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The biogeography of invasion in tropical and temperate seagrass beds: Testing interactive effects of predation and propagule pressure

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Abstract

Aim: Recent work has documented latitudinal gradients of biotic resistance, revealing diminished invasion success in the tropics as compared to the temperate zone. However, no studies have explored the biogeography of biotic resistance simultaneously with propagule pressure, which can greatly influence invasion dynamics and covary with latitude.

Location: 9–41° latitude, north-western Atlantic seagrass beds.

Methods: We conducted field experiments to test the interactive effects of propagule pressure (experimentally placed recruits) and biotic resistance (predation) on invader performance in temperate and tropical seagrass beds. For these experiments, we used marine invertebrate propagules from bryozoans (*Bugula neritina*) and tunicates (*Didemnum* spp.). We also quantified natural recruitment with and without exposure to predators.

Results: Surprisingly, predation substantially reduced invader survival at almost all latitudes. Overall, invaders experienced 15%–27% survival with predation as opposed to 75%–87% survival without predation. These patterns did not change when we increased local scale propagule pressure of *Bugula* by over 2-fold. However, predation had no effect on invader survival in Florida, where natural recruitment was up to 500-fold greater than other sites. We also measured substantial in situ recruitment of *Bugula* onto bare experimental surfaces that was not diminished with exposure to predators at mid-latitudes, suggesting a regional scale predator swamping effect.

Conclusions: Contrary to recent findings of latitudinal variation in biotic resistance, we found that predation strongly reduced invader success in both temperate and tropical seagrass beds. However, our results also indicate that propagule pressure (natural recruitment) can influence invasion at the regional scale to overwhelm native communities. Our data suggest that predation and propagule pressure act at varying spatial scales to affect biogeographic patterns of invasion. The importance of latitudinal variation in these interactions is largely untested but deserves attention given that globalization will continue to facilitate opportunities for invasion.

KEYWORDS
biogeography, biotic interactions hypothesis, biotic resistance, invasion, latitude, propagule pressure

1 | INTRODUCTION

The observation that species richness increases towards the equator is one of the most established patterns in nature (Hillebrand, 2004; Pianka, 1966). This latitudinal diversity gradient (LDG) is thought to be partly maintained by stronger species interactions in the tropics relative to temperate and polar zones ("biotic interactions hypothesis"; Mittelbach et al., 2007; Schemske, Mittelbach, Cornell, Sobel, & Roy, 2009). Strong species interactions in the tropics may contribute to the LDG by increasing rates of specialization and coevolution, and ultimately speciation (Schemske et al., 2009; Fine, 2015; but see Moles & Ollerton, 2016). A corollary of the biotic interactions hypothesis is that strong species interactions and a diversity of enemies (e.g., predators) in the tropics may also contribute to biotic resistance, the ability of native communities to reduce invasion by non-native species (Elton, 1958). Tropical biotic resistance may arise from diverse communities that are complementary in their resource use or predator hunting mode (Harvey, White, & Nakamoto, 2004; Stachowicz, Whitlatch, & Osman, 1999). Consistent with this view is the observation that introduced species richness declines in the tropics for many taxa (Hewitt, 2002; Sax, 2001). Over biogeographic scales, meta-analysis of biotic resistance suggests greater resistance from native predators and competitors at lower latitudes (Kimbro, Cheng, & Grosholz, 2013). Direct measurements from field experiments also demonstrate that predation by native communities greatly diminished non-native species richness in tropical sites relative to temperate sites (Freestone, Ruiz, & Torchin, 2013). However, herbivory on invasive plants was invariant across latitude in North American marshes (Allen et al., 2017; Cronin, Bhattarai, Allen, & Meyerson, 2015). Similarly, meta-analyses of birds and freshwater communities revealed that biotic resistance had no relationship with latitude (Alofs & Jackson, 2014; Blackburn & Duncan, 2001). These findings parallel the mixed support for stronger species interactions in the tropics (Coley & Barone, 1996; Moles, Bonser, Poore, Wallis, & Foley, 2011; Moles, Wallis, et al., 2011; Pennings & Silliman, 2005; Poore et al., 2012; Roslin et al., 2017; Schleuning et al., 2012). Thus, a clear understanding of mechanisms driving biogeographic variation in biotic resistance and species interaction strengths remains elusive.

A key gap in our understanding of these biogeographic patterns of biotic resistance is the role of propagule pressure, the intensity and frequency of arriving non-native recruits into the recipient community. Intense propagule pressure may overwhelm resistance from native consumers and competitors, swamping enemies with propagules and facilitating the colonization of non-native species (Lockwood, Cassey, & Blackburn, 2005; Simberloff, 2009; Williamson, 1996). Specifically, a large number of propagules (individuals per event) increase the probability that a colonizing population persists by counteracting demographic stochasticity or overcoming Allee effects. Greater propagule frequency (number of arrival events per unit time) reduces the probability of local extinction due to biotic and abiotic forces, diminishing the effect of environmental stochasticity. Propagule pressure may also overcome founder effects characteristic of non-native introductions and increase adaptive genetic variation that facilitates population establishment and proliferation (Roman, 2006; Saltonstall, 2002).

When tested together, the effects of propagule pressure and biotic resistance on invasion success remain unclear. Experiments have revealed that greater propagule pressure generally increases invasion success, whereas biotic resistance reduces invasion success in microbial and marine communities (Hedge, O'Connor, & Johnston, 2012; Jones, Ramoneda, Rivett, & Bell, 2017). On the other hand, propagule pressure can simply overwhelm biotic resistance from native communities, a pattern observed in both terrestrial and marine systems (Clark & Johnston, 2009; Hollebone & Hay, 2007; Thomsen, D'Antonio, Suttle, & Sousa, 2006; Von Holle & Simberloff, 2005). However, many of these studies were conducted in temperate or disturbed habitats that likely possess diminished species richness relative to tropical locations and perhaps a limited capacity for biotic resistance. The importance of propagule pressure and biotic resistance is unknown when considered across communities that substantially vary in species diversity, such as along latitudinal gradients. Broad scale experiments testing the role of propagule pressure and biotic resistance are needed to develop a mechanistic understanding of how these processes contribute to the ecological dynamics of invasion and explain patterns of community assembly at global scales.

One issue arising in biogeographic tests of biotic resistance and propagule pressure is that natural recruitment often covaries with latitude. For example, forest communities at higher latitudes of eastern North America recruit up to three times more trees than at lower latitudes (Godoy, Rueda, & Hawkins, 2015). Marine invertebrates also exhibit a seasonal, large recruitment pulse in high latitudes, whereas low latitudes produce a lower year-round recruitment signal (Connolly, Menge, & Roughgarden, 2001; Freestone, Osman, & Whitlatch, 2009). This covariation in recruitment regime can confound biogeographic observations of species interaction strength and resistance to invasion. Field experiments have the potential to address this covariation by manipulating propagule supply at the local scale, controlling propagule pressure within experiments (Von Holle & Simberloff, 2005). Ideally, this should be complemented with measurement of in situ regional recruitment rates to provide a more thorough assessment of biotic resistance and propagule pressure effects across latitude.

Despite the recognized importance of both biotic resistance and propagule pressure as mechanisms influencing invasion success (Hedge et al., 2012; Jeschke, 2014), to our knowledge, no study has measured their potential for interactive effects across a biogeographic scale. To address this, we used a comparative-experimental approach (sensu Menge et al., 2002), where we conducted replicated field experiments from 9 to 42° latitude in seagrass beds of the north-western Atlantic Ocean. Seagrass beds are a useful system for study because they are globally distributed in coastal zones and often located within or near estuaries with high invasion pressure from anthropogenic activities (Ruiz, Fofonoff, Carlton, Wonham, & Hines, 2000). Seagrass has also been used to examine biogeographic patterns of species interaction strength and the dynamics of community assembly (Duffy, Reynolds, et al., 2015; Reynolds et al., 2018). In this study, we tested the importance of biotic resistance (in the form of predation), propagule pressure and latitude in a series of manipulative field experiments that measured survival and performance of the non-native bryozoan *Bugula neritina* and two tunicates in the genus *Didemnum*. Our aims were to experimentally (a) quantify the effect of predation and propagule pressure on invasion across a latitudinal gradient and (b) measure naturally occurring recruitment of these species with and without exposure to predators.

2 | METHODS

2.1 | Study species and experimental preparation

We used the arborescent bryozoan *Bugula neritina* (hereafter *Bugula*) as a focal non-native species. *Bugula* is a useful model for tests of biotic resistance over large spatial scales because it is common and widely distributed in coastal marine systems (Mackie, Keough, & Christidis, 2006). *Bugula* is cryptogenic in the Caribbean and most likely introduced to the western north Atlantic (Fofonoff, Ruiz, Steves, Simkanin, & Carlton, 2018). Further, *Bugula* is amenable to experimentation because reproductive maturity can be rapidly assessed with visual examination, propagule release is easily achieved with light shocking, and the non-feeding larvae are competent to settle within a few hours (Clark & Johnston, 2005; Marshall, 2008). To complement experimental manipulation of *Bugula*, we also tested the colonization ability of two colonial tunicate species within the genus *Didemnum*. Few sessile marine species fully range throughout tropical and temperate oceans (*Bugula* is a rare exception), and the transplantation of non-native invertebrates with dispersive larval stages to new locations in marine systems is problematic. Therefore, we used non-native, congeneric and functionally similar *D. psammatodes* in the south (Panama, Belize and Florida) and *D. vexillum* in the north (Connecticut). This congeneric approach has long been used in biogeographic tests of species interaction strength in both terrestrial and marine systems when a single prey species is not distributed throughout the experimental domain (Jeanne, 1979; Pennings et al., 2009; Reynolds et al., 2018). Neither *Didemnum* species is found in Virginia (Fofonoff et al., 2018), so we only deployed *Bugula* in this region. Conversely, *Bugula* is not found in Belize, so we only deployed *D. psammatodes* at this location (see Appendices S1–S2 for a summary map and experimental metadata).

We created *Bugula* experimental units by spawning wild collected broodstock and settling larvae onto 100 cm^2 abraded polyvinyl chloride panels and holding them in the laboratory for 24 hours to complete metamorphosis (Lynch, 1947). We differentiated our experimental recruits from wild individuals by circling each initial *Bugula* recruit on each panel with a pencil and then photographing each panel to create a "map" of propagules (Appendix S3). We assigned each individual a unique identifier on the map to track individual performance. To test the effect of propagule pressure (i.e., number of *Bugula* recruits; hereafter propagule pressure) on invader survival, growth and reproduction, we used a regression approach and varied the number of experimental *Bugula* recruits placed on each experimental panel (7–19 individuals). We placed individual *Bugula* larva in drops of seawater on each panel until they adhered to the panel surface, and then, we submerged the panels in running seawater to allow them to finish metamorphosis. This approach allowed us to actively manipulate the number of recruits on each panel. There was no difference in the number of propagules deployed across regions (Poisson generalized linear mixed model, GLMM; Wald χ^2, $p = 0.137$), caging treatment ($p = 0.649$) or their interaction ($p = 0.696$). We deployed these *Bugula* panels at sites in Panama, Florida, Virginia and Connecticut.

To construct *Didemnum* experimental units, we used colony fragments as propagules instead of larval recruits for several reasons. Fragmentation is a major dispersal mechanism for clonal organisms (e.g., corals, bryozoans and tunicates), often exceeding the reproductive output of sexually produced larvae (reviewed in Jackson & Coates, 1986). In *Didemnum*, colonies produce long tendrils that can naturally pinch off and fall into the seabed from natural substrate, ship hulls and mooring lines (Valentine, Carman, Blackwood, & Heffron, 2007). Fragments are also generated from the cleaning of anthropogenic structures, fishing activities and storms (Reinhardt et al., 2012). Fragments may also survive and reproduce while rafting on flotsam in the water column for up to 3 weeks (Morris & Carman, 2012). Therefore, we collected wild *Didemnum* colonies from each site, excised 1 cm^2 colony sections and attached fragments to each experimental panel with cyanoacrylate glue. This technique has been successfully used to attach other tunicate species to experimental substrate (Young, 1989). Despite exhaustive searching, we found relatively few *Didemnum* colonies in Panama and Belize, limiting the broodstock material for fragmentation. Thus, we standardized the propagule treatment to four fragments on each panel for all *Didemnum* experiments. We deployed these experimental units into the field within 24 hours of collection to limit handling and fragmentation trauma.

2.2 | Predation experiments

We conducted three caging experiments to measure predation across latitude (for methodological details see Appendices S1–S3). The first experiment measured the survival, growth and reproduction of experimental bryozoan and tunicate propagules on fully caged panels (no predator access) and open panels without any caging (full predator access). The second experiment re-exposed the caged panels from the first experiment to measure survival of established colonies. In the third experiment, we deployed blank panels (caged and uncaged) to measure natural recruitment and colonization with and without the effect of native consumers. We deployed cage control treatments at a subset of sites due to limited availability of broodstock material for spawning and fragmentation. Cage control experiments indicated no difference in survivorship between cage control and open panel treatments for *Bugula* (Wald $Z = 0.409$, $p = 0.683$) and *Didemnum* (Wald $Z = 0.458$, $p = 0.647$; Appendix

S4). Retrospective power analyses based on binomial simulations (Johnson, Barry, Ferguson, & Müller, 2014) revealed that our experimental design reached an 80% power threshold when detecting an effect size (log odds ratio) of 2.7 and 2.8 (for *Bugula* and *Didemnum*, respectively). This was equivalent to an increase in survival of 6.7% and 19% from the open plots to the partial cage controls (for *Bugula* and *Didemnum*, respectively; Appendix S4). This suggests that our ability to resolve a caging artefact was reasonable for *Bugula* but coarse for *Didemnum*. Greater sampling surely would have increased our statistical power; however, we suggest that any potential caging artefact is not biologically meaningful when compared to the effect size of full predator exclusion cages. In the *Bugula* partial cage experiment, the odds of survival increase by 2.3 in the partial cage treatment, as opposed to the odds of survival increasing by 2,392 in the predator exclusion treatment (Appendix S4). For *Didemnum*, analysis estimated that the odds of survival increase by 2.6 in the partial cage treatment, as opposed to 40 in the full predator exclusion. Further, prior work testing the effects of five different caging treatments on invertebrate fouling communities revealed comparable results in this same experimental system (Freestone, Osman, Ruiz, & Torchin, 2011) and so we focused our analysis on the comparison between caged and open panels. We deployed all panels at 1–3 m depth and in seagrass beds dominated by turtle grass *Thalassia testudinum* (Panama, Belize and Florida) or eelgrass *Zostera marina* (Virginia and Connecticut).

In the first experiment, we deployed 256 experimental panels (2 genera * 2 predation treatments (open and caged) * 2 sites * 4 regions * 8 replicates; Appendices S1–S2). At each site, the species and predation treatments were randomly interspersed every 2 m along three parallel transects. Prior to deployment, we photographed every panel to track the fate of propagules. Experiments were deployed for 28–33 days of exposure to the recipient community (Appendix S2) after which time we recovered and photographed the experimental panels. For *Bugula*, we quantified the survival of propagules (alive or dead), growth (measured in branch bifurcations; Keough & Chernoff, 1987) and reproduction (fecundity as number of ovicells per colony) using a dissecting microscope. For *Didemnum*, we recorded the survivorship of the fragments (alive or dead) and quantified growth using change in total colony area per panel (cm^2) as measured by image analysis software (Schneider, Rasband, & Eliceiri, 2012). We quantified total colony size because distinguishing individual colony fragments was sometimes difficult (borders between colonies were difficult to observe). At the end of this experiment, we recovered 100% of the experimental panels, however, we excluded two *Bugula* panels from the analysis because they washed ashore in Florida. For *Didemnum*, we found high mortality (near 100%) within both open and caged panels at one site in Belize, and we therefore excluded that site since mortality may have been driven by handling stress or an ineffective caging treatment.

The second predation experiment was designed to measure predation on established colonies using experimental panels from the full cage treatments in the first predation experiment. After recovering the first experiment, we subjected predator exclusion panels to a brief holding (<24 hr) in the laboratory for photography and assessment of survival and performance and then redeployed these experimental panels into the seagrass bed without protection from predators (Freestone et al., 2011). We conducted this re-deployment at all sites except for Florida, where growth and survival of the initial propagules were extremely high and recruitment of wild *Bugula* was extraordinary, resulting in 100% cover of experimental and wild *Bugula* colonies (see below). We also reserved a small number of panels for laboratory assays of consumption, which resulted in replication for this experiment of 5–8 replicate panels per species and site (total = 76, mean = 6.9, *SD* = 1.45). After three days in the field, we recovered the panels and quantified survival as in the first experiment.

In the third experiment, we measured the effect of consumers on recruitment and colonization by deploying blank panels with and without predator exclusion cages at the same time as the first caging experiment. For each treatment and site combination, replication ranged from 4 to 8 panels (total = 84, mean = 5.3 per site and treatment, *SD* = 1.4). This experiment was spatially adjacent to the first experiment and deployed at the same time and for the same duration at each site. After recovery from the field, we photographed all panels and measured *Bugula* and *Didemnum* recruitment using dissecting microscopy. To identify potential predators within each region, we also conducted qualitative laboratory feeding assays with a range of consumers (e.g., urchins, crustaceans, gastropods; Appendix S5).

2.3 | Statistics

We used generalized linear mixed models (GLMMs) to quantify survival, growth and reproduction of invaders in the manipulative field experiments. For survival of *Bugula*, we modelled latitude (continuous), caging treatment, propagule pressure (continuous) and all possible interactions as fixed effects. For random effects, we specified experimental unit nested within site, and site nested within region. For survival of *Didemnum*, we created a model just as for *Bugula*, except without a propagule pressure fixed effect because *Didemnum* propagule pressure was fixed at four fragments per plate. To explore the effect of using two congeneric species of *Didemnum* across latitude, we also conducted analyses with and without *Didemnum vexillum* (deployed in Connecticut). For both species, we modelled the survival data in the form of zeroes and ones (Bernoulli trials) with binomial error and logit link functions. Because *Bugula* growth and reproduction were measured in the form of counts, we used a Poisson error distribution and log link function. We evaluated overdispersion (variance larger than mean) by calculating the sum of squared Pearson residuals, dividing this by the residual degrees of freedom and then conducting a chi-square test on the ratio. If the model was overdispersed, we used a negative binomial error distribution, which allows the variance to be larger than the mean with an overdispersion parameter. For *Didemnum* growth, a continuous response, we used a Gaussian error distribution and identity link function. We visually examined estimates versus residuals to evaluate the assumption of homoscedasticity and performed a log transformation if we observed fan shaped patterns within the residuals. Modelling *Bugula* recruitment was complicated by extreme variability in recruitment both within and among regions (e.g., variance of 2.6 in Panama as compared to 31,584 in Florida) and multicollinearity between the region and caging treatment predictors (variance inflation factors >10). To address these issues, we modelled the additive effect of cage treatment and latitude on *Bugula* recruitment with a negative binomial model with a random site effect. For all tests, we centred and scaled all continuous predictors (latitude and *Bugula* propagule pressure) prior to analysis. To generate the analyses and graphs, we used the packages "lme4," "lmerTest," "glmmTMB," and "ggplot2" within the R statistical computing environment (version 3.5.0; R Core Team 2018).

3 | RESULTS

The primary predictor of *Bugula* survival was predation (i.e., caging treatment). Across all sites, total survival was only 27.7% (214 of 773 propagules) in panels exposed to predators, as opposed to 82.9% total survival (656 of 791 propagules) in panels caged from predators (Figure 1a). One exception to these patterns occurred in Florida where total survival was 87.2% in open and 76.8% in caged treatments. The greater survival of *Bugula* in Florida was likely related to exceptionally high regional scale recruitment patterns that we observed in this experiment and the third experiment (see results below). However, at the local propagule pressure level, increasing the density of experimentally seeded recruits (within the manipulated

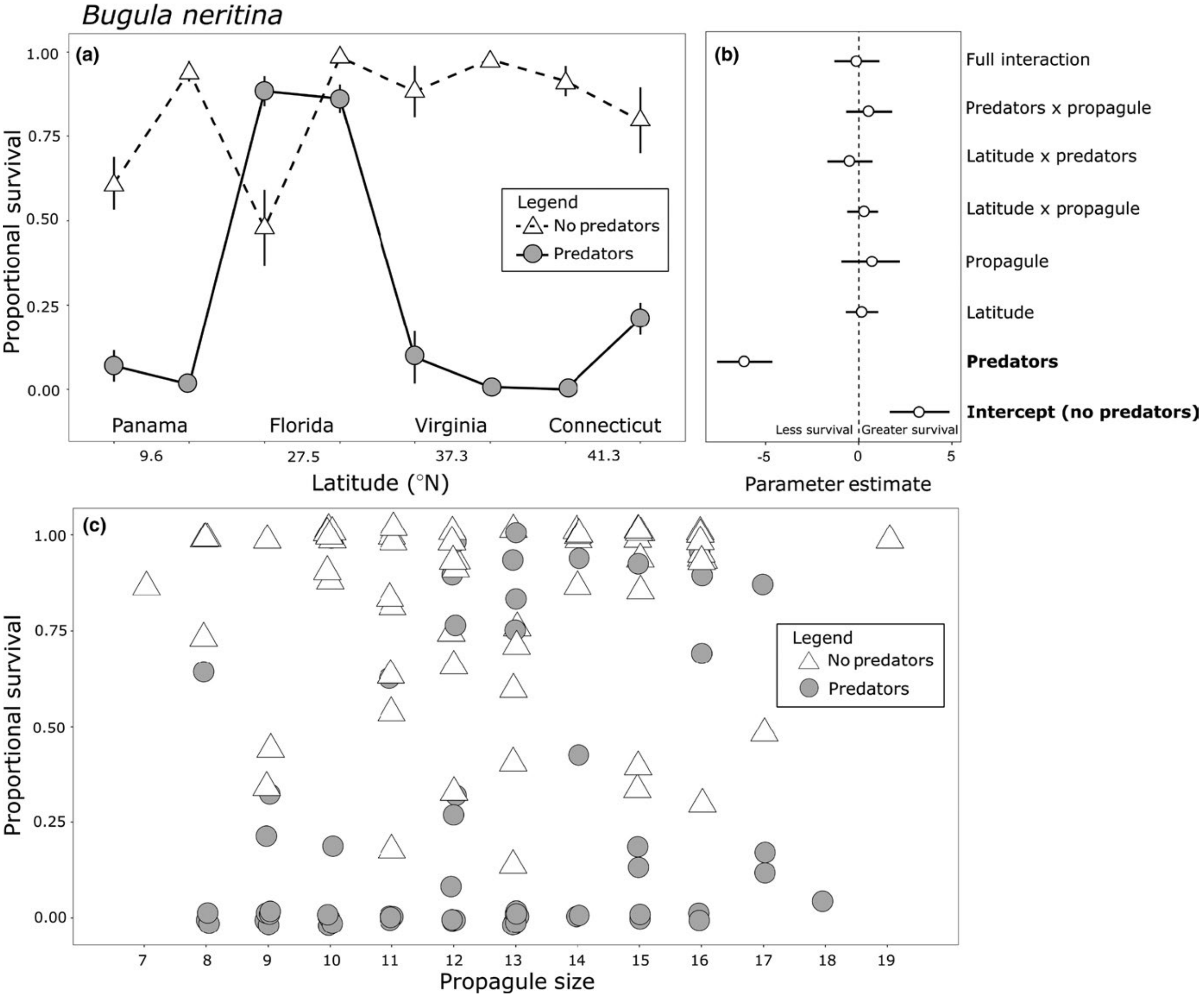

FIGURE 1 Predation Experiment 1. *Bugula* survival within predation experiment across latitude. (a) Survival from Panama to Connecticut inside predator exclusion (white triangles) and predator access treatments (grey circles). Points refer to mean proportional survival ±*SEM*. Note that locations are plotted categorically and that distances between them are not equal. (b) GLMM model results for the effects of caging, latitude, and propagules, and all interactions in predicting *Bugula* survival. Points refer to parameter estimates ±95% confidence intervals. Predictors that deviate from 0 are highlighted in bold. Positive estimates indicate greater survival, whereas negative estimates indicate decreased survival. (c) *Bugula* survival as a function of propagule size (number of colonizers per panel) in predator exclusion (white triangles) and predator access treatments (grey circles). Slight random jitter applied for clarity

range of propagules) did not have an effect on *Bugula* survival, nor did the latitude of the experiment (Figure 1b,c). There was also no evidence for two-way or three-way interactions among predation, propagule pressure or latitude (Figure 1b). Within the caged treatments (predator exclusion), *Bugula* exhibited greater growth with increasing latitude but there was no effect of propagule pressure or their interaction (Figure 2; Appendix S6). Reproductive output was unaffected by latitude, propagule pressure or their interaction (Figure 2; Appendix S6). *Bugula* propagules never reached reproductive maturity in Connecticut.

Predation was also the largest determinant of *Didemnum* fragment survival. Across all sites and with both species of *Didemnum*, total survival was only 15.6% (35 of 224 fragments) in panels exposed to predators, as opposed to 75.4% survival (169 of 224 fragments) in panels caged from predators (Figures 3a and 4). There was an overall main effect of predation that decreased survival of fragments (Figure 3b). However, there was no main effect of latitude or the interaction between latitude and predation on survival (Figure 3b). When excluding *Didemnum vexillum* (deployed in Connecticut) from analyses, we did find evidence for a positive effect of latitude on survival in plots exposed to predators (Interactive effect; $Z = 2.989$, $p = 0.003$). There was also an overall main effect that decreased survival of fragments when exposed to predators ($Z = -2.92$, $p = 0.004$). There was no effect of latitude on survival within the predator exclusion treatment ($Z = 0.559$, $p = 0.576$). In addition, *Didemnum* growth within the predator exclusion cages did not vary across latitude (Figure 3c, Appendix S6).

The second experiment tested for differences in established colony susceptibility to predation across latitude but found no evidence for such an effect. For *Bugula* and *Didemnum*, there was no effect of latitude on survival of established colonies over the 3-day deployment ($Z = 0.842$, $p = 0.400$ and $Z = -0.638$, $p = 0.524$, respectively). Upon re-deployment, established *Bugula* colonies appeared to experience greater overall survival than *Didemnum* (total 53.7%; 237 out of 441 total colonies). In contrast, out of a total of 122 *Didemnum* colonies redeployed across all sites, there was 100% mortality except for three experimental panels that had a total of 11 surviving colonies in Belize (Figures 4 and 5). Qualitatively, these high mortality rates were also experienced by other species of recruiting wild tunicates that developed within the predator exclusion treatment but then quickly perished upon exposure to predation (Figure 4; Appendix S3).

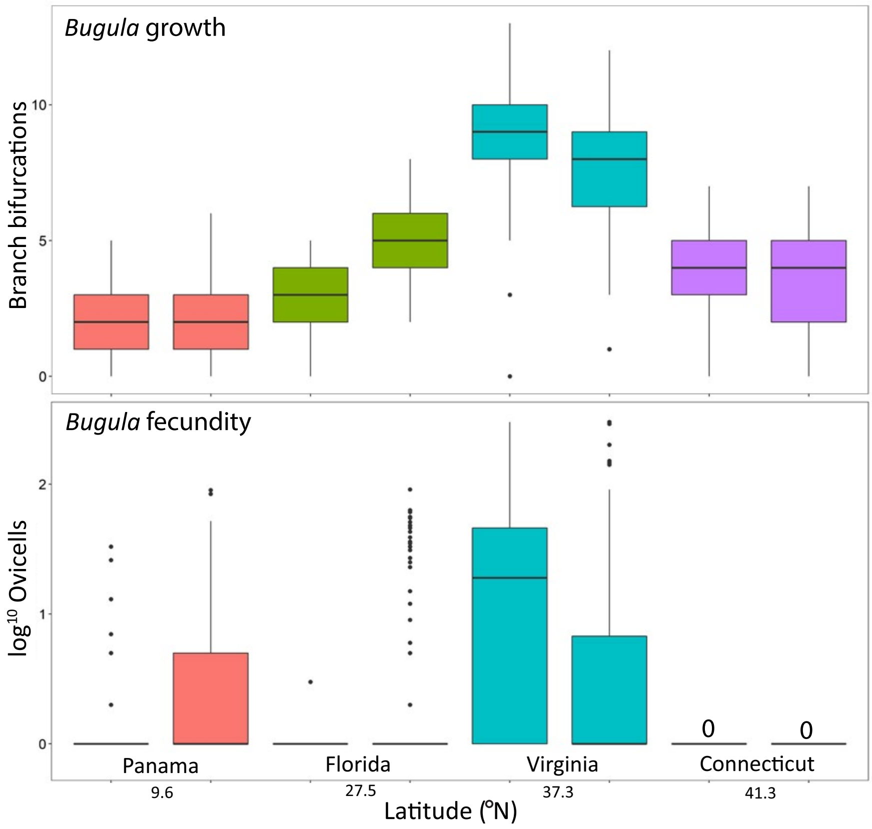

FIGURE 2 Boxplots of growth and fecundity of *Bugula* across latitude (within the predator exclusion treatments). Growth was measured as the number of branch bifurcations per colony, which is correlated to the total number of zooids (Keough & Chernoff, 1987). Fecundity is graphed as the $\log_{10}$ number of ovicells (externally visible reproductive structures) plus one per colony. The boxplots collapse to a flat line at some locations due to little variation (median and quartile values are the same). *Bugula* fecundity was zero in Connecticut, represented by annotations of 0. Note that locations are plotted categorically and that distances between them are not equal [Colour figure can be viewed at wileyonlinelibrary.com]

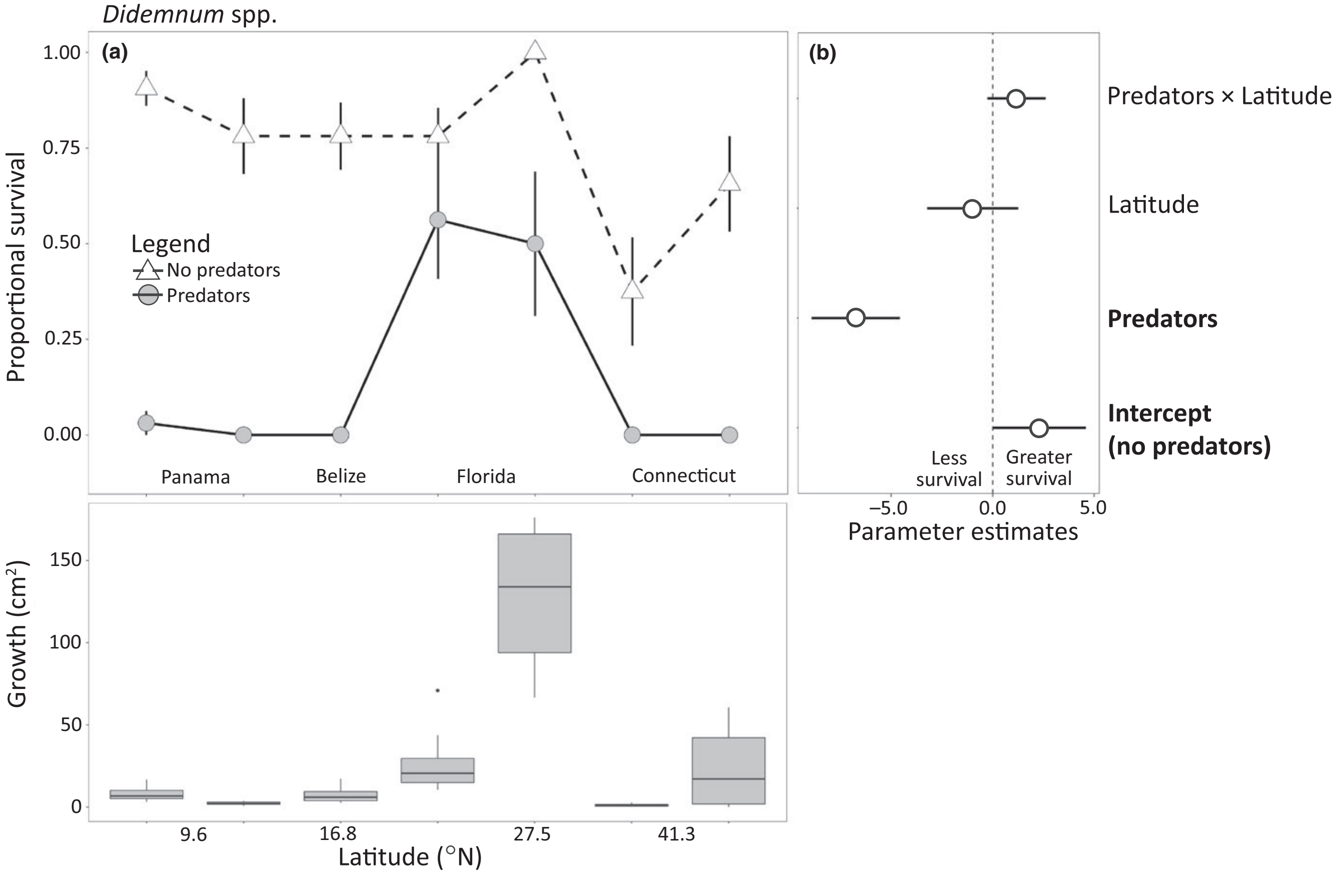

FIGURE 3 *Didemnum* survival and growth in predation Experiment 1. (a) Survival from Panama to Connecticut inside predator exclusion (white triangles) and predator access treatments (grey circles). Points refer to mean proportional survival ±*SEM*. (b) GLMM model results for the effects of predation (caging), latitude and their interaction in predicting *Didemnum* survival. Points refer to parameter estimates ±95% confidence intervals. Predictors that deviate from 0 are highlighted in bold. Positive estimates indicate greater survival, whereas negative estimates indicate decreased survival. (c) *Didemnum* growth within the caged treatments. In some instances, tunicates covered the entire surface of the panel and began growing onto the opposing surface, yielding sizes greater than 100 cm^2. Note that locations are plotted categorically and that distances between them are not equal

In the third experiment, we did not find a latitudinal or caging effect on *Bugula* recruitment (Figure 6; Appendix S7). There was also no evidence for an interaction between latitude and caging on *Bugula* recruitment (Appendix S7). Our experimental panels did measure an exceptional pulse of in situ recruitment in Florida and Virginia, whereas recruitment in Panama and Connecticut was virtually non-existent by comparison, which resulted in a hump shaped response of recruitment across latitude (Figure 6). Averaged across caged and uncaged treatments, Florida and Virginia had a mean of 167 and 126 *Bugula* recruits per panel (*SD* = 178, 131), respectively. In a few instances, we observed more than 500 recruits per panel. These values greatly exceeded the local propagule pressure manipulation of 7–19 *Bugula* recruits per panel. In contrast, Connecticut and Panama averaged 0.8 and 0.7 *Bugula* recruits per panel (*SD* = 1.6, 2.0), respectively. We did not record any *Didemnum* recruitment on bare panels, though we observed *Didemnum* settlers on *Bugula* experimental panels in a few instances. On bare predator exclusion panels, we also observed high recruitment of other fouling species (e.g., *Molgula manhattensis*, *Botrylloides violaceus*, *Botryllus schlosseri*) whereas predator exposed panels were generally devoid of tunicates (Appendix S3). Field observations and laboratory trials revealed a suite of predators that consume *Bugula* and *Didemnum* at virtually all sites, including fish, nudibranchs, gastropods, echinoderms and crustaceans (detailed list in Appendix S5).

4 | DISCUSSION

Our results indicate that predation was a primary determinant of invader survival and growth and that this effect was largely invariant across latitude. At most tropical and temperate locations, survival was near zero when propagules were exposed to the predator community. This was true even when we increased local propagule pressure of *Bugula* by over twofold. In addition, established *Bugula* and *Didemnum* colonies in the second predation experiment generally suffered high predation when exposed to the native community across most latitudes. However, we found that predation had limited effects on *Bugula* in Florida, which is explained by exceptionally high

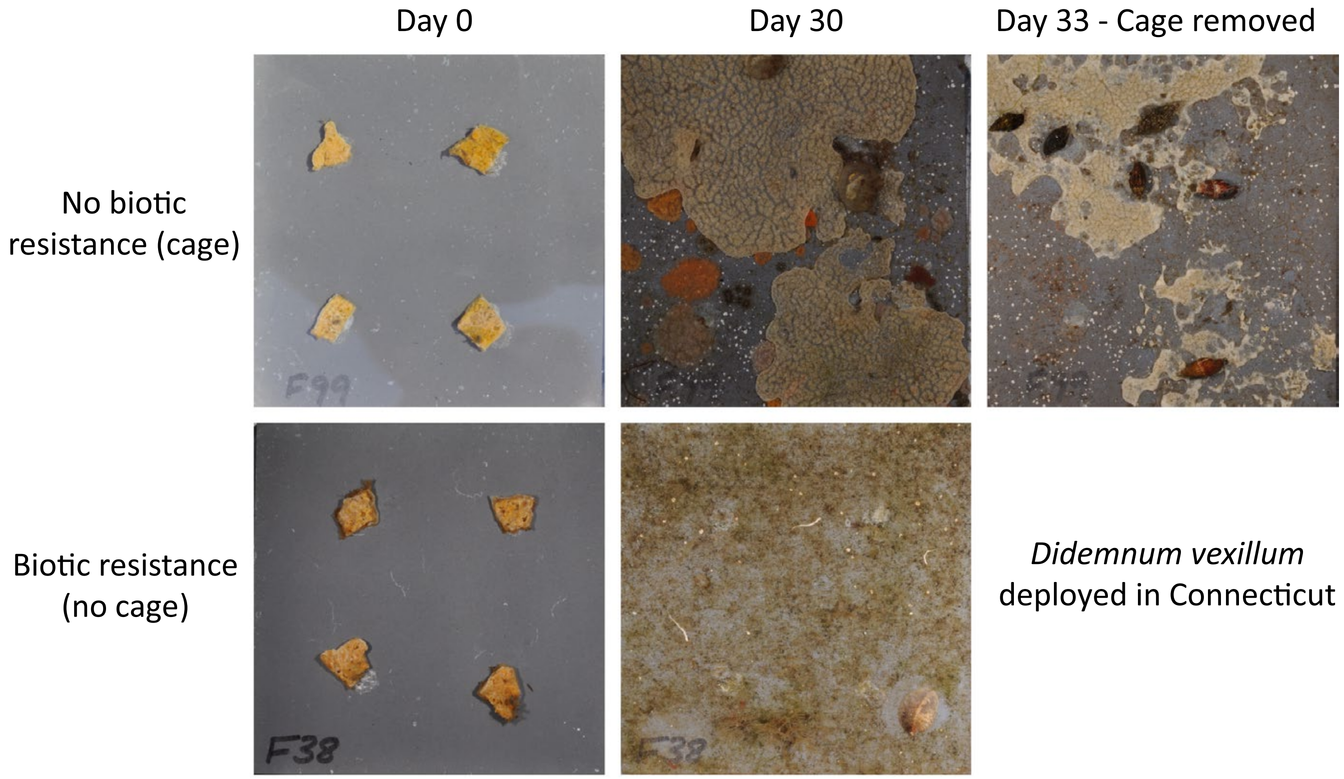

FIGURE 4 Time-series photograph mosaic of representative *Didemnum* panels deployed in Connecticut. Each column refers to a different time point. *Didemnum* fragments in the top row experienced no biotic resistance (predator exclusion cage) from day 0 to 30 (Experiment 1). At day 30, we subjected these panels to the predator community for three days (Experiment 2). Note the presence of predatory dove snails (*Alia* spp.) that were consuming *Didemnum* and the mortality of other tunicate species. The bottom row was exposed to the predator community for the entire experiment. All *Didemnum* recruits perished and only algae and one limpet were found (at lower right) [Colour figure can be viewed at wileyonlinelibrary.com]

in situ propagule pressure, reaching up to 500-fold greater wild recruitment than in other regions. This ambient propagule pressure may have resulted in predator satiation, decreasing the mortality of our experimental recruits via inverse density-dependent mortality, as seen in synchronized and periodic cicadas (Karban, 1982). In addition, predators did not reduce the recruitment of *Bugula* onto bare experimental panels in Florida and Virginia, regions that both exhibited exceptional densities of ambient propagules. Taken together, these results imply that biotic resistance (predation) and propagule pressure shape the dynamics of invasion at varying spatial scales. In our system, predation appears to be a major determinant of invasion at local spatial scales and when propagule pressure is reduced. In contrast, we suggest that propagule pressure operating at the regional spatial scale can overwhelm and swamp predators provided it has reached sufficient intensity.

Surprisingly, we found strong effects of predation on our experimental propagules in both tropical and temperate zones, suggesting that predation, at least on the species tested, is not correlated with latitude. These results were unexpected and contrast with previous reports of stronger marine biotic resistance (Freestone et al., 2013; Kimbro et al., 2013) and more generally, stronger species interaction strength at lower latitudes (Pennings & Silliman, 2005; Reynolds et al., 2018; Rodemann & Brandl, 2017). However, support for the biotic interactions hypothesis is mixed, with many examples of invariant species interaction strengths across latitude (Chen, Hemmings, Chen, & Moles, 2017; Kozlov, Lanta, Zverev, & Zvereva, 2015; Moles, Bonser, et al., 2011; Moles, Wallis, et al., 2011; Schleuning et al., 2012) or greater interaction strength at high latitudes (Poore et al., 2012). A possible factor contributing to debate over the biotic interactions hypothesis is seasonally varying interaction strength, which has been described in marine and aquatic systems where most predators are ectothermic and consumption is driven by seasonal water temperatures (Astudillo, Leung, & Bonebrake, 2016; Bishop, Rivera, Irlandi, Ambrose, & Peterson, 2005; Osman & Whitlatch, 1995). By necessity, we conducted our experiments during the seasons when *Bugula* was reproductively mature and *Didemnum* was prolific enough for collection. Thus, our experiments may have measured the peak of predation intensity across all sites. In contrast, previous latitudinal biotic resistance experiments measured the effect of predation on the colonization of invertebrate communities, sometimes recovering experiments in early and late autumn when water temperatures have cooled and consumptive activities may have declined at temperate sites (Freestone et al., 2011, 2013). One possibility is that that tropical species interaction strength is greater than in temperate ecosystems when time

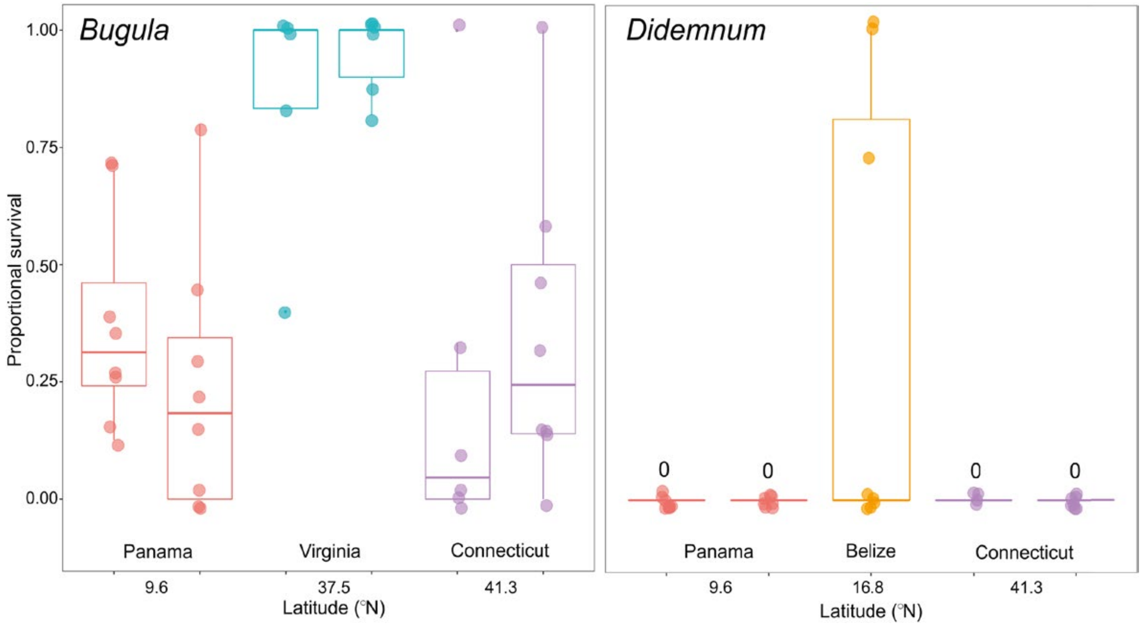

FIGURE 5 Predation Experiment 2. Survival of established (larger and older) *Bugula* and *Didemnum* after exposure to ambient predator communities for three days. Experimental animals previously resided within the predator exclusion treatment of predation Experiment 1. Proportional survival is depicted as boxplots overlaid with raw data points (slight random jitter applied for clarity). For *Didemnum* in Panama and Connecticut, there was zero survival for all plots, therefore the median and quartiles from the boxplots form a flat line and are annotated with "0." We did not re-deploy experimental units in Florida because of high survival for both species in the first experiment. Note that locations are plotted categorically and that distances between them are not equal [Colour figure can be viewed at wileyonlinelibrary.com]

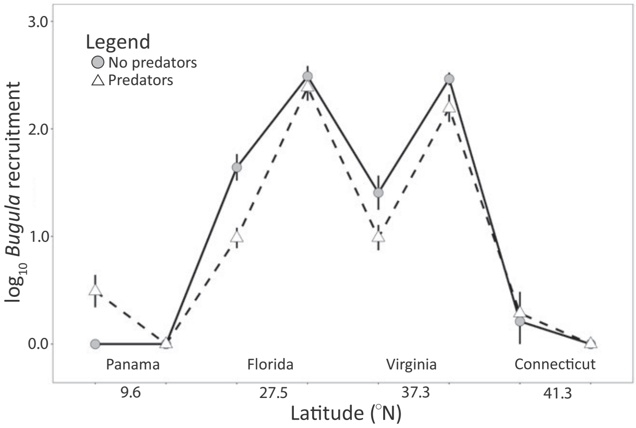

FIGURE 6 *Bugula* recruitment onto bare experimental panels across latitude and by caging treatment. Point estimates are means and error bars are ±*SEM* at the site level on the $\log_{10}$ scale. Note that locations are plotted categorically and that distances between them are not equal

averaged across the year, but this remains to be tested. In addition to species interaction strength, seasonality also influences patterns of recruitment, further complicating colonization dynamics (Connolly et al., 2001; Godoy et al., 2015). Given that high latitude sites exhibit greater temporal variation in environmental regime and propagule pressure than tropical sites, we expect that high latitude sites would be most sensitive to the timing of experimentation and sampling.

Greater propagule pressure of *Bugula* had no effect on invasion within the range of densities that we tested in Experiment 1. It is possible that our local scale manipulations did not reach a sufficient threshold for the invaders to establish. However, our range of manipulated propagules is comparable to the range used for other propagule pressure experiments (Sinclair & Arnott, 2016; Von Holle & Simberloff, 2005). We also observed that many of the consumers (e.g., parrotfish and urchins in Panama, crustaceans in Connecticut) foraged indiscriminately, scraping the experimental panels free of all growth, suggesting that even higher initial densities of locally placed propagules would have been insufficient to overcome this consumption pressure within our experiment. In Panama, we were able to capture video recordings of parrotfish that were able to completely consume 100 cm^2 colonies of *Didemnum* over the course of several hours. Likewise, in Connecticut, we observed crabs (*Libinia emarginata*) and snails (*Alia* spp.) that rapidly consumed *Bugula* and *Didemnum* in the field and laboratory. We suspect that predators are capable of regulating prey populations at these local spatial scales because there was little to no additional recruitment to drive the system towards predator satiation or recolonization following intermittent bouts of predation. In contrast, we suspect that high and persistent regional scale propagule pressure was the driver of *Bugula* population persistence in Florida. This can occur if regional recruitment is sufficiently high and there is no numerical predator response, such as the case in other systems exhibiting explosive recruitment of prey (e.g., synchronized cicada emergence and satiation of bird predators; Karban, 1982; Williams, Smith, & Stephen, 1993).

In Virginia, we measured intermediate *Bugula* recruitment, greater than Connecticut and Panama but less than Florida. We would have predicted that high recruitment of *Bugula* in Virginia in Experiment 3 should translate to high survival of experimental propagules during Experiment 1 (both experiments were conducted concurrently). In contrast, we observed poor survival of our experimental *Bugula* in Virginia during Experiment 1. Future biotic resistance experiments should explore the impact of a wider range of propagule pressure with greater temporal coverage to assess the overall capacity of native systems to resist invasion.

Our experimental manipulations of *Didemnum* provide additional evidence for the generality of native consumers to prey upon non-native species across latitude. *Didemnum* fragments were unable to persist on experimental panels without protection from predators at all sites except for Florida. However, even in Florida, *Didemnum* propagules exhibited greater survival and growth within predator exclusion cages (Figure 3). This susceptibility to predation was also apparent in Experiment 2, where nearly 100% of *Didemnum* prey perished in the 3-day "re-exposure" to predators. With respect to propagule pressure, the lack of wild broodstock material prohibited us from manipulating the propagule pressure of *Didemnum* within our experiments. However, we rarely measured natural *Didemnum* recruitment on our experimental panels, highlighting the important role of fragmentation and budding within this genus as a mechanism for spread (Jackson & Coates, 1986). One complicating factor in interpreting latitudinal variation in predation was our use of *Didemnum vexillum* in Connecticut and *Didemnum psammatodes* in Florida, Belize and Panama. When *Didemnum vexillum* was excluded from analyses, there was evidence for greater predation intensity at tropical sites for *Didemnum psammatodes*. Despite this exception, the majority of our data points to a large impact of predators across nearly all latitudes tested. We suggest that future studies employ this multipronged approach, using species found throughout the range tested when possible (e.g., *Bugula*) as well as congeneric and functionally similar species (e.g., *Didemnum* spp.) because few sessile marine invertebrate species are distributed in both the tropics and temperate zones. Given the ethical constraints of introducing new species, we feel that our complementary testing of both *Bugula* and *Didemnum* was a reasonable approach to quantifying biotic resistance across latitude. Future research may also consider employing non-living tissue or model prey to measure species interaction strength across broad spatial scales (Chen et al., 2017; Duffy, Ziegler, Campbell, Bippus, & Lefcheck, 2015; Roslin et al., 2017).

In conclusion, we provide evidence for the importance of predation as a widespread form of biotic resistance. We found unexpected levels of predation at almost all sites, without any latitudinal trend. Our results suggest that predation operates largely at the local scale to inhibit the invasion of *Bugula* and *Didemnum* in seagrass beds. In contrast, we found that propagule pressure had little effect at smaller experimental scales but likely operates at a much larger regional scale to potentially satiate and swamp native consumers. We suggest that the importance of latitudinal variation in biotic resistance and propagule remains largely untested but deserves future attention given that increased globalization and the associated propagule pressure has set the stage for the continued invasion of non-native species across the globe (Seebens et al., 2017). Further complicating the challenge of coping with invasion is the potential for climate change to facilitate novel trade routes (Miller & Ruiz, 2014) and intensify the consequences of invasive species (Cheng, Komoroske, & Grosholz, 2017; Sorte et al., 2013). Although our experiments focused on quantifying biotic resistance, our results contribute to the growing body of work suggesting that species interaction strength is not stronger at lower latitudes (Chen et al., 2017; Kozlov et al., 2015; Moles, Bonser, et al., 2011; Moles, Wallis, et al., 2011; Poore et al., 2012; Schleuning et al., 2012). Further experimentation and observation at broad spatial and temporal scales are critically needed to advance understanding of the mechanisms driving ecological patterns (e.g., latitudinal diversity gradient) as well as applied problems, such as biological invasions and associated changes to native biodiversity.

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DATA ACCESSIBILITY

Data are publicly available at Figshare https://doi.org/10.6084/m9.figshare.6985013.v3.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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