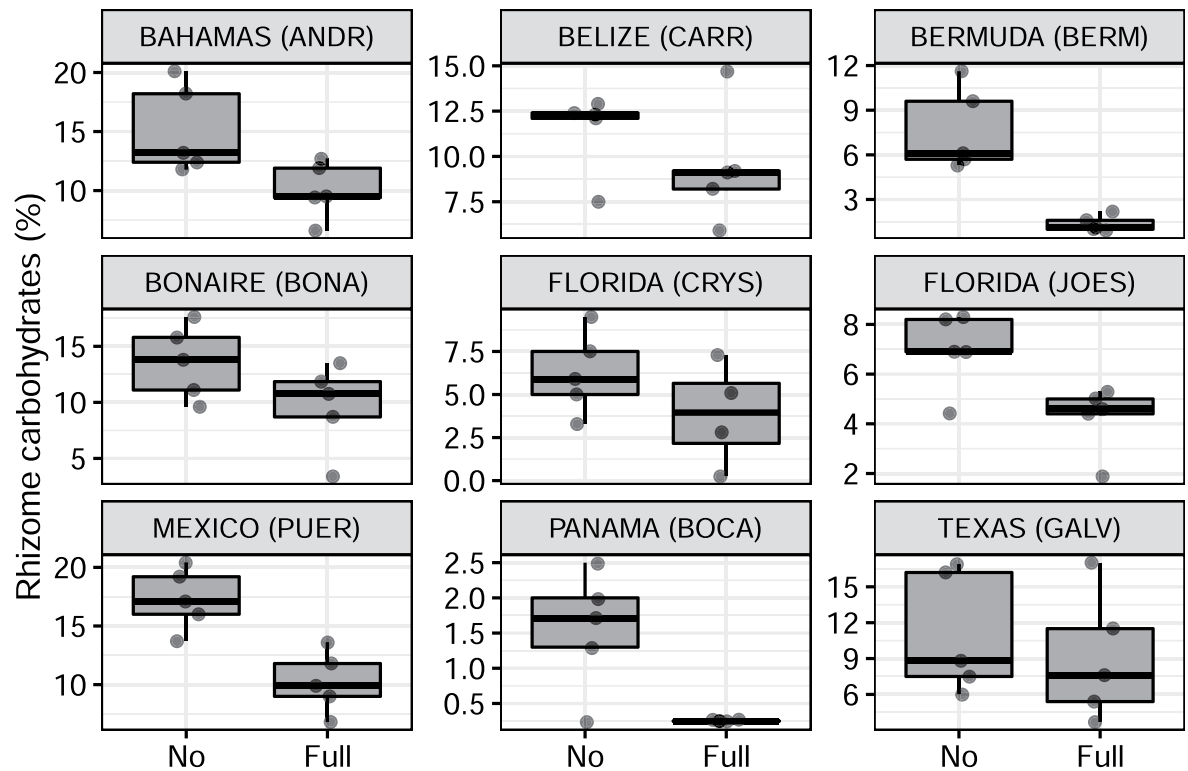


**Extended Data Fig. 4 | Temperature density distributions across sites.** Plots display frequency distributions of recorded temperatures at each site during the summer and winter seasons. Sites have been ordered from top to bottom in order of decreasing latitude.



**Extended Data Fig. 5 | Latitudinal trends in grazing.** Rates of seagrass grazing across latitude ( $^{\circ}$ N). Total grazing rate (left panel) represents the proportion of examined shoots with evidence of any grazing mark. Grazing rate – Fish only (right panel) represents the proportion of shoots with only characteristic fish

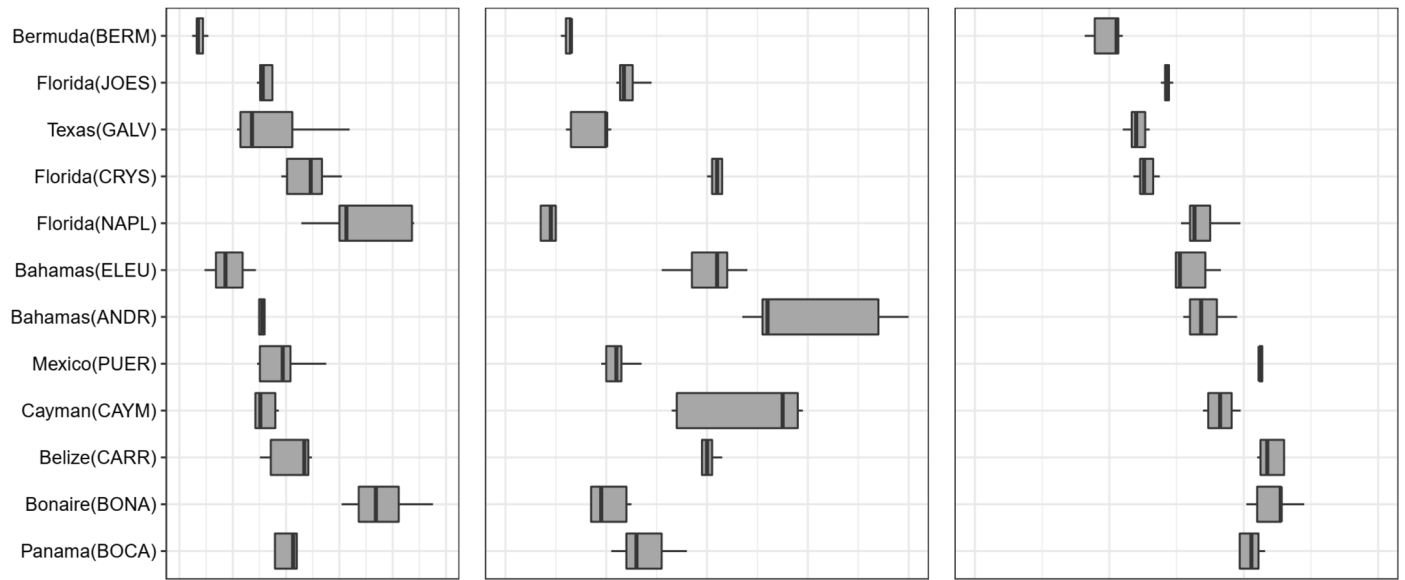
grazing marks (crescent shaped bite marks). Grazing rates were averaged across seasons. Trend lines represent fits of generalized additive models (GAMs) and grey shading displays 95% confidence intervals. Significance tests were two-sided.



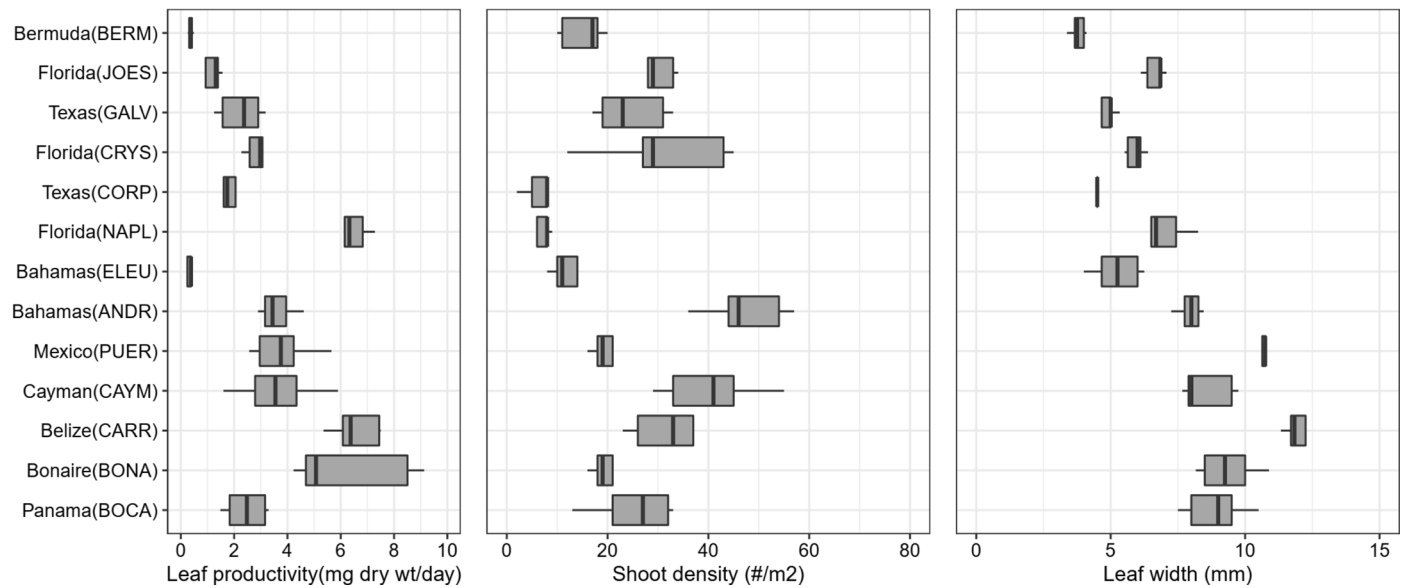
**Extended Data Fig. 6 | Main effects of simulated grazing on belowground non-structural carbohydrates.** Grazing effects (no clip vs full clip, only) on rhizome total non-structural carbohydrates. Samples were collected at the

experiment end after the winter season. Points represent individual plots and are jittered for clarity ( $n = 10$  plots/site). Description: vertical heavy lines (medians); solid boxes (interquartile range); whiskers (range of non-outlier data).

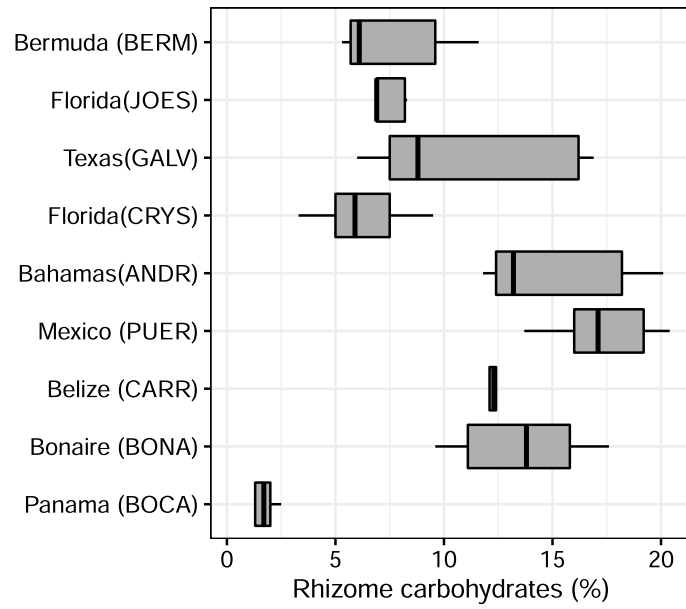
### Summer



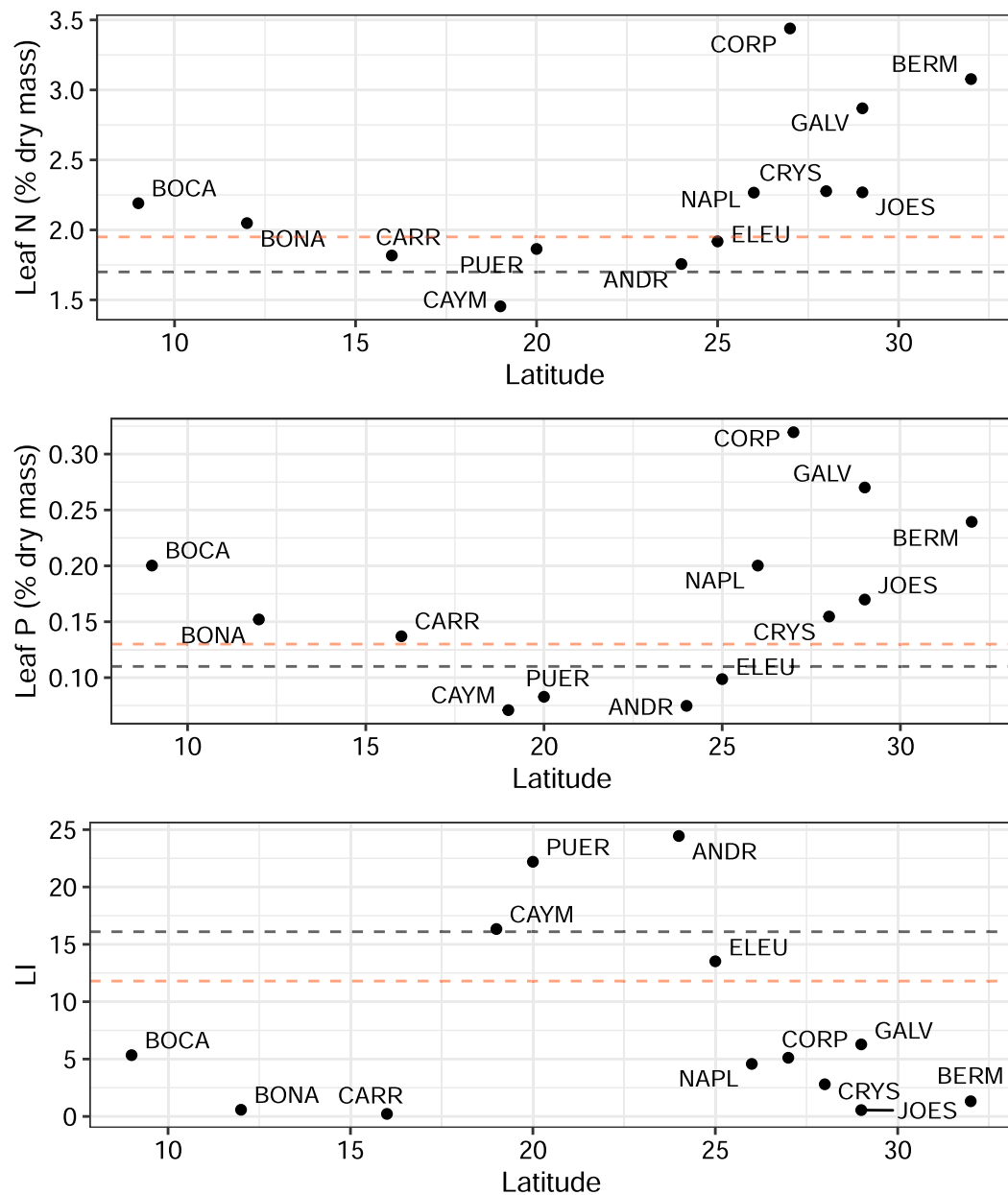
### Winter



**Extended Data Fig. 7 | Trends in leaf productivity, shoot density and leaf width across sites.** Boxplots of seagrass metrics measured in unmanipulated, open control plots (n = 5 plots/site) after the summer (upper panels) and winter (lower panels) seasons. Sites decline in latitude from top to bottom. Description: vertical heavy lines (medians); solid boxes (interquartile range); whiskers (range of non-outlier data).



**Extended Data Fig. 8 | Rhizome non-structural carbohydrates.** Boxplot of rhizome carbohydrates measured in control plots (n = 5 plots/site). Sites decline in latitude from top to bottom. Description: vertical heavy lines (medians); solid boxes (interquartile range); whiskers (range of non-outlier data).



**Extended Data Fig. 9 | Trends in leaf tissue nutrient content across latitude.** Values represent means of leaf tissue nitrogen (N) and phosphorus (P) content from the control, unmanipulated plots at each site across latitude ( $^{\circ}$ N) (data previously published<sup>86</sup>). The limitation index (LI) was calculated for each site

(see *Methods*). Note, higher LI values indicate seagrasses that are more nutrient-limited, thus a lower availability of ambient nutrients. For comparison, dashed red and black lines represent mean values from the enriched and unenriched open plots, respectively.

**Extended Data Table 1 | Site locations, codes, and environmental parameters**

Country	Site	Code	Latitude	Longitude	Limitation index	Aboveground biomass g dry mass m <sup>-2</sup>
Bermuda	Riddell's Bay	BERM	32°15'49.9"N	64°49'50.5"W	1.323	0.118
USA - Florida	St. Joseph Bay	JOES	29°42'05.0"N	85°19'34.6"W	0.552	0.432
USA - Texas	Galveston	GALV	29°02'41.8"N	95°10'15.7"W	6.280	0.613
USA - Florida	Crystal River	CRYS	28°42'50.4"N	82°49'08.4"W	2.803	4.347
USA - Texas	Corpus Christi	CORP	27°55'47.9"N	97°02'05.2"W	5.113	0.134
USA - Florida	Naples	NAPL	26°29'48.6"N	82°09'40.0"W	4.577	1.362
Bahamas	Eleuthera	ELEU	25°27'53.5"N	76°37'35.8"W	13.523	0.351
Bahamas	Andros	ANDR	24°53'54.3"N	77°54'25.2"W	24.444	4.488
Mexico	Puerto Morelos	PUER	20°52'04.5"N	86°51'35.4"W	22.198	0.803
Cayman Islands	Little Cayman	CAYM	19°40'14.6"N	80°03'21.3"W	16.337	2.186
Belize	Carrie Bow Cay	CARR	16°49'24.8"N	88°06'16.2"W	0.221	4.095
Bonaire	Lac Bay	BONA	12°06'44.3"N	68°13'42.0"W	0.580	1.746
Panama	Bocas del Toro	BOCA	9°21'05.8"N	82°15'27.8"W	5.342	0.824

Site	Mean daily summer light umol photons m <sup>-2</sup> s <sup>-1</sup>	Mean daily winter light umol photons m <sup>-2</sup> s <sup>-1</sup>	Mean summer temperature °C	Mean winter temperature °C
BERM	90.903	91.887	29.197	21.613
JOES	75.170	49.619	28.803	20.655
GALV	79.077	71.025	29.078	17.670
CRYS	114.463	82.676	30.170	22.676
CORP	N.D.	28.410	30.333	17.888
NAPL	132.877	145.735	30.093	26.597
ELEU	131.327	82.111	30.454	26.938
ANDR	116.112	69.079	29.514	26.896
PUER	84.951	65.118	29.409	28.233
CAYM	146.964	111.228	29.869	27.848
CARR	131.488	117.784	30.145	28.717
BONA	175.973	103.577	28.992	28.335
BOCA	57.250	73.146	30.638	28.964

Sites have been ordered by latitude. N.D.= No data.

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- For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
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- Estimates of effect sizes (e.g. Cohen's  $d$ , Pearson's  $r$ ), indicating how they were calculated

*Our web collection on [statistics for biologists](#) contains articles on many of the points above.*

### Software and code

Policy information about [availability of computer code](#)

- Data collection
- Data analysis

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio [guidelines for submitting code & software](#) for further information.

### Data

Policy information about [availability of data](#)

All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our [policy](#)



## Research involving human participants, their data, or biological material

Policy information about studies with [human participants or human data](#). See also policy information about [sex, gender \(identity/presentation\), and sexual orientation](#) and [race, ethnicity and racism](#).

Reporting on sex and gender	N/A
Reporting on race, ethnicity, or other socially relevant groupings	N/A
Population characteristics	N/A
Recruitment	N/A
Ethics oversight	N/A

Note that full information on the approval of the study protocol must also be provided in the manuscript.

## Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

Life sciences  Behavioural & social sciences  Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see [nature.com/documents/nr-reporting-summary-flat.pdf](https://www.nature.com/documents/nr-reporting-summary-flat.pdf)

## Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We used 650 experimental manipulative plots (distributed across a latitudinal gradient of 13 sites in the Western Atlantic) to explore (1) how grazing impacts the ecological functioning of a foundational marine ecosystem (seagrasses) and (2) how environmental context (light, temperature, nutrient availability) influences seagrass responses. At each of the 13 sites, grazing and nutrient availability were independently manipulated across 50 plots.
Research sample	Seagrass meadows at 13 sites across the Western Atlantic. Seagrasses at all sites were predominantly comprised of <i>Thalassia testudinum</i> (turtlegrass).
Sampling strategy	50 plots (10 treatments, n=5/treatment) were established at 13 sites across the Western Atlantic. All plots were sampled across two seasons (summer and winter). Levels of replication follow prior seagrass networks addressing similar questions (Campbell et al 2018, Journal of Ecology). The 13 sites were selected to represent the distributional range of the dominant seagrass species ( <i>Thalassia testudinum</i> )
Data collection	Data on seagrass productivity, shoot density, leaf morphology and rhizome carbohydrates were collected by all individuals in 2018 and 2019. See methods for a detailed description of the procedures
Timing and spatial scale	Experiment was conducted in 2018-2019. At each site, sampling was conducted at a single seagrass meadow (measuring 25m x 25m). Each manipulative plot was 0.5m x 0.5m.
Data exclusions	N/A
Reproducibility	This experiment was a massive, year-long networked project across 45 collaborators and 8 countries. Attempts to reproduce the findings were not made.
Randomization	Treatments within each site were randomly assigned across 50 plots. Across our 13 sites, light, temperature, standing stock biomass and nutrient availability were used as covariates in our analyses.
Blinding	Samples from individual plots were assigned a numerical identifier that obscured the assigned treatment.
Did the study involve field work?	<input checked="" type="checkbox"/> Yes <input type="checkbox"/> No

## Field work, collection and transport

Field conditions	Field work was conducted across 13 sub-tidal seagrass meadows in the Western Atlantic. All sites were <4m depth and dominated by the climax seagrass, <i>Thalassia testudinum</i> .
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Location	Please see Table S1 for GPS coordinates of all sites.
Access & import/export	This work was conducted under the following permits: at Eleuthera under permit #s MAMR/FIS/17 and MAMR/FIS/9 issued by the Department of Marine Resources; at Bonaire under permit #558/2015-2015007762 issued by Openbaar Lichaam Bonaire; at Belize under permit #0004-18 issued by the Belize Fisheries Department; and at Panama under permit #s SE/AP-23-17 and SE/AO-1-19 issued by the Ministerio de Ambiente de la Republica de Panama; at Andros by permits issued by The Bahamas National Trust and the Bahamas Environment, Science and Technology Commission; and at Cayman Islands by a permit issued by the Department of Environment.
Disturbance	Benthic voids created by our seagrass biomass cores were re-filled with sediment to facilitate recovery. All field materials were removed from the sites after the experiment.

## Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

### Materials & experimental systems

n/a	Involvement in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> Antibodies
<input checked="" type="checkbox"/>	<input type="checkbox"/> Eukaryotic cell lines
<input checked="" type="checkbox"/>	<input type="checkbox"/> Palaeontology and archaeology
<input checked="" type="checkbox"/>	<input type="checkbox"/> Animals and other organisms
<input checked="" type="checkbox"/>	<input type="checkbox"/> Clinical data
<input checked="" type="checkbox"/>	<input type="checkbox"/> Dual use research of concern
<input type="checkbox"/>	<input checked="" type="checkbox"/> Plants

### Methods

n/a	Involvement in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> ChIP-seq
<input checked="" type="checkbox"/>	<input type="checkbox"/> Flow cytometry
<input checked="" type="checkbox"/>	<input type="checkbox"/> MRI-based neuroimaging

## Dual use research of concern

Policy information about [dual use research of concern](#)

### Hazards

Could the accidental, deliberate or reckless misuse of agents or technologies generated in the work, or the application of information presented in the manuscript, pose a threat to:

No	Yes
<input checked="" type="checkbox"/>	<input type="checkbox"/> Public health
<input checked="" type="checkbox"/>	<input type="checkbox"/> National security
<input checked="" type="checkbox"/>	<input type="checkbox"/> Crops and/or livestock
<input checked="" type="checkbox"/>	<input type="checkbox"/> Ecosystems
<input checked="" type="checkbox"/>	<input type="checkbox"/> Any other significant area

### Experiments of concern

Does the work involve any of these experiments of concern:

No	Yes
<input checked="" type="checkbox"/>	<input type="checkbox"/> Demonstrate how to render a vaccine ineffective
<input checked="" type="checkbox"/>	<input type="checkbox"/> Confer resistance to therapeutically useful antibiotics or antiviral agents
<input checked="" type="checkbox"/>	<input type="checkbox"/> Enhance the virulence of a pathogen or render a nonpathogen virulent
<input checked="" type="checkbox"/>	<input type="checkbox"/> Increase transmissibility of a pathogen
<input checked="" type="checkbox"/>	<input type="checkbox"/> Alter the host range of a pathogen
<input checked="" type="checkbox"/>	<input type="checkbox"/> Enable evasion of diagnostic/detection modalities
<input checked="" type="checkbox"/>	<input type="checkbox"/> Enable the weaponization of a biological agent or toxin
<input checked="" type="checkbox"/>	<input type="checkbox"/> Any other potentially harmful combination of experiments and agents