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Temperature Drives Seagrass Recovery Across the Western North Atlantic

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ABSTRACT

Climate-driven shifts in herbivores, temperature, and nutrient runoff threaten coastal ecosystem resilience. However, ecological resilience, particularly for foundation species, remains poorly understood due to the scarcity of field experiments conducted across appropriate spatial and temporal scales that investigate multiple stressors. This study evaluates the resilience of a widespread tropical marine plant (turtlegrass) to disturbances across its geographic range and examines how environmental gradients in (a)biotic factors influence recovery. We assessed turtlegrass resilience by following recovery rates for a year after a simulated pulse disturbance (complete above- and belowground biomass removal). Contrary to studies in temperate areas, higher temperature generally enhanced seagrass recovery. While nutrients had minimal individual effects, they reduced aboveground recovery when combined with high levels of herbivore grazing (meso and megaherbivore). Belowground recovery was also affected by combined high levels of nutrients

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original work is properly cited and is not used for commercial purposes.

@ 2025 The Author(s). Global Change Biology published by John Wiley & Sons Ltd. and grazing (megaherbivores only). Light availability had minimal effects. Our results suggest that the resilience of some tropical species, particularly in cooler subtropical waters, may initially benefit from warming. However, continuing shifts in nutrient supply and changes in grazing pressure may ultimately serve to compromise seagrass recovery.

1 | Introduction

Understanding the ability of coastal ecosystems to resist and recover from disturbances, that is, ecosystem resilience (Folke et al. 2004), is essential in an era of rapid global change. Yet, we know very little about the impact of anthropogenic stressors on the resilience of foundation species that comprise our coastal zones. This is a cause for concern as global warming and other humaninduced stressors are increasingly driving large-scale ecosystem loss (Dirzo et al. 2014), and coastal ecosystems are among the most threatened systems on Earth (IPCC 2022; Woodruff et al. 2013). Often, empirical studies sample and compare resilience at a single location and focus on the effects of single stressors. This approach leads to an incomplete understanding of the impact of environmental drivers on ecosystem resilience across large spatial scales.

The resilience of coastal plant communities is under pressure from both global change stressors such as warming seas and intensifying storms, as well as human pressure from populationdense coastal zones (Gissi et al. 2021; He and Silliman 2019). Deterioration of coastal ecosystems will cause a concurrent loss of ecosystem services (James et al. 2023), such as efficient carbon storage capacity (Temmink et al. 2022) and coastal protection (Spalding et al. 2014). Because of thermal tolerance limits, population range shifts and mass mortality of coastal foundation species are expected under projected global change scenarios (Marbà et al. 2022; Saintilan et al. 2014). Furthermore, warming increases the frequency and intensity of heatwaves and storms (Knutson et al. 2010; Seidl et al. 2017), which may lead to declines (Serrano et al. 2021). Meanwhile, climate-induced poleward shifts of herbivores can lead to local changes in grazing pressure that can negatively impact coastal plants (Campbell et al. 2024; Vergés et al. 2016). Additionally, local impacts such as eutrophication due to urban and agricultural nutrient runoff (Horta et al. 2021) can cause loss through algal proliferation that results in light limitation in aquatic systems (Deegan et al. 2012). These factors that are often assessed singularly may interact and cause vegetation decline by compromising stability and thus ecological resilience (Gissi et al. 2021; Van Nes and Scheffer 2007). For example, temperate seagrasses weakened by eutrophication may be more vulnerable to heat stress (Pazzaglia et al. 2020), increasing the chance of meadow collapse.

Field-based methods testing the resilience of foundation species are rapidly developing. In particular, increasing evidence suggests that dynamic indicators, such as the recovery rate after a disturbance, can better serve to assess the resilience of an ecosystem than static indicators, such as cover or standing biomass (Cole et al. 2014; Ingrisch and Bahn 2018; Lam et al. 2017). It is rarely feasible to apply system-wide perturbations to experimentally assess resilience in vegetated habitats. Instead, measuring the recovery rate after a small-scale experimental perturbation can serve as a reliable indicator of ecosystem resilience (Scheffer et al. 2015; van de Leemput et al. 2018), where a low recovery rate after a physical disturbance may signal ecosystem vulnerability (Van Nes and Scheffer 2007). Disturbance and recovery experiments-mimicking pulse disturbances such as storms or anchoring damage (Oliver et al. 2015)-thereby provide a tool to determine the resilience of an ecosystem. In macrophyte-dominated marine ecosystems, the focus is often on measuring aboveground recovery (Castagno et al. 2021; Tassone et al. 2024). However, knowledge of belowground dynamics is key for understanding the resilience of these ecosystems (Nyman et al. 2006; Vonk et al. 2015) because belowground biomass includes the carbon reserves important for recovery potential (Campbell et al. 2024; Yang and Li 2022) and the rooting structure that provides stability and resistance to uprooting by waves and storms (De Battisti and Griffin 2022; Infantes et al. 2022). Therefore, both belowground dynamics and dynamic indicators such as recovery rates are essential to include in resilience assessments to conserve coastal ecosystems and to help build resilience in vulnerable ecosystems facing multiple threats.

The aim of this study is to investigate the effects of multiple key environmental drivers (temperature, light, nutrient availability, and grazing) that vary spatially and are expected to shift because of global change on the resilience of tropical foundational coastal ecosystems. Seagrass meadows, among the most threatened ecosystems worldwide (Dunic et al. 2021), were used as a model system. Since seagrass species traits, as well as the timing and temporal and spatial scale of the disturbance, play a large role in determining resilience (O'Brien et al. 2018; Sanmartí et al. 2021), we standardized these factors within a regionally coordinated experiment. Resilience to physical disturbances such as anchoring damage was assessed by measuring recovery rates of seagrass aboveground shoot abundance and biomass and belowground biomass after a small-scale pulse disturbance (complete biomass removal) across 10 sites in the subtropical-tropical Western North Atlantic, spanning $> 20^{\circ}$ of latitude. We focused on the foundational species turtlegrass (Thalassia testudinum), as its range extends over a large region in the Western North Atlantic and varying recovery times have been reported across studies that varied in site characteristics and their methodology (Dawes et al. 1997; Hammerstrom et al. 2007). We tested the effects of nutrient fertilization (mimicking chronic eutrophication) on seagrass recovery at each site, and also measured important environmental covariates (temperature, light, grazing pressure-both meso- and megaherbivores). Generalized linear mixed models were then used to assess the separate and interactive effects of fertilization and environmental covariates on ecological resilience.

2 | Material and Methods

2.1 | Study Site

This study was part of a larger coordinated research program, the *Thalassia* Experimental Network (TEN), which consisted of a series of sites across the geographic range of turtlegrass (*Thalassia*

testudinum) in the Western North Atlantic (9°N–32°N) (Campbell et al. 2024). At each site, seagrass meadows were selected based on the following criteria: (1) depth of <4 m, (2) dominated by turtlegrass (> 50% relative abundance), and (3) a minimum area of 25×25 m. Due to logistics, this experiment was performed at 9 out of the 13 sites that were part of TEN (Table S1, Figure 1A). To improve the latitudinal balance, we added one site that was not in the original network: Barcadera Bay, Aruba. Also, the original TEN site on Eleuthera became heavily grazed by turtles and was therefore not representative of the surrounding seagrass seascape (Smulders et al. 2023). Therefore, for this experiment, we established a second site (Eleuthera 2) outside of the grazed patch.

2.2 | Experimental Design

Ten experimental plots $(0.25 \times 0.25 \text{ m}, \text{ at least } 2\text{ m} \text{ apart in a})$ randomized design) were established at each site in the fall of 2018 (September-November, Table S1). In each plot, a disturbance was created by removing all above-and belowground biomass within a 15cm diameter circle, 20cm deep. After the biomass core was collected, the void was filled with local sediment, and bamboo skewers (~6 per plot) were used to mark the exact border where the biomass core was collected. Turtlegrass mainly recovers through clonal growth via elongation of horizontal rhizomes (van Tussenbroek et al. 2006). A replicated experiment was conducted at each site with two treatments, nutrient fertilized and unfertilized conditions (N = 5 plots per treatment). Every 2weeks to 2months (depending on logistics), the number of shoots regrown in the void was counted to investigate whether the shoot establishment rate was linear throughout the year. After about 1 year (10-14 months after disturbance) all biomass that had recovered within the marked void was collected.

Fertilization treatments were established by attaching a fiberglass mesh bag containing 300g of slow-release Osmocote fertilizer (Everris NPK 14:14:14) 30 cm above the sediment to a pole at a corner of each fertilized plot (N= 5), following (Campbell et al. 2024). Bags were replaced monthly to ensure consistent enrichment.

We set up control plots (0.06 m^2) directly surrounding the unfertilized plots (N=3). In these control plots, we assessed seagrass cover from photos taken both at the initiation of the experimental perturbation and at the end of the experiment. Due to high turbidity, this control procedure was not done at Galveston, but personal observations confirm no major changes in background seagrass cover during the experiment (pers. obs. JAG, ARA).

At the start and end of the experiment, all collected seagrass material was stored in a cooler and processed within 24h. The shoots were separated from the belowground biomass, leaves were scraped clean of epiphytes, and the above and belowground material were dried separately in an oven at 60° C. The number of foliar shoots within the core (= shoot abundance) was recorded as well as the dry weight of the above- and belowground biomass.

2.3 | Environmental Drivers of Seagrass Recovery

We measured several environmental factors at the site level as candidate drivers for seagrass recovery. Underwater loggers deployed in the seagrass canopy (HOBO UA-002064) recorded the water temperature every 6 min at each site. From these measurements, an average annual temperature was calculated, as well as its seasonality (SD of temperature among months). Light intensity was measured by a light sensor (Odyssey Submersible PAR Logger) deployed at the same location, with the same measuring interval and duration as the temperature loggers, and averaged annually. Ambient leaf N and P content was obtained



FIGURE 1 | (A) A map of our study sites (B) Seagrass shoot abundance recovery (% compared to pre-disturbance \pm SE) in unfertilized plots along a latitudinal gradient. Average annual water temperatures are visualized in color on the bar chart and on the map. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

by analyzing the green leaf tissue from the unfertilized (N=5)plots at the start of the experiment. Additionally, all green leaf material of both unfertilized (N=5) and fertilized plots (N=5)obtained at the end of the experiment was analyzed for N and P content. Dried leaf material was homogenized to a fine powder using a mortar and pestle. The ground leaf material was subsequently analyzed for nitrogen content on an elemental analyzer (Thermo Flash 1112) and for phosphorus content on an autoanalyzer (SKALAR San++) after a digestion using sulphuric acid and selenium (Novozamsky et al. 1983). Since sites may be either P- or N-limited (Fourqurean et al. 2023), we used an index to indicate the overall magnitude of nutrient limitation. The Limitation Index (LI) was calculated as the absolute deviation of ambient leaf molar N:P from the balanced 30:1 ratio (Campbell et al. 2024). LI indicates ambient nutrient availability, where higher LI values signal a larger degree of either N- or P-limitation.

We estimated both megaherbivore (turtle) and mesoherbivore (fish) grazing pressure per plot. Fish grazing on turtlegrass results in crescent-shaped bitemarks from the sides and top of the leaves (Figure S1). Therefore, fish grazing pressure was estimated by counting the average number of fish (crescent) grazing marks per shoot of (a maximum of) 10 shoots collected in each plot at the end of the experiment (fall 2019). Turtles crop the leaves from above, resulting in a straight cut (Figure S1). Therefore, turtle grazing pressure was estimated by calculating the proportion of leaf area that was removed in each of the plots relative to the mean leaf area of the unfertilized caged plots of the TEN experiment (Campbell et al. 2024). The outcome was validated by comparing it with known turtle abundances at the study sites (Pers. obs. LMRB, AMM, FOHS, SAM). We chose to estimate grazing pressure from seagrass leaves instead of measuring actual densities of fish and turtles near the study sites since herbivores do not always spread evenly over space and time, resulting in local heterogeneity in grazing pressure (Smulders et al. 2022, 2023).

2.4 | Data Analysis

We used multi-model inference to examine which local and across-site environmental factors were important for our recovery response variables, which were based on measured shoot abundance, aboveground biomass, and belowground biomass (Smulders et al. 2025). Because the timing of the end-harvest varied across sites (between 293 and 433 days after the start of disturbance), shoot abundance, aboveground biomass, and belowground biomass recovered at the end of the experiment were standardized (multiplied by experiment duration and divided by 365 days). For this, we assumed linear growth based on a recent overview (Tassone et al. 2024) and results of regression analysis at the site level. The median R^2 values of these linear regressions were 0.74 (range: 0.29-0.99; Table S2). We then calculated the percentage recovery as the ratio of the standardized plot-specific response variables to the pre-disturbance value, multiplied by 100.

Latitude and seasonality were both correlated with average annual temperature and therefore excluded from the main models (Table S3), and are presented in the Supporting Information S1 (Tables S5 and S6). Average temperature was selected over latitude and seasonality since it is the candidate driver reported to increase with global warming.

For all response variables (shoot abundance recovery, aboveground biomass recovery and belowground biomass recovery), we included the covariates "temperature," "fish grazing," "turtle grazing," "light" and "LI". The models also included fertilization as a fixed factor to observe any significant interactions between fertilization and fish herbivory, turtle herbivory, and LI (Eq. S1). We standardized our covariate values by subtracting the mean and dividing by the standard deviation. All covariates had variance inflation factors < 5, indicating low collinearity. We fitted the full models for all response variables using generalized linear mixed models (GLMMs) with site as a random effect and a Tweedie distribution used for continuous data with non-normal distributions and zero inflation (our response variables had between 13% and 26% zeroes and were tested for zero-inflation using the DHARMa package) using the glmmTMB package. All full models were examined for model fit by plotting the residuals versus the fitted values, the fitted values versus the observed data and the residuals versus the treatment "fertilization". The model fit, specifically the ability of the models to cope with the large numbers of zeroes, as well as outliers, dispersion and uniformity were tested using the DHARMa package. We ranked the resulting potential models with AICc using the "dredge" function in the MuMIn package in R. Because the top models were performing equally well, we performed model averaging to arrive at consistent parameter estimates of the most important explanatory variables in the full GLMM, by averaging a set of top models which share similarly high levels of parsimony (Table S7 for the selection of top models). We defined the top models as those that fell within 2 AIC units of the model with the lowest AIC value, as is recommended when factors may have weak interactions with the response (Grueber et al. 2011) with the model.avg. function in the MuMIn package, and we present the conditional averages. Standardized coefficient plots are visualized in Figure S3. For data visualization of aboveand belowground biomass recovery, we created a dataset using the "predict" function for each specific significant variable while the remaining variables were set at their average value.

To test whether fertilization increased leaf N and P content, we fitted a linear mixed effects model with a gaussian distribution (using glmmTMB) to plot-specific leaf N and P data, with site as a random effect and fertilization as a fixed factor. Model validation was conducted as described above.

To test the difference in the effect of the environmental factors on traditional static indicators versus dynamic indicators, we compared the response of static indicators: aboveground biomass (g DW m⁻²) and shoot density (shoots m⁻²) as measured before the experimental disturbance, to dynamic indicators: aboveground biomass recovery and shoot recovery percentages as obtained at the end of the experiment in the unfertilized plots (total of 50 plots). For shoot density and (log-transformed) aboveground biomass, linear mixed models were used, fitted with a gaussian distribution (using the lme4 package). Residuals were visually inspected using Q-Q plots and residual-versus-fitted plots, confirming approximate normality and homoscedasticity. For shoot and aboveground biomass recovery, we fit generalized linear mixed models with a Tweedie distribution as previously described (using glmmTMB). Model fit was assessed with the DHARMa package, and diagnostic plots indicated no major deviations from distributional assumptions.

To explore the variation in recovery rates irrespective of initial conditions, we first divided the end measurement of both aboveground and belowground biomass by the area of the created gap (0.018 m²) and then by the duration of the experiment. Additionally, the estimated time to full recovery was calculated as the ratio of the initial total biomass to the final total biomass, multiplied by the experiment duration and scaled to 1 year (divided by 365 days). Plots that showed zero recovery (12% of total plots, spread over five sites; Table S4) were removed for this calculation.

To investigate the relationships among the above and belowground seagrass recovery response variables, and to assess whether seagrass recovery was affected by initial conditions, we performed correlation analysis using Kendall's tau rank correlation with the "cor" function in R.

To test whether the seagrass cover at the site remained stable over the course of the experiment, we compared the control plots between the start and end of the experiment using pairwise *t*-tests with a Bonferroni correction. All data analyses were performed in R (v.4.2.2).

3 | Results

3.1 | Above- and Belowground Seagrass Recovery

Aboveground biomass recovery rates (calculated from biomass cores taken after 1 year of recovery) in unfertilized plots ranged 100-fold from 0.003 ± 0.001 (Bermuda) to 0.30 ± 0.06 (Bonaire)

g DW m⁻²day⁻¹ with an average of 0.06 ± 0.01 g DW m⁻²day⁻¹ (Figure 2A). Belowground biomass recovery rates per site ranged 10-fold from 0.04 ± 0.02 (Galveston, USA) to 0.42 ± 0.07 (Bonaire) g DW m⁻²day⁻¹, with an average of 0.19 ± 0.03 g DW m⁻²day⁻¹ (Figure 2B).

The average percentage of above- and belowground biomass recovered in the unfertilized plots after 1 year was lowest for Crystal River, USA, with 2.11% ±1.2 and 3.61±1.9, respectively, and highest for Bonaire with 195.88%±81.8 and 49.25±6.5, respectively. Comparing above to belowground responses per site and then averaging across sites, we found that belowground recovery rates (in g DW m⁻²day⁻¹) were 6.8 times higher than aboveground recovery rates, but the percentage of aboveground biomass recovered was, on average, 1.4 times higher than that of belowground biomass.

Additionally, we extrapolated the years needed to achieve full recovery (restoring the values to those of initial measurements). Years needed for full recovery (both above- and belowground) were lowest for Bonaire $(1.5\pm0.18$ years) and highest for Galveston $(13.7\pm3.16$ years), with an average of 4.3 years across all sites (Figure 2C).

The percentage of shoots and aboveground biomass recovered after 1 year was positively correlated with the percentage of belowground biomass recovered after 1 year (Kendall's tau rank correlation test, tau=0.41, p < 0.001 and tau=0.50, p < 0.001 respectively). Aboveground recovery was independent of initial conditions, while initial belowground biomass correlated negatively with the percentage of belowground biomass recovered (tau=-0.24, p < 0.001, Figure S4).

There was no difference in seagrass cover in the control plots between the start and end of the experiment.



FIGURE 2 | Boxplots of (A) aboveground and (B) belowground biomass recovery rates and (C) estimated total recovery time of turtlegrass in unfertilized plots in years. The order of the study sites corresponds to the latitudes from low latitude (bottom) to high latitude (top). Middle vertical lines of the boxes represent boxplot medians, left and right vertical lines represent the 25th and 75th percentiles, whiskers represent the smallest and largest measured values within the 1.5 interquartile range from the box and dots represent the outliers outside the interquartile range.

3.2 | The Effects of Fertilization and Environmental Factors on Seagrass Shoot Abundance Recovery

We found no effect of fertilization alone on the percentage of recovered shoots of turtlegrass after 1 year (Table 1). Across the geographic range of turtlegrass, the percentage of shoots recovered increased with temperature (p=0.03, standardized coefficient of 0.34) (Figure 1B and Figure S5). Significant interactions were observed between fertilization and both types of grazing pressure (fish and turtles). The percentage of recovered shoots increased with increasing fish grazing pressure in the unfertilized, but not in the fertilized plots (p=0.002). With increasing turtle grazing pressure in the fertilized plots, the percentage of recovered shoots decreased (p=0.013), while no relationship was found in the unfertilized plots. Fertilization therefore reduced shoot recovery at high grazing pressure for both types of grazers (see Figure S2 For trends in fish and turtle herbivory across sites).

Running the same set of models using seasonality and latitude instead of average annual temperature, we found that shoot abundance recovery decreased with seasonality, but not with latitude (Tables S5 and S6).

3.3 | The Effects of Fertilization and Environmental Drivers on Seagrass Above- and Belowground Biomass Recovery

Similar to shoot recovery, the percentage of aboveground biomass recovered increased with temperature (p = 0.001, std. coef. 0.45) (Figure 3, Table 1), and significant interactions were found between fertilization and grazing pressure. The positive relationship between fish grazing pressure and aboveground biomass recovery was reduced by fertilization (p < 0.001). Additionally, the positive relationship between turtle grazing pressure and aboveground biomass recovery was reduced by fertilization, resulting in a negative relationship (p=0.007). Aboveground biomass recovery decreased with latitude and with seasonality (Tables S5 and S6).

The percentage of belowground biomass recovered also increased with temperature (p = 0.009) (Figure 3, Table 1). Additionally, significant interactions were found between the nutrient limitation index (LI) and the fertilization treatment (p = 0.013) and between turtle grazing and the fertilization treatment (p = 0.022), indicating that fertilization decreased belowground biomass recovery when higher levels of nutrient limitation or turtle grazing were present. Belowground biomass recovery decreased with seasonality, but not with latitude (Tables S5 and S6).

One year after disturbance, total biomass recovery increased with temperature in a pattern similar to belowground biomass recovery (p=0.003) (Table 1). The standardized coefficients for temperature for total and belowground biomass recovery were 0.50 and 0.52, respectively, in the averaged models. Interactions were observed between LI and fertilization (p=0.015), as well as turtle grazing and fertilization (p=0.019). These interactions suggest that fertilization reduced total recovery rates under higher nutrient limitation or intense turtle grazing. While total

biomass recovery decreased with seasonality, it was unaffected by latitude (Tables S5 and S6).

Fertilization increased leaf N content (p < 0.001), but not leaf P content (p = 0.91) (Table 1) in seagrass leaves taken from biomass cores at the end of the experiment (see Figure S6 for trends in %N, %P, C:N and C:P across sites).

When we compared the response of static versus dynamic indicators to the environmental drivers, we found that temperature would not have been revealed as an important factor had we focused on static indicators (Table S8). None of the drivers had a significant impact on static shoot density.

4 | Discussion

The capacity of coastal ecosystems to recover after disturbances depends on various local environmental factors, most of which are increasingly affected by global change (Jones et al. 2021; Wernberg et al. 2010). Here, we evaluated the ecological resilience of a widespread (sub)tropical marine plant by measuring the response to a pulse disturbance across its geographic range and along gradients in environmental factors. Our results provide the first experimental evidence that both above- and belowground recovery of a marine plant increases with temperature after a disturbance. Specifically, we found that cooler temperatures at subtropical sites may limit resilience, increasing vulnerability to acute physical disturbances and potential for meadow collapse (Scheffer et al. 2015; van de Leemput et al. 2018). Fish and turtle herbivory influenced aboveground recovery, depending on local nutrient availability. We find that while rising temperatures may serve to increase the resilience of tropical species at the cool edge of their range, eutrophication and food web alterations may compromise the resilience to future disturbances anticipated under global change scenarios.

By measuring dynamic indicators, we found that a combination of temperature and the interaction between herbivory and fertilization drives the resilience of turtlegrass. Temperature increased recovery of seagrass shoot abundance, aboveground and belowground biomass recovery but did not affect the static indicator aboveground biomass. None of the measured environmental drivers significantly impacted the static indicator shoot density, which, along with cover, is commonly used as a seagrass response indicator (Nowicki et al. 2017; Tassone et al. 2024). These results add to the evidence that dynamic indicators respond differently to environmental factors than static indicators (Lam et al. 2017) and may thus better serve to predict responses of seagrasses to future disturbance (Connolly et al. 2018; Nowicki et al. 2017). Additionally, we found that aboveground biomass recovered 1.4 times faster than belowground biomass, indicating that aboveground biomass production is followed by belowground biomass recovery. We want to highlight that, unlike aboveground recovery, belowground biomass recovery correlated negatively with initial biomass conditions and responded differently to climate change-related drivers compared to shoot abundance and aboveground biomass recovery. Therefore, dynamic responses of aboveground variables may not reflect those of the whole plant, and we recommend incorporating dynamic measures of belowground parts to understand the health

Response	Factor	Estimate	SE	р
(A) Shoot recovery (% shoots compared to pre-disturbance) (4 top models)	Temperature	0.338	0.156	0.030*
	Fish grazing	0.296	0.119	0.013*
	Turtle grazing	-0.349	0.157	0.026*
	Turtle grazing:Fertilization	-0.340	0.137	0.013*
	Fish grazing:Fertilization	-0.253	0.081	0.002**
	LI:Fertilization	0.214	0.123	0.082
	Light	-0.115	0.134	0.391
	LI	-0.091	0.172	0.598
	Fertilization	0.014	0.010	0.890
(B) Aboveground biomass recovery (% g DW compared to pre-disturbance) (3 top models)	Temperature	0.448	0.139	0.001**
	Fish grazing	0.439	0.121	0.0003***
	Turtle grazing: Fertilization	-0.341	0.127	0.007**
	Fish grazing:Fertilization	-0.235	0.109	0.030*
	LI:Fertilization	0.139	0.135	0.299
	Fertilization	-0.018	0.112	0.874
	Turtle grazing	-0.005	0.146	0.970
(C) Belowground biomass recovery (% g DW compared to pre-disturbance) (10 top models)	Temperature	0.524	0.202	0.009**
	Turtle grazing:Fertilization	-0.235	0.103	0.022*
	LI:Fertilization	-0.221	0.089	0.013*
	Light	0.187	0.183	0.306
	Fish grazing	0.140	0.142	0.326
	LI	0.132	0.194	0.497
	Turtle grazing	-0.124	0.163	0.445
	Fertilization	0.044	0.098	0.647
(D) Total biomass recovery (% g DW compared to pre- disturbance) (13 top models)	Temperature	0.503	0.169	0.003**
	Turtle grazing:Fertilization	-0.233	0.010	0.019*
	LI:Fertilization	-0.216	0.089	0.015*
	Light	0.0190	0.141	0.179
	Fish grazing	0.196	0.139	0.160
	LI	0.091	0.157	0.560
	Turtle grazing	-0.081	0.142	0.570
	Fertilization	0.040	0.095	0.674
(E) % N (DW)	Fertilization	0.228	0.048	0.000002***
(F) % P (DW)	Fertilization	-0.001	0.010	0.905

TABLE 1 | Statistical results for averaged generalized linear mixed models testing the impact of fertilization treatments and environmental drivers on seagrass recovery and nutrient content.

Note: The number of top models ($\leq \Delta 2$ AICc) is reported, along with the coefficient estimates and standard errors of the standardized regressors. Temperature is the average yearly water temperature at canopy level. Turtle and fish grazing is a grazing index assessed from the leaves. LI is the nutrient limitation index. Light is the yearly average input of light in the system. Nutrient fertilization was simulated by adding both N and P to the water column. Since only one factor, fertilization, was tested against nitrogen and phosphorus content, model averaging was not performed on those two models. ***p < 0.001.

*p<0.05.



FIGURE 3 | Summary of the results of the averaged generalized linear mixed models for above and belowground biomass recovery (% compared to pre-disturbance). The line represents the average value of the model response, with the 95% confidence interval, and is plotted on top of the measured data points. Arrows point from an environmental factor to either above or belowground biomass recovery and indicate a positive (green) or negative (red) significant or neutral (black) impact on recovery rates either as main effect or in the interaction with fertilization (+ NP) based on the coefficients from the models where p < 0.05. For example, fish grazing pressure in nutrient enriched plots decreased aboveground biomass recovery relative to ambient conditions. Arrow letters correspond to the plots (A–F). Averaged model results are presented in Table 1.

and resilience of coastal foundation species (Lam et al. 2017; Sanmartí et al. 2021) and their adaptability to a changing environment (Cole et al. 2014), whenever possible.

The positive relationship between temperature and seagrass recovery contrasts with the negative effects of prolonged high temperatures that are regularly reported for seagrasses (Aoki et al. 2021; Strydom et al. 2020) and for other coastal foundation species (Smale 2020; Wernberg et al. 2010). While temperate seagrass meadows are especially vulnerable to warming (Marbà et al. 2022), turtlegrass, primarily found at tropical latitudes, may benefit from warming at the cool edges of its distribution. Previous studies suggest mild temperature increases enhance the seagrass photosynthetic rate (Lee et al. 2007) and shoot formation through clonal growth (Lee and Dunton 1996). However, beyond certain temperature thresholds, respiration can exceed photosynthesis, reducing growth rates (Nguyen et al. 2021) and overall resilience for species growing near the upper limits of their thermal distribution or in areas prone to heatwaves (Fraser et al. 2014; Marbà et al. 2022; Wiens 2016). Earlier work shows that T. testudinum can grow in temperatures of up to 35°C (Zieman 1975) with reported optimal temperatures ranging between 23°C and 31°C (Lee et al. 2007). Therefore, we assume that at our tropical sites, high temperatures were not yet limiting growth. However, continued increases in temperature may serve to compromise tropical species at the warm edge of their distribution as temperature optimums are more regularly exceeded. The relatively low recovery in Panama was unexpected since it was the site with the highest mean temperature. However, other studies have also shown compromised seagrass meadows at this site (Campbell et al. 2024), potentially driven by intensive agriculture from the surrounding watershed (Seemann et al. 2014). Our study suggests that within the examined temperature range, which did not include heatwaves, slight increases in mean annual temperature can enhance the recovery potential of subtropical seagrasses, just as has been found for salt marsh plants in a warming experiment (Smith et al. 2022). Experimental testing of increasing temperature impacts on subtropical seagrass resilience is needed to confirm the correlative relationships found in this study and to assess whether withinsite variations in temperature can also drive recovery rates.

Subtropical sites experience higher seasonality, due to low surface irradiance and temperatures in winter, and therefore shorter

growing seasons (van Tussenbroek et al. 2014). We found that higher annual temperature variability, similar to lower annual temperature, reduces recovery rates. A longer growing season due to ocean warming may therefore increase seagrass resilience at subtropical latitudes, depending on local grazing pressure and light and nutrient availability. Recent work has demonstrated that subtropical seagrasses in the Western North Atlantic are relatively sensitive to high grazing pressure compared to tropical seagrasses and that light can play a key role in regulating responses to overgrazing (Campbell et al. 2024). However, in this study, we found instead that temperature played a stronger role. One reason accounting for this distinction across studies may be the use of different plant metrics (leaf growth rates vs. whole shoot recovery). However, in sum, both studies document an increased vulnerability of tropical seagrasses at the cooler boundary of their range.

Our results highlight the importance of distinguishing types of grazers and their impact on seagrass recovery rates. Grazing pressure is expected to rise, especially in the subtropics, due to the indirect effects of rising temperatures on herbivore habitat range and metabolism (Vergés et al. 2016; Zarco-Perello et al. 2020). We found that fish grazing can positively impact aboveground recovery. The underlying mechanism could be that fish grazing stimulates compensatory growth (summarized by Valentine and Heck 2021). An alternative explanation is that, similar to terrestrial grasslands (Borer et al. 2014), grazing may open up the canopy, thereby increasing light availability for shoots from surrounding seagrasses to grow into the gap. Migrating herbivores from tropical to subtropical sites may therefore increase local meadow resilience, up to a grazing pressure limit where intensive grazing prevents regrowth (Bennett et al. 2015). However, the positive relationship between aboveground recovery and fish grazing was predominantly driven by high grazing pressure at the Bonaire site (Figure S2). This study did not assess herbivore densities. Therefore, to confirm the relationships found between grazing pressure and seagrass recovery, future studies should include both a broader range of sites with varying grazing pressures and measures of herbivore density. For larger herbivores such as green turtles, we found that grazing reduced the recovery in fertilized plots. At one of our sites on Eleuthera, heavy turtle grazing (Smulders et al. 2023) resulted in a > 50%reduction in shoot recovery compared to a nearby ungrazed site. Our results, combined with reports of increasing overgrazing events at subtropical sites in the Western Atlantic (Fourqurean et al. 2019; Rodriguez and Heck 2021) suggest reduced meadow resilience and ecosystem functioning in turtle-dense environments (Christianen et al. 2023; Gangal et al. 2021).

Theory suggests that the capacity of plant communities to recover after disturbances likely depends on local nutrient status (Boada et al. 2017; Wasson et al. 2017). In our study, fertilization reduced belowground biomass recovery in nutrient-limited plots, potentially because seagrass invests less in belowground tissues when nutrients are abundant (Campbell et al. 2024; Romero et al. 2006). Additionally, grazing by both turtles and fish reduced the aboveground recovery in fertilized plots, likely due to increased grazing pressure on nutrient-enriched leaves (Smulders et al. 2022). Fertilization-induced grazing pressure by turtles also decreased belowground recovery. Thus, highlatitude sites, currently less resilient due to temperature and seasonality effects, may become more vulnerable to consumer pressure fueled by eutrophication, as was found for other coastal wetlands (He and Silliman 2015). Intensive grazing has been found in other studies to affect belowground vegetation dynamics, including carbohydrate reserves (Campbell et al. 2024) and biomass (Christianen et al. 2014; O'Dea et al. 2022). The resulting reduction in biomass could then affect key ecological services such as shoreline protection, habitat provision for commercially valuable species, nutrient cycling, and carbon sequestration (Christianen et al. 2023; Fourgurean et al. 2023; James et al. 2020), and can lead to loss of entire seagrass meadows (Fourqurean et al. 2019; Gangal et al. 2021). Therefore, it is important to monitor how subtropical seagrasses respond to expected increases in temperature and grazing pressure to determine if they will be able to maintain resilience under an altered climate. We propose that management aiming to restore herbivorous fish and turtle abundances include repeated assessments of grazing pressure and nutrient mitigation strategies in order to maintain ecosystem resilience and thus important ecosystem services.

5 | Conclusions

Our study demonstrates that (1) temperature can increase (sub) tropical seagrass resilience at the cool edge of the range boundary, (2) eutrophication combined with fish or turtle herbivory can decrease seagrass meadow resilience, and (3) measuring belowground biomass in addition to aboveground biomass contributes to the understanding of the resilience of coastal foundation species. Dynamic indicators like recovery rate are more suitable for estimating ecosystem resilience than static indicators, and our findings underscore the value of replicated experiments across large environmental gradients. Ecologically based strategies are needed to enhance the resilience of coastal ecosystems and maintain their roles as ecosystem engineers in a changing world.

Author Contributions

Fee O. H. Smulders: conceptualization, data curation, formal analysis, funding acquisition, investigation, visualization, writing - original draft, writing - review and editing. Justin E. Campbell: conceptualization, formal analysis, funding acquisition, investigation, writing - original draft, writing - review and editing. Andrew H. Altieri: funding acquisition, investigation, writing - review and editing. Anna R. Armitage: investigation, writing - review and editing. Elisabeth S. Bakker: conceptualization, writing - review and editing. Savanna C. Barry: investigation, writing - review and editing. S. Tatiana Becker: investigation, writing - review and editing. Enrique Bethel: investigation, writing review and editing. James G. Douglass: investigation, writing - review and editing. Hannah J. van Duijnhoven: investigation, writing - review and editing. Jimmy de Fouw: investigation, writing - review and editing. Thomas K. Frazer: investigation, writing - review and editing. Rachael Glazner: investigation, writing - review and editing. Janelle A. Goeke: investigation, writing - review and editing. Gerrit Gort: formal analysis, investigation, writing - review and editing. Kenneth L. Heck: funding acquisition, investigation, writing - review and editing. Olivier A. A. Kramer: investigation, writing - review and editing. Ingrid A. van de Leemput: conceptualization, writing - review and editing. Sarah A. Manuel: investigation, writing - review and editing. Charles W. Martin: investigation, writing - review and editing. Isis G. Martinez López: investigation, writing - review and editing. Ashley M. McDonald: investigation, writing – review and editing. Calvin J. Munson: formal analysis, investigation, writing – review and editing. Owen R. O'Shea: investigation, writing – review and editing. Valerie J. Paul: funding acquisition, investigation, writing – review and editing. Laura K. Reynolds: investigation, writing – review and editing. O. Kennedy Rhoades: formal analysis, investigation, writing – review and editing. Lucia M. Rodriguez Bravo: investigation, writing – review and editing. Amanda Sang: investigation, writing – review and editing.

Yvonne Sawall: investigation, writing – review and editing. **Khalil Smith:** investigation, writing – review and editing. **Jamie E. Thompson:** investigation, writing – review and editing. **Brigitta van Tussenbroek:** investigation, writing – review and editing. **William L. Wied:** investigation, writing – review and editing. **Marjolijn J. A. Christianen:** conceptualization, funding acquisition, investigation, writing – original draft, writing – review and editing.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Dryad data repository at https://doi.org/10.5061/dryad.2280gb602.

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Supporting Information

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