



RESEARCH ARTICLE

Predation shapes invertebrate diversity in tropical but not temperate seagrass communities

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Abstract

1. The hypothesis that biotic interactions are stronger at lower relative to higher latitudes has a rich history, drawing from ecological and evolutionary theory. While this hypothesis suggests that stronger interactions at lower latitudes may contribute to the maintenance of contemporary patterns of diversity, there remain few standardized biogeographic comparisons of community effects of species interactions.
2. Using marine seagrasses as a focal ecosystem of conservation importance and sessile marine invertebrates as model prey, we tested the hypothesis that predation is stronger at lower latitudes and can shape contemporary patterns of prey diversity. To further advance understanding beyond prior studies, we also explored mechanisms that likely underlie a change in interaction outcomes with latitude.
3. Multiple observational and experimental approaches were employed to test for effects of predators, and the mechanisms that may underlie these effects, in seagrass ecosystems of the western Atlantic Ocean spanning 30° of latitude from the temperate zone to the tropics.
4. In predator exclusion experiments conducted in a temperate and a tropical region, predation decreased sessile invertebrate abundance, richness and diversity on both natural and standardized artificial seagrass at tropical but not temperate sites. Further, predation reduced invertebrate richness at both local and regional scales in the tropics. Additional experiments demonstrated that predation reduced invertebrate recruitment in the tropics but not the temperate zone. Finally, direct observations of predators showed higher but variable consumption rates on invertebrates at tropical relative to temperate latitudes.
5. Together, these results demonstrate that strong predation in the tropics can have consequential impacts on prey communities through discrete effects on early life stages as well as longer-term cumulative effects on community structure and diversity. Our detailed experiments also provide some of the first data linking large-scale biogeographic patterns, community-scale interaction outcomes and direct observation of predators in the temperate zone and tropics. Therefore, our results support the hypothesis that predation is stronger in the tropics, but also elucidate

some of the causes and consequences of this variation in shaping contemporary patterns of diversity.

KEYWORDS

biotic interactions hypothesis, diversity, invertebrates, latitude, predation, seagrass, *Thalassia*, *Zostera*

1 | INTRODUCTION

The latitudinal diversity gradient, with species richness peaking at low tropical latitudes, is among the most well-established patterns in ecology (Fischer, 1960; Hillebrand, 2004; Kinlock et al., 2018; Pianka, 1966). Stronger biotic interactions at lower latitudes have been proposed as a central mechanism to help explain both the evolutionary origin and ecological maintenance of the latitudinal diversity gradient and high tropical biodiversity (Dobzhansky, 1950; Mittelbach et al., 2007; Schemske, 2002; Schemske, Mittelbach, Cornell, Sobel, & Roy, 2009). For predation in particular, the strength and generality of a change in interaction strength with latitude are receiving increased empirical interest (Lavender, Dafforn, Bishop, & Johnston, 2017; Reynolds et al., 2018; Roslin et al., 2017; Sheppard-Brennand, Dworjanyn, & Poore, 2017), but standardized biogeographic comparisons remain few. We are also at the early stages of understanding community consequences of a change in interaction strength across latitude and the role of predation in shaping contemporary patterns of diversity (Freestone & Inouye, 2015; Freestone, Osman, Ruiz, & Torchin, 2011).

The mechanisms that underpin stronger effects of predators at lower latitudes also remain unresolved. Predator consumption rates, both species-specific and cumulative, may drive latitudinal change in predation pressure as much as or more than predator diversity, per se (Guidetti, 2007). Other mechanisms could also reinforce or mitigate interaction outcomes. For instance, prey recruitment can also vary with latitude and be orders of magnitude lower at lower latitudes (Connolly, Menge, & Roughgarden, 2001; Freestone, Osman, & Whitlatch, 2009). While predation at early life stages may reduce recruitment (Menge, 1991), high recruitment rates may also subsidize prey populations, moderating observed effects of even strong predation.

Seagrasses, complex ecosystems of conservation importance (Orth et al., 2006; Waycott et al., 2009), are ideal to test for differences in predator–prey interactions across latitude, the mechanisms that underlie them, and effects on patterns of diversity. As ecosystem engineers, seagrasses provide structurally complex foundation habitat for a rich biota, including a diversity of sessile invertebrates that grow on seagrass blades (Borowitzka, Lavery, & van Keulen, 2010). Predators are known to shape the structure and function of seagrass communities, and predation pressure in seagrass ecosystems can be stronger at lower latitudes (Bostrom & Mattila, 1999; Freestone et al., 2011; Heck & Wilson, 1987; Peterson, Thompson, Cowan, & Heck, 2001). More studies are needed, however, to

understand the geographic scope of predator–prey interactions in seagrass ecosystems across latitude, the underlying drivers of these interactions and the resulting consequences for patterns of diversity in ecological communities.

To test for biogeographic differences in predator–prey interaction outcomes, effects on contemporary patterns of diversity and underlying mechanisms, we focused on temperate, subtropical and tropical seagrass ecosystems, spanning 30° of latitude along the Atlantic coast of North and Central America. Using a suite of observational and experimental approaches, we tested the hypothesis that predation would be stronger in the tropics than in the temperate zone. To examine interaction strength, we explored the effect of predation on prey community abundance and diversity (i.e., interaction outcomes) at two spatial scales, as well as the intensity (i.e., frequency) of predation events. Specifically, we hypothesized that predation would have stronger effects on patterns of prey abundance and diversity in a tropical relative to a temperate seagrass ecosystem. To understand mechanisms underlying a change in interaction outcome with latitude, we hypothesized that (a) prey recruitment would be more strongly reduced by post-settlement predation in the tropics than the temperate zone; and (b) predator consumption rates would be higher in the tropics than in the temperate zone. Together, our tests of these hypotheses provide some of the first data linking large-scale biogeographic patterns, community-scale interaction outcomes and direct observation of predators in the temperate zone and tropics.

2 | MATERIALS AND METHODS

2.1 | Study system

Seagrass ecosystems provide an exceptional, and particularly timely, model for understanding biogeographic variation in predator–prey interaction outcomes and effects on prey diversity. With a distribution that spans temperate and tropical coastlines (Short, Carruthers, Dennison, & Waycott, 2007), seagrasses are one of the most broadly distributed marine foundation species. Seagrass epibionts, along with the seagrasses themselves, significantly contribute to coastal productivity and are important basal prey species in these ecosystems (Borowitzka et al., 2010). Seagrass habitat, however, is in global crisis, with rates of decline that rival losses to other foundation species such as coral (Orth et al., 2006; Waycott et al., 2009). The loss of key seagrass species can have dramatic effects on their associated

communities (Hughes, Williams, Duarte, Heck, & Waycott, 2009; Micheli, Bishop, Peterson, & Rivera, 2008), yet their invertebrate epibionts remain understudied, with only a few studies exploring diversity of this assemblage (Borowitzka et al., 2010). Using invertebrate epibionts on seagrasses to test our hypotheses also extends inference beyond research studies that use simplified model systems that lack the complexity of natural habitats (Freestone et al., 2011).

2.2 | Biogeographic comparison of seagrass communities across latitude

To examine biogeographic differences among seagrass communities, we collected seagrasses and the associated sessile invertebrates growing on the blades of the seagrass (e.g., ascidians, bryozoans, tube-building polychaetes, bivalves) from three regions along the western Atlantic Ocean and Gulf of Mexico: temperate New Jersey, USA (three sites; 39°N), subtropical Gulf Coast of Florida, USA (three sites; 26°N), and tropical Bocas del Toro, Panama (two sites; 9°N) (Appendix S1). Collections and experiments overlapped with the temperate and subtropical summer, when the majority of primary production and recruitment of sessile invertebrates occurs; growth and reproduction occur year round in the tropics. Seagrass beds were subtidal and shallow (<1 m at low tide). Seagrass composition varied among the regions; temperate seagrass beds were dominated by *Zostera marina*, and subtropical and tropical seagrass beds were dominated by *Thalassia testudinum*. We collected five seagrass samples at random per site from circular plots with a diameter of 30 cm separated by >1 m. Each sample consisted of ten blades of seagrass, *Z. marina* in New Jersey and *T. testudinum* in Florida and Panama. Morphological metrics (length, width) were recorded for each blade. Sessile invertebrate individuals growing on the leaf surface were enumerated and identified to the lowest taxonomic group possible using external diagnostic characteristics. Two metrics of diversity—taxonomic richness and a diversity index that accounts for both richness and relative abundance (Shannon–Wiener Index, hereafter diversity)—and numbers of individuals were calculated per sample.

2.3 | Predator exclusion experiments

To test the hypothesis that predation is stronger in the tropics than the temperate zone, we used predator exclusion experiments in seagrass meadows at two sites in temperate New Jersey, USA, and two sites in tropical Bocas del Toro, Panama (Appendix S1), using two treatment comparisons. A full cage with a mesh size of 1 mm (hereafter termed small mesh) was compared to two control treatments: a partial cage control (two sides and a top) with small mesh and a control with no cage. A full cage with a mesh size of 6.35 mm (hereafter termed large mesh) was compared to a partial cage control with large-mesh and the no-cage control. Since the no-cage control was shared between the two comparisons, we had a total of five treatments. The small-mesh cage was previously shown to exclude nearly

all predators in seagrass ecosystems, while the large-mesh cage still allows micro- and mesopredators (e.g., small crustaceans, flatworms, nudibranchs) access to the caged community (Freestone et al., 2011). These mesh sizes can therefore produce different results, particularly in regions such as the tropics where small predators can be important (Freestone et al., 2011). Partial cages are a procedural control to account for any artefacts of the cage itself beyond its effect on predator access.

These treatments were applied to circular plots of natural and artificial seagrass, interspersed at random within a contiguous seagrass meadow at each site. All plots were 30 cm in diameter, delineated by plastic landscape edging that was buried approximately 10 cm into the sediment, and were separated by >1 m. Clear mesh cages were attached to the edging, extended 50 cm above the sediment, and could be opened from the top for maintenance. To ensure that enclosures did not trap any predators, we removed all visible predators, applied slow-release insecticide to deter small crustaceans (Poore, Campbell, & Steinberg, 2009; Whalen, Duffy, & Grace, 2013) to all plots for six days prior to the onset of the experiment, and then maintained enclosures weekly (Appendix S2).

Artificial seagrass (Bostrom & Mattila, 1999) was used to standardize both a time frame for prey community development and substrate for invertebrates to control for differences in seagrass morphology among sites and regions. Artificial seagrass was fabricated from green polypropylene ribbons, 30 cm long and 4.7 mm wide, attached to plastic mesh that was staked onto the sediment surface within the circular plot. Artificial seagrass density was 30 blades per plot (based on natural seagrass shoot densities; Kennish, Haag, & Sakowitz, 2009), and blades were haphazardly arranged. Unlike natural seagrass that had an existing epibiont community when the experiment was initiated, artificial seagrass was deployed clean.

We deployed all five treatments on natural and artificial seagrass plots at two sites in New Jersey and two sites in Panama (Appendix S1). A smaller experiment consisting of three treatments (small-mesh full and partial cages and no cage) on natural seagrass was deployed at a third site in New Jersey. We replicated all treatments on natural and artificial seagrass 4–5 times per site for a total of 185 experimental plots.

After 8 weeks, we collected 10 natural or artificial seagrass blades at random from each plot. Morphological metrics (length, width) were recorded for natural seagrass. Invertebrate individuals were enumerated and identified to the lowest taxonomic group possible using external diagnostic characteristics. Taxonomic richness, diversity and numbers of individuals were calculated per seagrass sample (10 blades of seagrass).

2.4 | Recruitment and predator consumption rates

To quantify effects of predation on post-settlement recruitment rates, settlement panels were used as standardized collectors (Freestone et al., 2011) at three sites in New Jersey and two sites

in Panama (Appendix S1). Panels were fabricated from 100-cm² grey PVC that was abraded on one side to facilitate settlement by invertebrates. Panels were oriented horizontally, facing the sediment to reduce algae growth and facilitate invertebrate recruitment, and were elevated approximately 15 cm off the sediment with stakes. Three clean settlement panels were deployed with and without small-mesh cages and sampled with replacement every 2 weeks during the 8-week experimental period, for a total of four deployment rounds ($N = 24$) at each site. Prior recruitment studies showed that invertebrate abundances do not differ systematically between partial cages and no-cage panels (A. L. Freestone, unpublished data), and therefore, no-cage panels were used as the sole control. Cages were cleaned weekly. Upon retrieval every 2 weeks, individuals were enumerated and identified to the lowest taxonomic group possible.

To quantify predator consumption rates directly, invertebrate communities on five settlement panels per site were allowed to develop in the absence of predators (inside small-mesh cages) for 8 weeks and were then exposed to predation and monitored with video. Exposure experiments were conducted at three sites in New Jersey, two sites in Florida and two sites in Panama (Appendix S1). Clean panels were deployed, as in the recruitment study, at the onset of the 8-week predator exclusion experiments. Cages were cleaned weekly. At the end of the experimental period, the cages were removed to expose communities to predation. All exposed panels at a site were attached to large mesh in a vertical array that was secured into the seagrass bed with stakes. Panels were oriented vertically to increase the ambient light needed for filming. The array was then monitored using a Go Pro underwater video camera for 51–210 min during 3–5 separate morning and afternoon exposure intervals at each site. Exposures were conducted between 8 a.m. and 6.30 p.m. Cameras required sufficient ambient light, and therefore, only diurnal predators were observed. Panels that were not visible during exposures due to camera angle or poor visibility, including one afternoon deployment at one site in New Jersey, were excluded from analysis. In between exposure intervals, panels were caged to prohibit predation.

Videos were then used to quantify predator consumption rates on invertebrates. Each contact (e.g., fish strike) by a predator was recorded as a predation event. For analyses, an experimental unit was a single panel deployed for a continuous exposure interval. We were largely unable to detect predation events during exposure experiments at four sites, one site in Panama, one site in Florida and two sites in New Jersey (Appendix S1). This lack of observed predation occurred despite intensive sampling effort: only eight predation events were observed at these four sites during 62 panel exposures that were sampled for a total of 7,839 panel-minutes. Thus, we focused the analysis on the remaining three sites where predation was more common during exposures, including one site per region (Appendix S1; intervals ranged from 106 to 172 min). New Jersey data included 15 panel exposure experiments totalling 2,170 min, Florida had 13 panel exposure

experiments totalling 1,885 min, and Panama had 20 panel exposure experiments totalling 2,525 min.

2.5 | Data analysis

To understand broad biogeographic differences in seagrass communities, we first compared seagrass and invertebrate samples collected from uncaged natural seagrass in the three regions. Seagrass surface area and invertebrate abundance (i.e., numbers of individuals), taxonomic richness, and diversity per sample were compared among regions using mixed models with a fixed factor of region and a random factor of site nested within region. Seagrass surface area and invertebrate diversity data were analysed using ordinary least-squares mixed models, as appropriate for non-integer data. Integer data on numbers of individuals and richness were modelled using generalized linear mixed models (GLMM). For these and all subsequent GLMMs, AIC values were used to select among Gaussian, Poisson and negative binomial distributions with appropriate link functions. A negative binomial distribution with a log link function and a Gaussian distribution provided the best fit for numbers of individuals and richness data, respectively. To account for variation in numbers of individuals, richness and diversity that could be attributed to natural differences in the surface area of seagrass, surface area (cm²) of the 10 blades per sample was then included as an offset in the mixed models. Offsets are used to calculate the rate of increase in the dependent variable per unit increase of a known constant (here, surface area). Offsets were retained in models only when they improved model fit, as determined using AIC values. An offset was retained only for the model for numbers of individuals. Regional means were then compared with post hoc multiple comparison methods (Holm for GLMM, Tukey HSD for ordinary least squares). One-tailed tests were conducted for richness and diversity, which were hypothesized to be higher at lower latitudes in accordance with the latitudinal diversity gradient. Two-tailed tests were used for all other comparisons.

To test for regional variation in the responses of invertebrates to predators, we used planned contrasts to compare treatments with and without predator exclusions. Planned contrasts allow for the comparison of treatment groups that are identified a priori and provide a strong test for whether caged treatments differ from both the treatment and procedural controls. Response variables were invertebrate numbers of individuals, taxonomic richness and diversity. Planned contrasts compared the full cage treatment of each mesh size to the performance of the two controls (no-cage treatment and the respective partial cage treatment for each mesh size) in New Jersey and Panama. We hypothesized that predators would reduce invertebrate numbers of individuals, richness and diversity (*sensu* Freestone et al., 2011), so one-tailed tests were used in each case. Contrasts were performed on mixed models with fixed effects of region, treatment and region*treatment, and random effects nested within region of site and site*treatment.

Data for natural and artificial seagrass were analysed separately. For artificial seagrass, small- and large-mesh cage comparisons in New Jersey and Panama were tested in a single analysis. Because numerous replicates from the natural seagrass experiment at one site in New Jersey were lost, data for the small-mesh and large-mesh comparisons were analysed separately, using data from the remaining two New Jersey sites to compare against the two sites in Panama (Appendix S1). As described above, diversity data were analysed with ordinary least-squares mixed models, and data on invertebrate richness and individuals were analysed with GLMMs after a model selection procedure. Models for natural seagrass data were then tested with and without an offset for seagrass surface area for improved model fit. For the GLMMs, a negative binomial distribution with a log link function was used for numbers of individuals on both natural and artificial seagrass, a Gaussian distribution was used for richness on artificial seagrass, and a Poisson distribution with a log link function was used for richness on natural seagrass. An offset for seagrass area was retained only for the large-mesh treatment comparison of numbers of individuals on natural seagrass.

To understand the effect of predation on richness at a larger spatial scale, species accumulation curves were used to estimate regional richness (pooled among replicates and sites) for treatment groups. Sample-based species accumulation curves were calculated with observed species richness values and permuted 9,999 times to produce a mean ($\pm SD$) curve. Since accumulation curves did not level off in Panama, richness was rarified to a standard sample size for comparison.

Invertebrate recruitment data (i.e. total number of recruited invertebrate individuals per panel per 2-week period) were modelled using a GLMM with a negative binomial distribution and a log link function. The model included fixed effects of region and treatment, and the interaction. Random effects were site (nested within region), deployment round (nested within site and region) and site*treatment (nested within region). Treatment means in New Jersey and Panama were compared with a one-tailed Holm test for multiple comparisons to test the hypothesis that predation decreased recruitment.

Predator consumption rates (i.e., number of predation events per panel exposure) were compared among New Jersey, Florida and Panama with a GLMM with a negative binomial distribution and a log link. The model included a fixed effect of region, and random effects of panel and exposure interval, both nested within region. An offset of exposure duration was included in the model based on improved model fit to control for the number of minutes a panel was exposed. Regional means were compared using one-tailed tests to assess the hypothesis that lower latitude regions had higher predator consumption rates.

All mixed models were completed in R version 3.6.0 (R Core Team, 2019) using the lme4 version 1.1-21 package (Bates, Machler, Bolker, & Walker, 2015) and the glmmTMB version 0.2.3 package (Brooks et al., 2017). Contrasts and multiple comparisons in R were performed with the multcomp version 1.4-10 package (Hothorn,

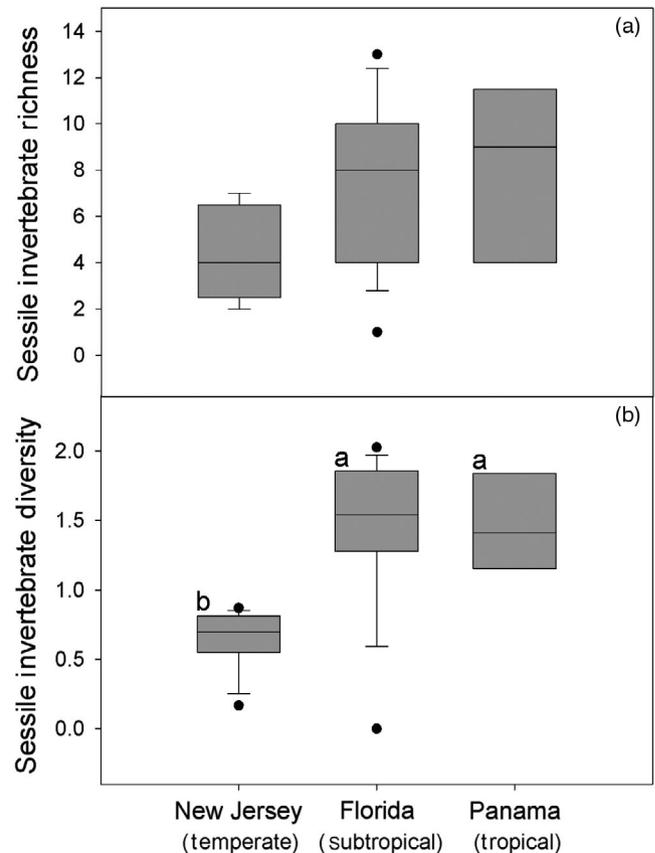


FIGURE 1 Sessile invertebrate (a) richness and (b) diversity (Shannon–Wiener Index; $R^2 = .59$, Region: $F_{2/5,347} = 8.37$, $p = .023$) per sample (10 blades) of natural seagrass in temperate New Jersey, subtropical Florida and tropical Panama. Data are pooled by region for three sites in New Jersey, three sites in Florida and two sites in Panama for visual comparison. Data are shown as box plots, with the lower boundary of the box indicating the 25th percentile, the line within the box indicating the median and the upper boundary of the box indicating the 75th percentile. The bars below and above the box show the 10th and 90th percentiles, respectively. Outliers are indicated with individual data points. Different letters above each box plot indicate significant differences in diversity among regions at $\alpha = .05$. No differences in richness were observed among regions

Bretz, & Westfall, 2008). Species accumulation curves were produced in PRIMER 6 v. 6.1.13.

3 | RESULTS

3.1 | Biogeographic comparison of seagrass communities across latitude

The sessile invertebrate communities observed were composed of solitary and colonial ascidians, cnidarians (i.e., anemones, hydroids), sabellid and serpulid worms, bivalves, bryozoans, barnacles and sponges. Diversity of sessile invertebrates collected at a local (i.e., plot) scale from uncaged natural seagrass in temperate New Jersey, subtropical Florida and tropical Panama showed

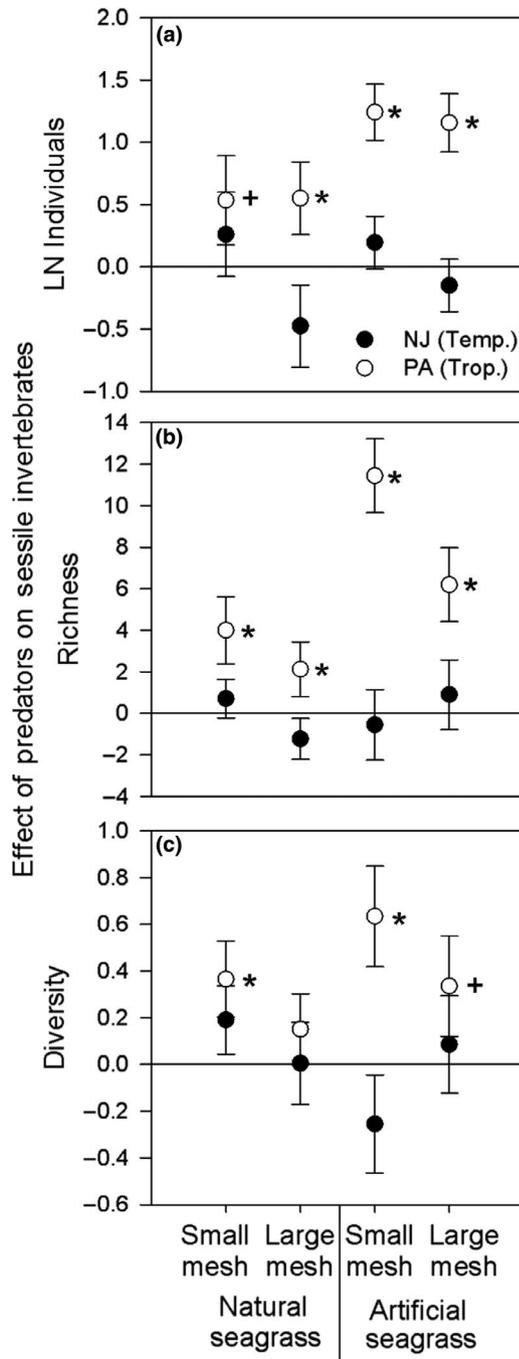


FIGURE 2 Effect of predators on sessile invertebrates as represented by differences (mean \pm SE) between full cage and control treatments (i.e., parameter estimates from mixed models) in (a) LN individuals, (b) richness and (c) diversity of invertebrates per sample (10 blades of seagrass). Filled circles represent temperate New Jersey (NJ), and open circles represent tropical Panama (PA). Significance tests indicate difference from zero (i.e., no effect of predation on an invertebrate variable within a region). Positive values indicate an increase in the variable in the full cages in comparison with controls. Symbols: (+) indicates trends in the data ($p < .1$) and (*) indicates significance at $\alpha = .05$

a weak relationship with latitude. Invertebrate richness at the plot scale did not differ among regions (Figure 1a), but diversity (expressed as an index) was higher in Panama and Florida than in New

Jersey (Figure 1b). *T. testudinum* provided greater seagrass surface area per plot and harboured a much lower density of invertebrate individuals in Florida and Panama than *Z. marina* did in New Jersey (Appendix S3 and S4).

3.2 | Predator exclusion experiments

Predator exclusion generally increased invertebrate abundance, richness and diversity in Panama, with no effect in New Jersey (Figure 2). For natural seagrass in Panama, numbers of individuals were higher in large-mesh enclosures than controls, with small-mesh enclosures producing a more modest marginal increase. Both types of enclosures on natural seagrass in Panama had higher invertebrate richness, and small-mesh enclosures were also more diverse than controls. For artificial seagrass in Panama, both types of enclosures had more individuals and higher invertebrate richness than controls. Enclosures on artificial seagrass in Panama also resulted in more diverse invertebrate communities, with stronger effects observed with the smaller mesh size. In contrast to Panama, however, predator exclusion had no effect on invertebrate communities in New Jersey. No treatment effects on individuals, richness or diversity on natural or artificial seagrass were observed in New Jersey.

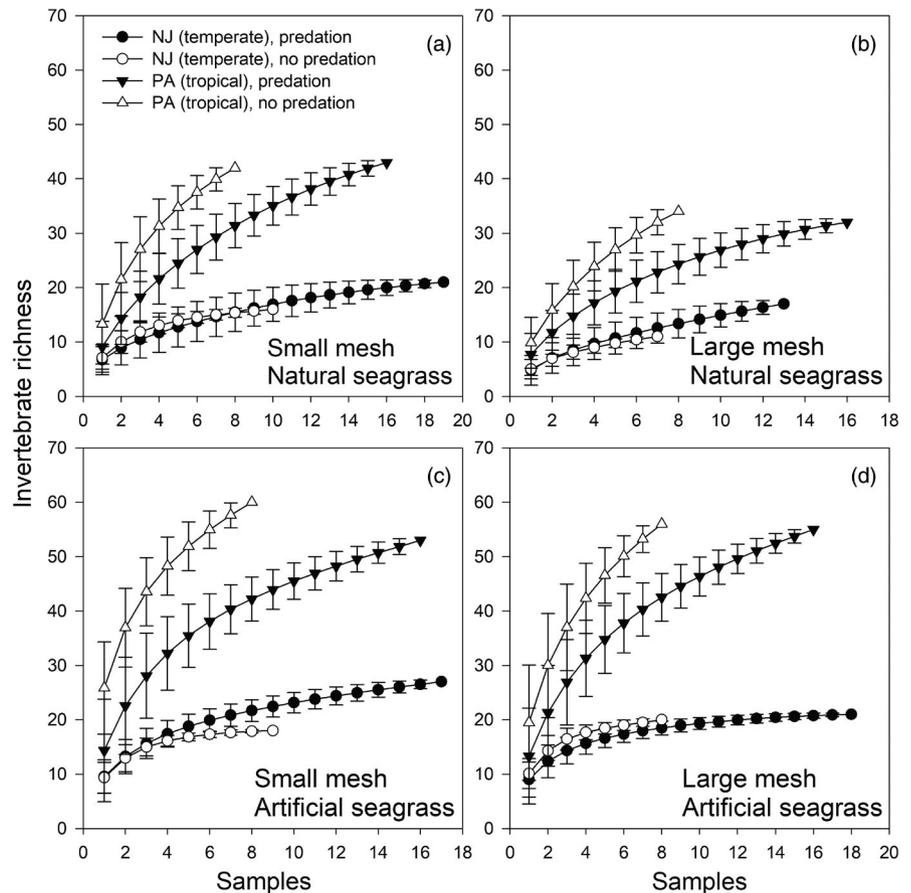
Predator exclusion also increased regional richness of invertebrates on natural and artificial seagrass in Panama, but not New Jersey (Figure 3). When regional richness was rarified to seven samples for all treatment groups, richness was nearly identical between full cage and control treatment in New Jersey, with mean treatment differences ranging from 0.4 to 3.2 taxa. In Panama, however, regional richness was always substantially higher in full cage treatments than controls, with mean treatment differences ranging from 9.2 to 17.3 taxa. Therefore, across all treatment comparisons, the mean effect of predator exclusion on regional richness was 7.5 times greater in Panama than in New Jersey. Regional richness patterns were also consistent with the latitudinal diversity gradient, with regional richness in Panama being consistently greater than in New Jersey.

3.3 | Recruitment and predator consumption rates

The recruitment rate of all taxa over 2-week intervals was two to three orders of magnitude higher in temperate New Jersey than tropical Panama (Figure 4a). These experiments were conducted during the peak recruitment season in the seasonal temperate zone, however, and recruitment in the temperate zone tapers off substantially at other times of year (A. L. Freestone, unpublished data). Therefore, the results do not imply annual recruitment rates. While post-settlement predation did not affect recruitment in New Jersey (Figure 4b), predation reduced recruitment in Panama (Figure 4c).

Predator exposure experiments demonstrated higher predator consumption rates (predation events/minute) in Panama than in

FIGURE 3 Invertebrate species accumulation curves for experimental plots in temperate New Jersey (circles) and tropical Panama (triangles), comparing small-mesh treatments and controls on (a) natural and (c) artificial seagrass, and comparing large-mesh treatments and controls on (b) natural and (d) artificial seagrass



New Jersey (Figure 5). A total of 33 predation events were observed in New Jersey, 112 in Florida and 258 in Panama. The observed predator guild in all three regions included fish, but also grass shrimp (*Palaemonetes pugio*) in New Jersey, and crabs in New Jersey and Panama. Most events in all three regions were discrete strikes by fish (Florida and Panama) or shrimp (New Jersey), but grazing events also occurred sometimes extending for several minutes.

4 | DISCUSSION

Across our study regions, predators shaped sessile invertebrate diversity more strongly in the tropics than in the temperate zone. Predation reduced local abundance, taxonomic richness and diversity of invertebrates in seagrass communities in the tropical but not the temperate region. Furthermore, predation shaped patterns of invertebrate richness not only at the local scale but also at the regional scale in the tropics. These results were largely consistent on both natural and artificial seagrass and for both predator exclusion mesh sizes. Furthermore, taxonomic richness was broadly consistent with known scale-dependent patterns of the latitudinal diversity gradient, with more striking differences among biogeographic regions emerging at regional rather than local scales (Hillebrand, 2004; Kraft et al., 2011; Witman, Etter, & Smith, 2004). These data were collected in a complex and ephemeral natural habitat across sites and biogeographic regions that varied not only in latitude, but other

important ecological characteristics as well, including the dominant species of seagrass, the composition of the predator and prey communities, and abiotic conditions. Given this natural variability, it is noteworthy that these results are consistent with both theoretical expectations (Mittelbach et al., 2007) and prior experimental studies on simplified model systems that span broader latitudinal gradients (Freestone & Osman, 2011; Freestone et al., 2011; Rodemann & Brandl, 2017; Roslin et al., 2017), demonstrating the potential generality of these patterns.

Consistent with prior studies (Freestone et al., 2011), we found that strong predation in the tropics can decrease diversity in a given habitat over ecological time, and our results are consistent with an emerging conceptual model for larger-scale coexistence in the bio-diverse tropics. While predation can increase diversity through the control of competitive dominants (Paine, 1966), in our study, predation limited the local distribution and abundance of prey species in seagrass ecosystems in the tropics. With predation limiting local diversity of prey, regional diversity of prey in the tropics is likely maintained by spatial and temporal variation in composition among local communities. In the tropics, seagrass blades that were exposed to predators (control treatments) harboured a rich diversity of invertebrates; however, an even greater diversity was present in refugia (full cage treatments) at both local and regional scales. Indeed, the reduction of regional richness by predators was 7.5 times greater in tropical Panama than temperate New Jersey. Given the structural complexity of seagrasses and their associated species, it is likely that

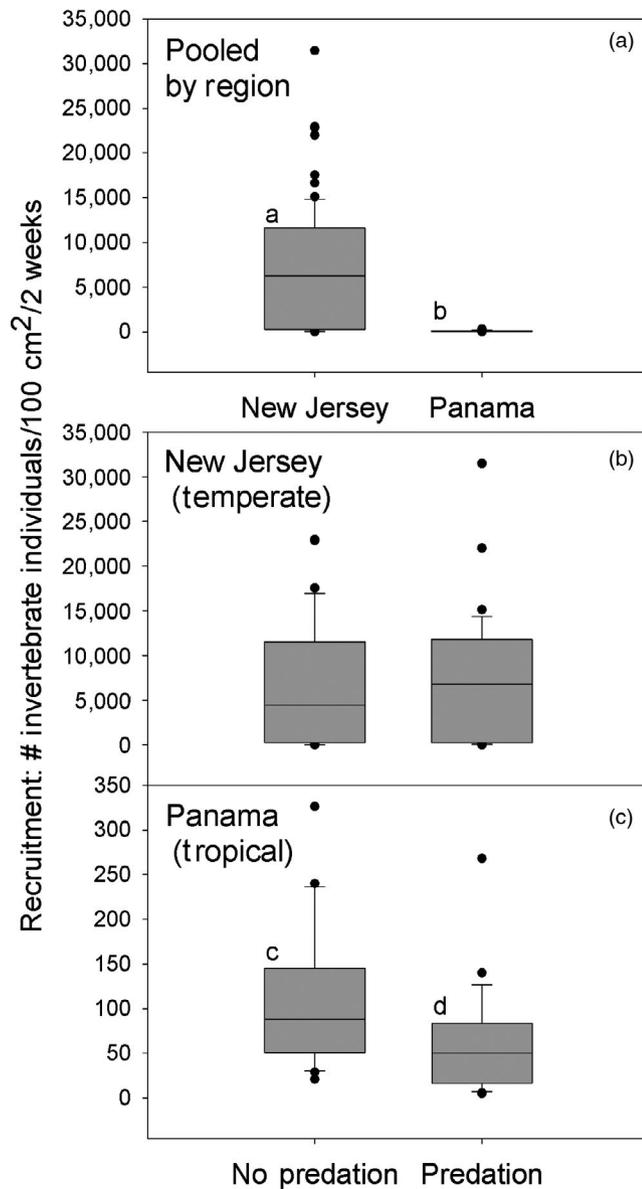


FIGURE 4 Number of invertebrate recruits on 100-cm² settlement panels per 2-week interval (a) in temperate New Jersey and tropical Panama (control and caged panels are pooled by region), and (b, c) observed in the presence (control panels) or absence (caged panels) of predators in each region. Data were collected in four consecutive 2-week intervals at two sites per region, but data are pooled by region for visual interpretation. Each data point represents recruitment on one panel deployed for 2 weeks. Data are shown as box plots, with the lower boundary of the box indicating the 25th percentile, the line within the box indicating the median, and the upper boundary of the box indicating the 75th percentile. The bars below and above the box show the 10th and 90th percentiles, respectively. Outliers are indicated with individual data points. Different letters above each box plot indicate significant differences at $\alpha = .05$. Overall, New Jersey had higher recruitment than Panama (panel a, χ^2 region: 4.202, $p = .04$). While predator exclusion treatments had no effect on recruitment in New Jersey (panel b), recruitment was higher in predator exclusions than in controls in Panama (panel c, $t = 3.83$, $p = .0002$)

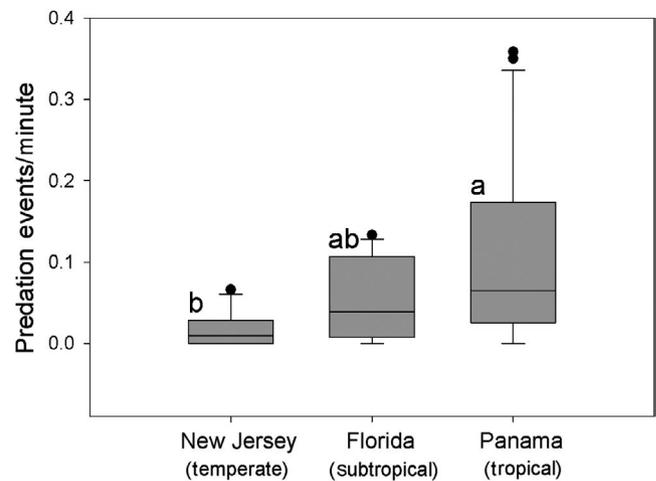


FIGURE 5 Predation events per minute for each of the three regions. Data are from one site per region where sufficient predator activity was observed. Each data point represents predation observed on invertebrates on a settlement panel during a single predator exposure ($N = 48$). Data are shown as box plots, with the lower boundary of the box indicating the 25th percentile, the line within the box indicating the median, and the upper boundary of the box indicating the 75th percentile. The bars below and above the box show the 10th and 90th percentiles, respectively. Outliers are indicated with individual data points. Different letters above each box plot indicate significant differences at $\alpha = .05$. Predation events/minute were higher in Panama than New Jersey ($p = .02$)

ample microhabitats exist in nature that are protected from predation, thereby providing refuges for predator-susceptible species and increasing regional diversity (Freestone et al., 2011; Freestone & Osman, 2011). Patchy distributions of predators and prey (Sheppard-Brennand et al., 2017) and uneven impacts of specialist predators (Mittelbach et al., 2007; Schemske, 2002) are likely to further contribute to compositional variability among prey communities in the tropics. In sessile marine invertebrate communities, non-random community assembly, which can result from strong predator-prey interactions, can drive higher community variability (i.e., beta diversity) in tropical environments and contribute to regional coexistence (Freestone & Inouye, 2015). Therefore, we predict that local and biogeographic variation in predation pressure is likely to have fundamental importance to the maintenance of multiscale patterns of diversity.

While predators shaped invertebrate epibiont diversity on natural seagrass in the tropics, results were sometimes stronger on artificial seagrass. Epibiont communities are inherently ephemeral, settling on seagrass blades as they emerge, grow and ultimately senesce. Integrity of leaf tissue can vary, even within a single blade, due to herbivore damage or physiological deficiency. Blades also vary in size and density, and these characteristics can also vary in time as the seagrass grows or senesces. Therefore, seagrass as a substrate is spatially and temporally heterogeneous. Artificial seagrass, in comparison, while structurally complex like natural seagrass, provided a standardized substrate that controlled for differences in morphology, history and substrate condition. Also, while natural seagrass had an epibiont community present at

the onset of the experiments, artificial seagrass were deployed clean. Therefore, any effects of the predator enclosure experiment on natural seagrass were overlaid on a backdrop of existing substrate and epibiont variability, perhaps resulting in more noise in the data and a weaker treatment signal. Nonetheless, even with this background variability, predation had a measurable effect on invertebrate communities on natural seagrass in the tropics.

Our detailed experiments also yielded novel insight into mechanisms that underlie predator–prey interaction outcomes. First, we examined patterns of initial (post-settlement) prey recruitment. We found that summer recruitment rates were orders of magnitude greater in temperate New Jersey than tropical Panama. The low recruitment rates observed in tropical Panama in comparison with temperate New Jersey may be the result of strong predation on planktonic invertebrate larvae in the tropics, combined with stronger selective pressure at high latitudes for accelerated reproduction during the comparatively shorter growing season (Dobzhansky, 1950; Menge, 1991). High recruitment rates in New Jersey may offset any losses of individuals to predators during early life stages or may swamp predators resulting in dampened observed effects. We further demonstrated, however, that predators decreased recruitment rates in our tropical, but not in our temperate region. The effect of predators on recruitment rates in Panama coupled with our other experimental results suggests that predation at the recruitment life stage in the tropics likely contributes to strong effects on invertebrate communities over longer periods of time. Since invertebrate individuals at later life stages in the tropics can also undergo strong predation pressure (Freestone et al., 2011), the effect of predators on community diversity and structure is likely an aggregate effect of mortality at multiple life stages, beginning at settlement or even before.

To complement experiments on interaction outcomes, we also used a separate experiment to directly document predator consumption rates. The hypothesis of stronger predation in the tropics has a rich history, but many studies explore effects of predators using enclosure experiments rather than direct observations of predator activity. We combined both approaches to develop a deeper understanding of how these interactions unfold in nature. We found higher predator consumption rates on invertebrate communities in the tropics, which likely underlie the stronger cumulative effect of predators on community assembly and further support the hypothesis that predation is stronger in the tropics. While our predator data are limited to diurnal time periods and a single site per region (once sites with insufficient observed predator activity were omitted), and conclusions must be drawn with caution, the patterns are intriguing. Our direct observations suggest that strong predation can result from a relatively low number of species (and possibly individuals) that have high consumption rates, despite the strong likelihood of a diverse predator community in the tropics given the generality of the latitudinal diversity gradient (Hillebrand, 2004). Out of the 258 diurnal predation events observed at the site in Panama, nearly all (234 events) were by four-eye butterflyfish (*Chaetodon capistratus*). Indeed, occurrence patterns of key predator taxa, along with different functional traits of prey, can influence spatial variability

in predation outcomes (M. Repetto, D. Lopez, A. Freestone, unpublished data). We present predator consumption rates of the predator guild as a whole due to the difficulty of assessing per capita rates with fixed-area video (as unmarked individuals leave and re-enter the field of view), but per capita rates may also be higher in the tropics given the expectation of increased metabolic activity in warmer ocean waters (Iles, 2014). Nearshore predation rates, however, can be more strongly predicted by annual mean temperatures than in situ temperatures at the time of predation assays, suggesting the interaction between predation and temperature may be more complex than simply increased metabolic demands (Reynolds et al., 2018). Field observations and data presented here suggest, however, that predator activity can be quite spatially and temporally variable in the tropics. Therefore, while strong cumulative effects of predators over time in the tropics may be common, predation at any single location or point in time may be difficult to predict.

5 | CONCLUSIONS

Invertebrate communities are an important component of the diverse and complex seagrass ecosystem, which is the base of economically important food webs (Heck, Hays, & Orth, 2003). Invertebrate diversity in this system was shaped more strongly by predators at our tropical sites relative to our temperate sites. The effect of predation started at early stages of community assembly and manifested in aggregate differences in more mature communities over the experimental period. High consumption rates by key predator taxa likely underlie strong cumulative effects of predators on prey community diversity in the tropics. Therefore, biogeographic differences in the nature and outcome of species interactions represent important ecological mechanisms that shape contemporary patterns of diversity.

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AUTHORS' CONTRIBUTIONS

A.L.F., G.M.R. and M.E.T. conceived the ideas; A.L.F. designed methodology; A.L.F., K.J.P. and E.W.C. collected the data; A.L.F. and B.J.S. analysed the data; A.L.F. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Data Repository: <https://doi.org/10.5061/dryad.kh189321p> (Freestone et al., 2019).

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SUPPORTING INFORMATION

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