

Stronger predation in the tropics shapes species richness patterns in marine communities

AMY L. FREESTONE,^{1,2,4} RICHARD W. OSMAN,² GREGORY M. RUIZ,² AND MARK E. TORCHIN³

¹*Department of Biology, Temple University, Philadelphia, Pennsylvania 19122 USA*

²*Smithsonian Environmental Research Center, Edgewater, Maryland 21037-0028 USA*

³*Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Panama*

Abstract. Species interactions are widely assumed to be stronger at lower latitudes, but surprisingly few experimental studies test this hypothesis, and none ties these processes to observed patterns of species richness across latitude. We report here the first experimental field test that predation is both stronger and has a disproportionate effect on species richness in the tropics relative to the temperate zone. We conducted predator-exclusion experiments on communities of sessile marine invertebrates in four regions, which span 32° latitude, in the western Atlantic Ocean and Caribbean Sea. Over a three-month timescale, predation had no effect on species richness in the temperate zone. In the tropics, however, communities were from two to over ten times more species-rich in the absence of predators than when predators were present. While micro- and macro-predators likely compete for the limited prey resource in the tropics, micropredators alone were able to exert as much pressure on the invertebrate communities as the full predator community. This result highlights the extent to which exposure to even a subset of the predator guild can significantly impact species richness in the tropics. Patterns were consistent in analyses that included relative and total species abundances. Higher species richness in the absence of predators in the tropics was also observed when species occurrences were pooled across two larger spatial scales, site and region, demonstrating a consistent scaling relationship. These experimental results show that predation can both limit local species abundances and shape patterns of regional coexistence in the tropics. When preestablished diverse tropical communities were then exposed to predation for different durations, ranging from one to several days, species richness was always reduced. These findings confirmed that impacts of predation in the tropics are strong and consistent, even in more established communities. Our results offer empirical support for the long-held prediction that predation pressure is stronger at lower latitudes. Furthermore, we demonstrate the magnitude to which variation in predation pressure can contribute to the maintenance of tropical species diversity.

Key words: *biotic interactions; coexistence; diversity; latitude; local; marine invertebrates; predation; regional; scale; species richness; temperate; tropic.*

INTRODUCTION

The latitudinal diversity gradient, with higher species richness at low latitudes than at high latitudes, is one of the clearest patterns in ecology and is consistent in both terrestrial and marine systems (Hillebrand 2004*a, b*). However, the underlying ecological (Willig et al. 2003, Currie et al. 2004) and evolutionary (Mittelbach et al. 2007) drivers have been debated for decades. One evolutionary hypothesis that is receiving renewed attention is the biotic interactions hypothesis. This hypothesis has roots in classic ecology and evolutionary biology and predicts that species interactions are stronger at lower latitudes (Pianka 1966, Coley and Barone 1996, Schemske et al. 2009), contributing to both

the origin and maintenance of higher tropical species diversity. Over evolutionary timescales, strong biotic interactions at low latitudes are predicted to result in higher diversification rates and ultimately high tropical biodiversity (Dobzhansky 1950, Fischer 1960, Schemske 2002, Mittelbach et al. 2007). Over ecological timescales, strong interactions are thought to compress niche space in the tropics allowing for greater species coexistence (MacArthur 1969, Connell 1970, Janzen 1970).

However, empirical ecological data to test the comparative magnitude and effects of interaction strength along broad geographic gradients are surprisingly limited (Schemske et al. 2009). In terrestrial systems, for example, herbivory (Coley and Barone 1996, Pennings and Silliman 2005) and predation by ants (Jeanne 1979) were shown to be stronger at low latitudes than high latitudes. Similarly in marine systems, herbivory by fishes at low latitudes resulted in more potent chemical defenses and reduced palatability in some algal and sponge species compared to higher

Manuscript received 27 December 2009; revised 13 August 2010; accepted 3 September 2010; final version received 4 October 2010. Corresponding Editor: J. F. Bruno.

⁴ E-mail: amy.freestone@temple.edu

latitudes (Bolser and Hay 1996, Ruzicka and Gleason 2008). Strong predation pressure at lower latitudes in marine systems was also shown to promote stronger physical (Vermeij 1978) and behavioral (Bertness et al. 1981, Fawcett 1984) defenses.

While stronger predation pressure at lower latitudes in comparison to higher latitudes has also been shown to impact predation rates on focal taxa (Heck and Wilson 1987, Peterson et al. 2001, Sanford et al. 2003), latitudinal shifts in interaction strength among *communities* of predators and prey will likely also have important emergent consequences for prey community structure and species richness. However, existing experimental comparisons of interaction strength across latitude have not generally examined community-level consequences. One such study compared results from separate tropical and temperate experiments and found support for stronger predation in the tropics, driving species abundances among habitats in a marine intertidal system (Menge and Lubchenco 1981). Another recent study on subtidal marine invertebrate communities across latitudes found that structurally complex habitats in the tropics harbored more diverse communities than less complex habitats that were more exposed to predators, while no such pattern was found in the temperate zone (Freestone and Osman 2010). In addition to species sorting among local scale habitats in response to predation pressure (Wulff 2005, Garcia and Mittelbach 2008), predation can also limit the realized regional pool of species that are able to establish in a particular habitat, thereby dictating how species richness is partitioned among both habitats and spatial scales (Chase et al. 2009). However, no studies to date have experimentally examined the relative impact of predation on observed patterns of species richness across latitude. This gap in our empirical understanding is surprising considering the critical role predation is thought play in maintaining species diversity in the tropics (Paine 1966, MacArthur 1969, Connell 1970, Janzen 1970).

Tremendous progress has been made in understanding how species richness covaries with latitude as a factor of scale, taxonomic grouping, mode of dispersal, and trophic level (Hillebrand 2004a, Witman et al. 2004), but understanding the role of species interactions, such as predation, in structuring patterns of species richness across latitude requires large-scale systematic experimental approaches. However, studies that employ such approaches are extremely rare. A particular challenge has been the use of experiments that control for potential confounding effects of habitat type, timescales, community history, and methodology.

In this study, we report the first experimental field test that predation is stronger at lower latitudes and will have a disproportionate effect on observed patterns of species richness in the tropics. Using experimental plots in communities of sessile marine invertebrates, we measured the effects of predator exclusion on species

richness, while controlling for key variables including habitat, community developmental timescale, and community history. More specifically, we employed two experimental approaches to ensure results were robust to both spatial scale and community age. First, we examined the effects of predator exclusion on community development, conducting standardized and simultaneous experiments across 32° of latitude, from the temperate zone to the tropics. We analyzed the results at three spatial scales to examine effects of predation on community patterns and the implications of community dynamics for regional coexistence. Second, we exposed more established communities to different levels of predation in the tropics to confirm that effects of predation were large, rapid, and consistent across multiple experiments.

METHODS

Study system

Communities of sessile marine invertebrates provide an ideal model system to test hypotheses on comparative effects of predation on species richness. These communities (1) are globally ubiquitous in their distribution; (2) are experimentally tractable due to their rapid community developmental timescales and the feasibility to conduct experiments on meaningful spatial scales; and (3) represent a diversity of taxa including ascidians, bryozoans, tube-building polychaetes, sponges, barnacles, bivalves, and a variety of cnidaria (hydroids, sea anemones, and coral) with different reproductive strategies, growth forms, feeding behaviors, and predator defense adaptations. These attributes have made sessile invertebrate communities an important system for testing ecological theory over the past 50 years (Connell 1961, Paine 1966, Stachowicz et al. 1999, Freestone and Osman 2010), and we now apply this system to temperate-tropical comparisons of predation effects on species richness.

Effects of predation across latitude

We conducted a large-scale predator exclusion experiment on marine invertebrate communities across 32° of latitude along the western coast of the Atlantic Ocean and Caribbean Sea (Table 1). Three-month experiments were performed simultaneously in four focal regions: Connecticut (Long Island Sound; 41° N, 72° W), Florida (Indian River Lagoon; 27° N, 80° W), Belize (Mesoamerican Reef; 16° N, 88° W), and Panama (Bocas del Toro; 9° N, 82° W), with additional experiments in the tropics.

Experiments were deployed at two sites per region in shallow (<4 m depth) seagrass habitat. Seagrasses are one of the few coastal marine habitats that span the entire range of our latitudinal gradient. While dominant seagrass species change with latitude (*Zostera marina* in temperate regions and *Thalassia testudinum* in the tropics), our focus on a single habitat type across the latitudinal gradient provided continuity among very

TABLE 1. Summary of experimental design.

Experiment type and region	Duration	Deployment date	Treatment	<i>N</i>
Community development with and without predation across latitude				
Connecticut	3 months	July 2008†	all	48
Florida	3 months	August 2008†	all	24
Belize	3 months	April 2008	all	50
Belize	3 months	July 2008†	all	50
Belize	3 months	October 2008	S, PS, O	40
Panama	3 months	September 2008†	all	52
Panama	3 months	December 2008	S, O	56
Exposure of three-month-old communities to predation in tropics				
Belize	7 days	January 2009	E, C	20
Panama	9 days‡	December 2008	E, C	8
Panama	7 days‡	April 2009	E, C	13
Panama	3 days	April 2009	E, C	27
Panama	1 day‡	April 2009	E	6

Notes: All five predation treatments were employed except where noted (key to abbreviations: S, screened; PS, partial screen; O, open). Treatments for exposure experiments were: E, exposed; C, controls. *N* indicates total number of replicates retrieved.

† Simultaneous deployments of community development experiment.

‡ One site was used for these experiments. All other experiments were conducted at two sites per region.

distinct biogeographic regions. Seagrass beds are also considered critical habitat for many marine species (Waycott et al. 2009) and a refuge and nursery for juvenile fishes and invertebrates (Heck et al. 2003), and thus we expected predation to be strong in these environments.

Using 100-cm² PVC settlement panels as standardized experimental habitat (substrate), we manipulated predation using five enclosure treatments for three-month intervals (Appendix A). We used enclosures of two mesh sizes (1 and 5 mm) to exclude predators of different size classes. Five mm enclosures were constructed from plastic vexar marine-grade mesh, referred to as “caged” treatments, and allowed micropredators access to the developing communities. One-millimeter enclosures were constructed by encasing the vexar mesh cages with fiberglass window screening, referred to as “screened” treatments, and eliminated nearly all predation. Our expectation was that both types of predator exclusions would produce a treatment effect in the tropics, with the exclusion of all predators demonstrating the strongest effect. Partial cages were designed to control for shading and hydrodynamic changes that may occur with the predator exclusions, but to ensure access to all predators. These treatments consisted of a top and two sides and were constructed with both types of caging materials (“partial cage” and “partial screen”). Additional panels had no caging material and are termed “open.”

Panels were mounted on plastic vexar stands with the experimental surface facing perpendicular to the seafloor (Appendix A). The vexar stands (not the panels) were in contact with the seafloor to maximize access to the communities by benthic predators but reduce sedimentation on the panels. Panels were deployed haphazardly

with respect to their orientation to the dominant current.

This experimental design controlled for several key factors. Habitat type and area were standardized using 100-cm² settlement panels deployed in seagrass beds. Community history and developmental timescale were also controlled in that all communities developed in situ on clean settlement panels during the three-month experiments. Another potential confounding effect is latitudinal differences in historical anthropogenic alteration of food web structure through over-harvesting of important predators (Witman and Sebens 1992). However, the primary predators in our system are not under strong pressure from fisheries, and we do not expect historic overfishing to bias our comparison.

We conducted simultaneous experimental deployments in all regions to coincide with the period of peak recruitment in the temperate zone, occurring in late summer (Table 1). In the tropics however, temporal variation in recruitment is poorly resolved (Freestone et al. 2009). Since there was no a priori expectation for how community dynamics would vary with time of year in the tropics, iterative deployments were conducted to both coincide with the temperate experiments (for the simultaneous deployments) and test predator effects at other times of year (two additional deployments in Belize, one in Panama; Table 1).

The full suite of treatments was employed during the first deployment in Belize (April) and all late-summer (simultaneous) deployments. Initial deployments in the tropics indicated that open, partial cage, partial screen, and caged treatments all produced comparable results. Therefore, a subset of treatments was employed for the last deployment in Belize (screened, partial screen, and open) and Panama (screened and open; Table 1) to allow increased replication of target treatments for use in

experiments on established communities. Treatments were replicated at least five times at each site in each region.

After three months, panels were retrieved and communities of invertebrates were examined live using a dissecting microscope to quantify species richness and percent cover. For species richness estimates, organisms were identified to the lowest possible taxonomic group (species whenever possible) or received a morphospecies classification based on commonly used external diagnostic characteristics. Relative abundances were recorded as percent cover of species using a point count grid of 100 points for all deployments except for the first Belize deployment (April) when relative abundances were recorded as number of individuals or colonies.

Species richness patterns were analyzed at the community (panel) scale and across all communities at a given site (site scale). At the community scale, an index of species diversity (Shannon-Wiener diversity index, H') and percent cover were also analyzed. To test the hypothesis that predation effects were stronger at low latitudes, variables were modeled with nested mixed models using fixed effects of region, treatment, and region \times treatment, with the interaction term being of key importance, and the random effects of site (nested within region) and the interaction between treatment and site (nested in region). Since our primary comparison was between temperate and tropical latitudes and since Belize and Panama were more climatically similar in their temperature and seasonality, the two tropical regions were expected to differ from the northern regions but not necessarily from each other. Point count data were used to estimate percent cover and were arcsine square-root transformed to meet assumptions of the test. To analyze species richness patterns at the Site scale, species occurrences among replicate communities within each treatment were pooled by site (therefore, each site harbored a single treatment observation) and modeled as above. When additional (more than five) replicates were retrieved, species occurrences were pooled for five random replicates only. Data from all deployments were included in the full models, with the exception that data from the first Belize deployment (April) were excluded from the percent cover analysis because relative abundances were measured using different methods. Species occurrences within treatments were further pooled at the regional scale for qualitative comparison. All analyses were conducted in JMP 8.0 (SAS Institute, Cary, North Carolina, USA).

Predation in the tropics

To examine the effect of predation on more established communities in the tropics, and to confirm results from the previous experiments, we removed predator exclosures from communities after three months and then exposed communities to predation. Screened communities were redeployed either without the protective screening to allow access to predators (exposed

treatment) or rescreened as controls. Exposure experiments were conducted for seven days at each of two sites in Belize in January 2009 and at one site in Panama in April 2009. Additional exposure experiments were conducted in Panama for one-, three- (April 2009), and nine-day (December 2008) intervals (Table 1). Communities were processed as above, and data were analyzed using matched pair comparisons of species richness and percent cover before and after exposure to predation.

RESULTS

Throughout our study, 39 species were observed in Connecticut, 70 in Florida, 145 in Belize (April deployment, 87; July deployment, 81; October deployment, 105), and 145 in Panama (September deployment, 102; December deployment, 110).

Effects of predation across latitude

Predation was stronger and shaped species richness patterns in the tropics but not the temperate zone across the three month developmental timeframe. This pattern was consistent for both species richness (Fig. 1A, Appendix B) and diversity (Shannon-Wiener, Fig. 1B, Appendix B). While there was no effect of predation on species richness in the temperate and subtropical regions, in the tropics, communities that were protected from all predators (1-mm screened treatments) were two to over 10 times more species rich than communities without predator exclosures (Fig. 2A) and were more species rich than all other treatments. Tropical communities that were protected only from larger predators (5-mm caged treatments) were less species rich than communities that were protected from all predators (1-mm screened treatments), indicating the importance of micropredators in this system, most likely juvenile fish, crustaceans, flatworms, and snails (A. Freestone, *personal observation*). However, while the diversity index means trended in the same direction as the species richness means in the tropics, the screened and caged treatment diversity index values were not statistically different (Appendix B). This pattern showed a similar increase in the evenness of abundances in the absence of either all predators or micropredators only. While sample size among treatments and regions varied because of additional deployments in the tropics and some losses from storms in Florida, including the loss of all screened replicates from one site in Florida, overall patterns were robust to these differences. The region \times treatment interaction remained significant regardless of whether the Florida data or the additional tropical data were excluded from the model. No differences ever occurred among treatments in the temperate zone, while consistent differences occurred in the tropics (Figs. 3 and 4).

Predation also slowed community development (percent cover) in the tropics. In Panama, screened communities without predators achieved higher cover

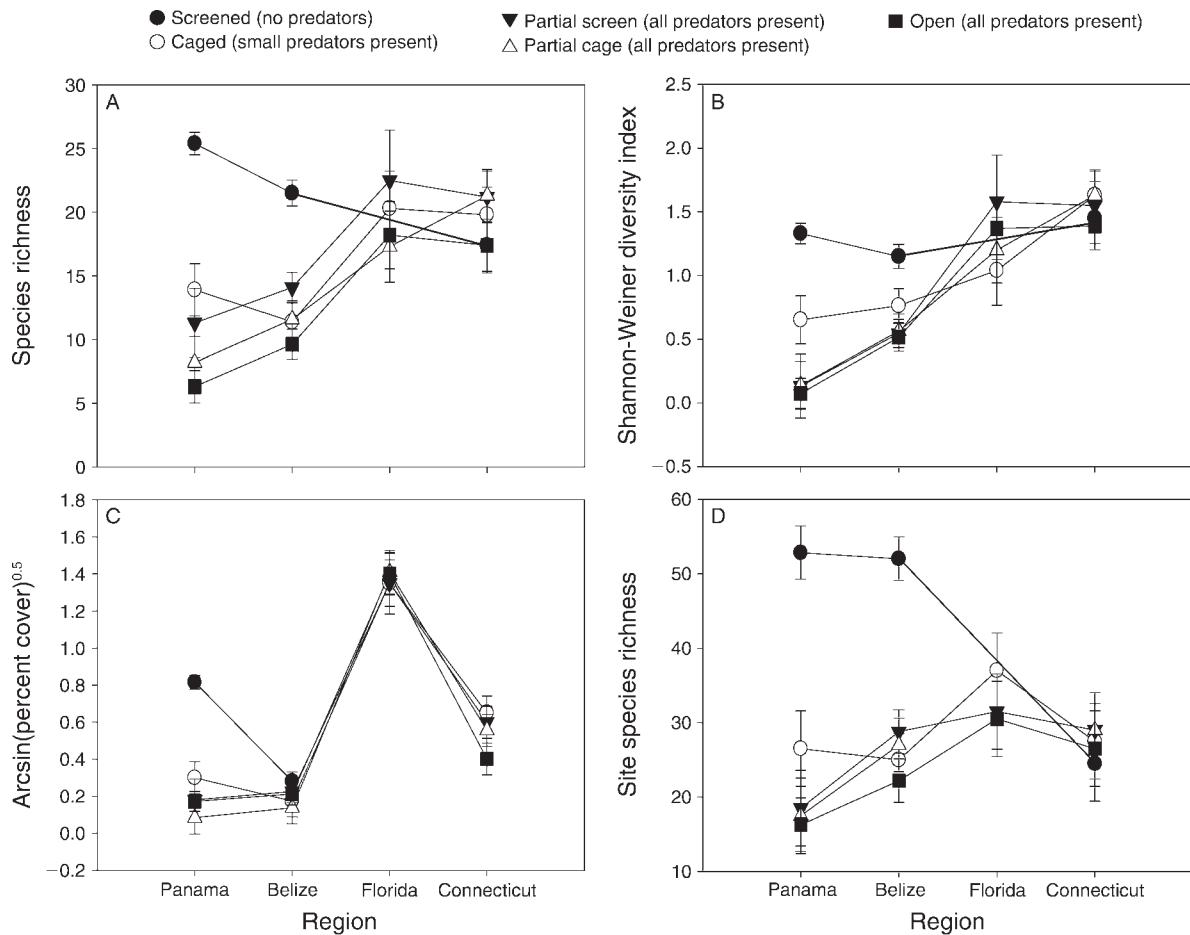


FIG. 1. Interaction plots with least squares (LS) means for treatment (predation pressure) × region (latitude). This figure demonstrates the strength of the interaction term by plotting LS means (\pm SE) for the dependent variable, as defined by the nested mixed model, by region. Arithmetic means are provided in Appendix B. (A) Community species richness model: $R^2_{adj} = 0.66$, $F_{38,281} = 17.3$, $N = 320$, $P < .0001$; region \times treatment, $F_{12,25.2} = 4.39$, $P = 0.0009$; treatment, $F_{3,57.1} = 4.11$, $P = 0.01$; region, $F_{2,3.36} = 7.09$, $P = 0.06$; site, $F_{3,19.5} = 2.55$, $P = 0.09$; site \times treatment, $F_{15,218} = 2.50$, $P = 0.002$. (B) Community Shannon-Wiener model: $R^2_{adj} = 0.49$, $F_{38,281} = 9.06$, $N = 320$, $P < 0.0001$; region \times treatment, $F_{12,30.4} = 2.73$, $P = 0.01$; treatment, $F_{3,81.0} = 0.8$, $P = 0.5$; region, $F_{2,3.38} = 15.7$, $P = 0.02$; site, $F_{3,21.8} = 3.34$, $P = 0.04$; site \times treatment, $F_{15,281} = 1.73$, $P = 0.04$. (C) Community percent cover model: $R^2_{adj} = 0.75$, $F_{38,231} = 22.1$, $N = 270$, $P < 0.0001$; region \times treatment, $F_{12,26.0} = 4.80$, $P = 0.0004$; treatment, $F_{3,56.0} = 0.67$, $P = 0.6$; region, $F_{2,3.21} = 7.27$, $P = 0.06$; site, $F_{3,22.3} = 4.16$, $P = 0.02$; site \times treatment, $F_{15,231} = 2.12$, $P = 0.01$. (D) Site species richness model: $R^2_{adj} = 0.73$, $F_{37,20} = 5.24$, $N = 58$, $P = 0.0001$; region \times treatment, $F_{12,29.0} = 2.83$, $P = 0.01$; treatment, $F_{2,33.9} = 1.35$, $P = 0.3$; region, $F_{2,4.30} = 1.65$, $P = 0.3$; site, $F_{3,22.0} = 1.38$, $P = 0.3$; site \times treatment, $F_{14,20} = 1.03$, $P = 0.5$.

than any other treatment, but no treatment effect occurred in other regions (Fig. 1C, Appendix B). However, cover on screened panels in Panama was similar to treatments at the highest latitude sites in Connecticut (only differed from open communities in Connecticut), demonstrating that tropical communities can achieve comparable cover to temperate communities in the absence of predation. While no effect of predation on percent cover was observed in Belize, cover among all treatments was very low.

Higher community species richness in the absence of predation in the tropics was also reflected across communities at each site. When species richness was calculated by treatment at the site scale (species occurrences pooled among replicate communities in a

given treatment), the interaction between region and treatment was again significant, and screened communities collectively harbored 1.5 to over eight times more species than open treatments in the tropics (Fig. 1D and 2B), substantially contributing to observed regional species richness (Fig. 2C). While tropical communities in the absence of predation achieved richness values comparable to temperate communities (Fig. 1A), at the site scale, richness in the tropics was higher than in the temperate zone (Fig. 1D).

Predation in the tropics

All established tropical communities experienced significant reductions in species richness when exposed to predation regardless of the exposure duration or time

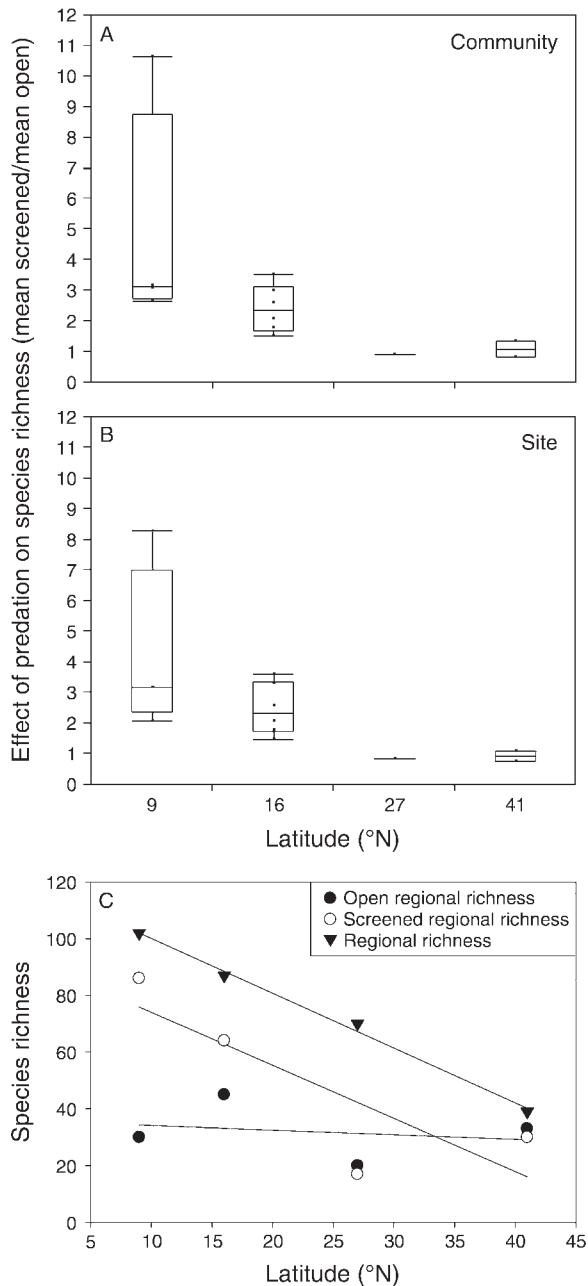


FIG. 2. (A) Ratio of species richness in communities without predation (screened treatment) to those open to predation (open treatment) to illustrate relative effect size. Means by site are presented for each region. The ratio was only calculated for one site in Florida, due to the complete loss of all screened replicates from the second site. For the box plots, the upper and lower components of the box indicate the 75th and 25th quartiles, respectively. The middle line indicates the median value. Lines extend to the highest and lowest data values that are still within $1.5 \times$ interquartile range of the upper and lower quartiles. (B) Same as above with species occurrences pooled by site. (C) Species richness pooled at the regional scale for communities in the presence (open treatments) and absence (screened treatments) of predators, compared to overall regional richness (total observed across all treatments). Due to the limited replication at the regional scale, trend lines are provided to aid in visual interpretation only. Treatment values

of year, although predation was spatially and temporally variable (Table 2). Species richness was reduced from 10% in December (nine-day exposure) to 65% in April (seven-day exposure) in Panama. A seven-day exposure in Belize in January showed an intermediate effect size with communities losing 21–35% of species present (Table 2). Among-site variability also occurred in both tropical regions, but interestingly, the magnitude of the differences was consistent between regions. Percent species loss differed by 14% between sites in Belize for a seven-day exposure, while losses differed by 16% between sites in Panama for a three-day exposure. While there were species losses and gains in all communities, controls consistently underwent a net gain of species, which indicates that organisms were recruiting during these time periods as well. Therefore, the percentages reported do not include species that may have recruited and subsequently been consumed from the exposed communities during the deployments. Total percent cover was also reduced in all exposed communities in Panama (matched pairs, $P < 0.05$; see Plate 1 and Appendix C). Cover was not reduced on exposed communities in Belize most likely because initial cover (Fig. 1C) was already quite low (matched pairs, $P > 0.05$).

DISCUSSION

Our experimental results support the hypothesis that predation in this habitat is stronger and has a greater impact on species richness in the tropics than in temperate regions. At the community scale, we found that predation reduced species richness in the tropics by two to over ten times, while predation had no effect on species richness of subtropical and temperate communities. Furthermore, our results were consistent across communities (panels) at the scale of individual sites in the tropics, which exhibited up to eight times more species in the absence of predators compared to when predators were present. Additional experiments in the tropics further demonstrated that predation not only reduced species richness in more established communities but that these changes can occur rapidly over the course of one to several days. Our results are consistent with the limited but growing literature that suggests species interactions are stronger at lower latitudes (reviewed in Schemske et al. [2009]) and that these differences can differentially impact community structure across latitude (Menge and Lubchenco 1981, Freestone and Osman 2010).

← for Florida are given for one site only. However, overall regional richness is shown for both sites, which is a more appropriate comparison with the other regions. Therefore, the discrepancy in richness between the treatment values and the overall regional value in Florida is attributed to the richness observed at the second site. Data are presented for late-summer deployments only to standardize for sampling effort.

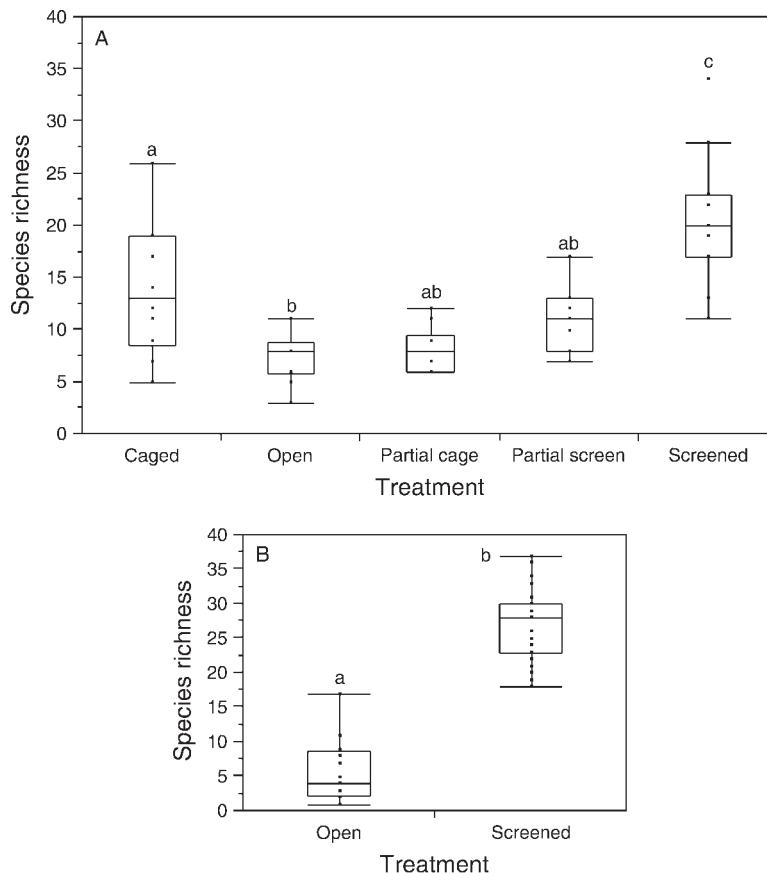


FIG. 3. Species richness among treatments in Panama for two three-month deployment intervals: (A) September–December 2008 and (B) December 2008–March 2009. Treatments that share letters indicate lack of statistical difference at $\alpha = 0.05$ (Tukey hsd).

Our interpretations are further supported by the result that richness did not increase until all predators were removed from the community (screened panels). Contrary to our original expectations, species richness was not higher in the 5mm cages that excluded only macropredators and was similar to treatments open to all predators. This result is consistent with other studies that have demonstrated the important impact micropredators can have on recruitment, composition, and cover of sessile marine invertebrate communities (Osman et al. 1992, Whitlatch and Osman 2009, Nydam and Stachowicz 2007). At our tropical sites, micropredators, such as juvenile *Mithrax sculptus* crabs, were very abundant and likely play a key role in the predation effects documented here. For example, in laboratory trials, *M. sculptus* were found to reduce species richness on screened panels down to levels observed on open panels over the course of only a few days (A. Freestone, unpublished data).

This result does not, however, demonstrate that larger predators are not important; rather, that in the absence of large predators that would otherwise compete for the limited prey resource or consume the micropredators themselves, small predators can have a comparable

impact on species richness as the full predator community. It was not possible to separate the relative importance of the different predator size classes in structuring the prey communities when the full predator community was present, given the strong effects of the micropredators alone and because effects of large and small predators are probably not additive. However, these results strongly support our hypothesis that predation is stronger at lower latitudes in that when communities are exposed to any amount of predation, either small predators alone or the full predator community, sizable effects on species richness occur. While subtle differences in water flow and shading, even among treatments and controls, are possible in any predator exclusion experiment and could impact experimental results, by exposing our diverse screened communities to predation, we were able confirm the significant impact the full predator community can have on species richness in the tropics.

Our patterns not only represent a consistent scaling relationship in the tropics, but also highlight the importance of predation in shaping patterns of species richness across latitude. The latitudinal diversity gradient is widely recognized as being scale dependent

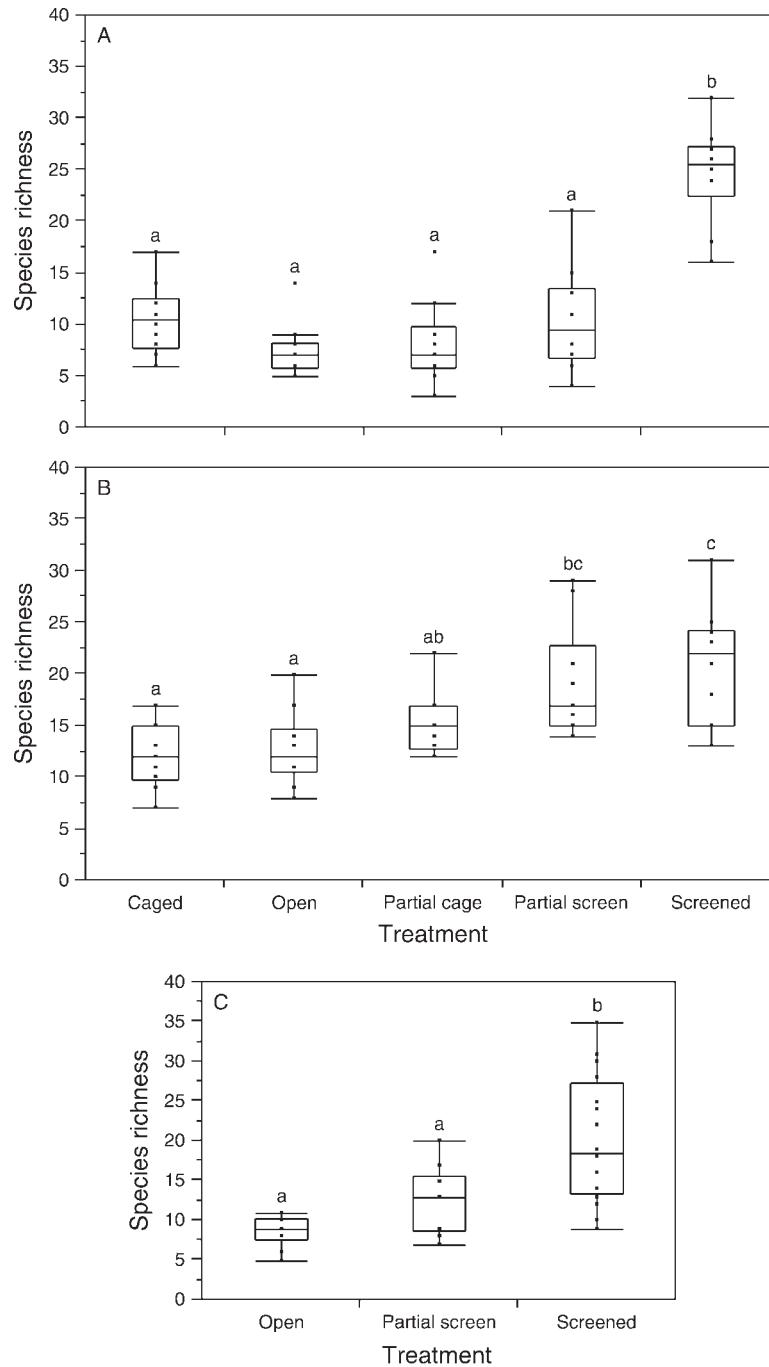


FIG. 4. Species richness among treatments in Belize for three three-month deployment intervals: (A) April–July 2008, (B) July–October 2008, and (C) October 2008–January 2009. Treatments that share letters indicate lack of statistical difference at $\alpha = 0.05$ (Tukey hsd).

(Hillebrand 2004a, Witman et al. 2004), with diversity at larger spatial scales more strongly correlated with latitude. Our work contributes a mechanistic element to these patterns and suggests that an increase in intensity of predation may limit local richness and abundance of species in the tropics while also shaping patterns of regional coexistence. Predation limited local

diversity in the tropics to the extent that communities that were exposed to predation exhibited an inverse latitudinal diversity gradient with fewer species co-occurring at small spatial scales than in the temperate zone (Fig. 1A). Even at larger scales (site and region), species that were observed in the presence of predators did not demonstrate a clear relationship with latitude

TABLE 2. Results of experimental exposures of three-month-old communities to predation (all $P < 0.05$).

Region, deployment date, and site	Exposure duration (d)	Species loss on exposed communities		Species gains on controls	N
		Number of species	%		
Belize, January 2009					
Twin Cays	7	4.2 of 20	21	2.8	10
Carrie Bow	7	7.2 of 20.5	35	1	10
Panama, December 2008					
Solarte	9	1.8 of 17.3	10	4.2	8
Panama, April 2009					
Solarte	7	16.4 of 25	65	4.5	13
Solarte	3	14.9 of 25.6	58	4.5	13
STRI Pt.	3	12 of 28.7	42	2	14
STRI Pt.	1	2.5 of 28	9		6

Note: The one-day exposure at STRI Pt. did not have a control, so no value is given for species gains on controls.

(Fig. 1D, 2C). However, in the absence of predators, species richness scaled from having a very weak relationship to latitude at the community scale (Fig. 1A), potentially indicating an upper limit to local richness, to a clear negative relationship with latitude at larger scales (Fig. 1D, 2C). Thus, only in the absence of predators did diversity patterns conform to the expected scale-dependent latitudinal diversity gradient (e.g., Witman et al. 2004) and it was these species that drove the cline of total observed regional species richness with latitude (Fig. 2C). In this system, strong predation likely promotes niche partitioning among species that utilize spatial variation in exposure to predation, as demonstrated here with our experimental “refuges,” as a mechanism of regional coexistence in the tropics. While interpreting latitudinal diversity gradients among a few regions should be done with caution, our study provides the first experimental evidence both for the magnitude of impact predation can have on limiting local diversity in the tropics in comparison to the temperate zone and the significant contribution predator-susceptible species have to the observed regional species pool in the tropics.

While our results did not demonstrate an effect of predation on species richness in the temperate zone, predation has been shown to increase species richness in temperate marine communities by limiting abundances of competitive dominants (Paine 1966). However, while space is an important limiting resource in these communities (Stachowicz et al. 1999, Barnes 2000), space was generally not limiting during the three-month experiments (Appendix B), suggesting that competition for space was relatively low over this timescale. Nevertheless, competitive hierarchies can be strong at high latitudes (Barnes 2006), and the role of predation in the coexistence of competitively inferior species may also increase both with latitude and timescale.

Latitudinal differences in other key variables, notably recruitment, may also interact with and be a consequence of consumer pressure. Recruitment rates can be

one to two orders of magnitude higher in the temperate zone compared to the tropics (Freestone et al. 2009). While these differences may mediate the impact of consumer pressure on species abundances, lower recruitment at low latitudes may in turn result from strong predation during the planktonic larval, settlement, and/or reproductive adult life stages (Menge 1991). However, regardless of these differences, over a three month timescale predation did not result in the complete elimination of community constituents at the local scale in the temperate zone, as it did in the tropics, nor did predator exclusions harbor unique species that substantially contributed to regional richness. Communities in Connecticut and Florida showed no difference among treatments in total percent cover or diversity estimates that incorporate relative abundances of species. In contrast, both diversity and percent cover were significantly reduced by predation in Panama. Thus, while predation is undoubtedly occurring at higher latitudes, our results suggest that the effect on the community is much greater in the tropics.

Importantly, while predation pressure was strong in the tropics, interaction strength was variable, both within and among tropical regions and times of year (Table 2; Figs. 2, 3, and 4). Spatial and temporal variation in interaction strength is a critical assumption of hypotheses that attribute strong biotic interactions in the tropics to higher rates of diversification (Schemske 2002) as well as coexistence over ecological time (Chesson 2000). However, while the relative effect varied among our experiments in the tropics, the presence of an effect was consistent, suggesting that predation plays a key role in shaping species richness patterns in the tropics.

Strong species interactions in the tropics have also been proposed to explain biogeographic patterns of species invasion. Lower nonnative species richness has been documented in the tropics, and one hypothesis attributes this pattern to stronger biotic resistance to invasion at low latitudes (Sax 2001, Hewitt 2002). Our

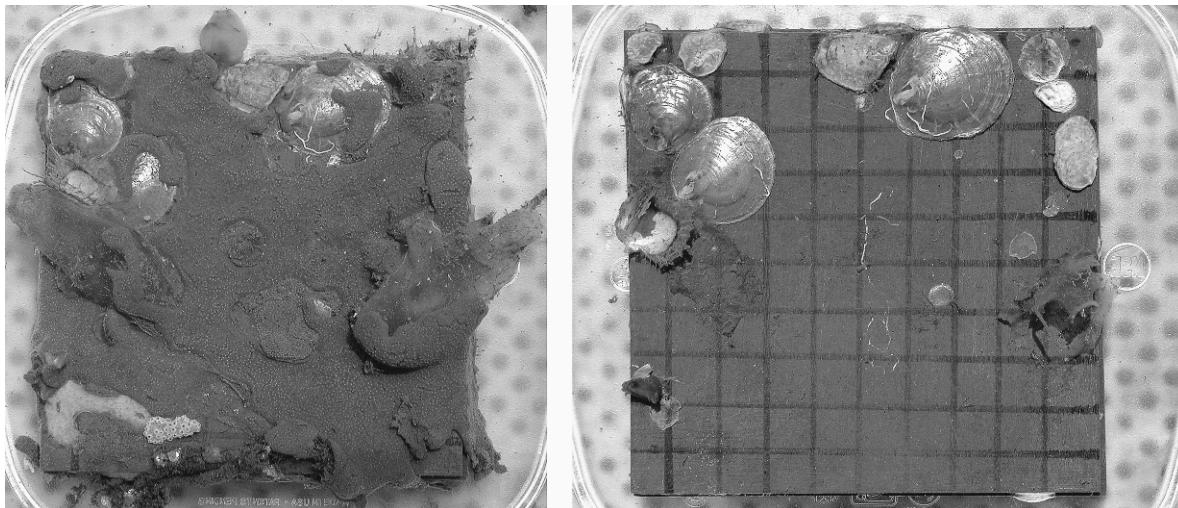


PLATE 1. Example of a community that developed without predators (screened treatment) for three months and was then exposed to predation for three days. Photographs are of the community (left) before and (right) after exposure at Solarte, Panama, in April of 2009. Panels are 100 cm². The underlying grid on the panel is only visible in the photograph on the right after predators consumed most of the invertebrates. The dominant colonial tunicate which is covering most of the panel in the photograph on the left is *Didemnum psammathodes*. See Appendix C for color versions of these photographs. Photo credit: A. L. Freestone.

results illustrate that community membership can be limited by predation at low latitudes, and this has three important implications for predicting the frequency and impact of species invasions in the tropics: (1) stronger predation could render tropical communities less susceptible to invasion relative to temperate communities, (2) establishment of nonnative species could be limited to spatial or temporal refuges from predation, and/or (3) strong predation could select for nonnative species that are well-defended against predation. We are at the beginning stages of experimentally linking local scale species interactions to regional diversity of both native and nonnative species, but the observed shift in interaction strength with latitude will be critical to understanding these dynamics.

ACKNOWLEDGMENTS

We are grateful to G. Ashton, K. Larson, S. Reed, C. Schloeder, and B. Sewall for field assistance and helpful discussion, and to S. Harrison and H. Cornell for reviewing an earlier draft of the manuscript. We also greatly appreciate the assistance of the faculty and staff at UCONN Avery Point, particularly R. Whitlatch, Smithsonian Marine Station at Fort Pierce, Caribbean Coral Reef Ecosystems Program, and STRI Bocas del Toro research station. Funding was provided by the Smithsonian's Marine Science Network Postdoctoral Fellowship (A. Freestone) and Scholarly Studies (G. Ruiz and M. Torchin) programs. This is Smithsonian Marine Station at Fort Pierce Contribution No. 834 and Smithsonian Caribbean Coral Reef Ecosystems Program Contribution No. 893.

LITERATURE CITED

- Barnes, D. K. A. 2000. Diversity, recruitment and competition on island shores at south-polar localities compared with lower latitudes: encrusting community examples. *Hydrobiologia* 440:37–44.
- Barnes, D. K. A. 2006. Temporal-spatial stability of competition in marine boulder fields. *Marine Ecology Progress Series* 314:15–23.
- Bertness, M. D., S. D. Garrity, and S. C. Levings. 1981. Predation pressure and gastropod foraging: a tropical-temperate comparison. *Evolution* 35:995–1007.
- Bolser, R. C., and M. E. Hay. 1996. Are tropical plants better defended? Palatability and defenses of temperate vs. tropical seaweeds. *Ecology* 77:2269–2286.
- Chase, J. M., E. G. Biro, W. A. Ryberg, and K. G. Smith. 2009. Predators temper the relative importance of stochastic processes in the assembly of prey metacommunities. *Ecology Letters* 12:1210–1218.
- Chesson, P. 2000. General theory of competitive coexistence in spatially-varying environments. *Theoretical Population Biology* 58:211–237.
- Coley, P. D., and J. A. Barone. 1996. Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics* 27:305–335.
- Connell, J. H. 1961. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecological Monographs* 31:61–104.
- Connell, J. H. 1970. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pages 298–313 in P. J. den Boer and G. R. Gradwell, editors. *Dynamics of populations*. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.
- Currie, D. J., G. G. Mittelbach, H. V. Cornell, R. Field, J. F. Guegan, B. A. Hawkins, D. M. Kaufman, J. T. Kerr, T. Oberdorff, E. O'Brien, and J. R. G. Turner. 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters* 7:1121–1134.
- Dobzhansky, T. 1950. Evolution in the tropics. *American Scientist* 38:209–221.
- Fawcett, M. H. 1984. Local and latitudinal variation in predation on an herbivorous marine snail. *Ecology* 65:1214–1230.
- Fischer, A. G. 1960. Latitudinal variations in organic diversity. *Evolution* 14:64–81.

- Freestone, A. L., and R. W. Osman. 2010. Latitudinal variation in local interactions and regional enrichment shape patterns of marine community diversity. *Ecology* 92:208–217.
- Freestone, A. L., R. W. Osman, and R. B. Whitlatch. 2009. Latitudinal gradients in recruitment and community dynamics in marine epifaunal communities: implications for invasion success. *Smithsonian Contributions to the Marine Sciences* 38:247–258.
- Garcia, E. A., and G. G. Mittelbach. 2008. Regional coexistence and local dominance in *Chaoborus*: species sorting along a predation gradient. *Ecology* 89:1703–1713.
- Heck, K. L., G. Hays, and R. J. Orth. 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. *Marine Ecology Progress Series* 253:123–136.
- Heck, K. L., and K. A. Wilson. 1987. Predation rates on decapod crustaceans in latitudinally separated seagrass communities: a study of spatial and temporal variation using tethering techniques. *Journal of Experimental Marine Biology and Ecology* 107:87–100.
- Hewitt, C. L. 2002. The distribution and diversity of tropical Australian marine bioinvasions. *Pacific Science* 56:213–222.
- Hillebrand, H. 2004a. On the generality of the latitudinal diversity gradient. *American Naturalist* 163:192–211.
- Hillebrand, H. 2004b. Strength, slope and variability of marine latitudinal gradients. *Marine Ecology Progress Series* 273:251–267.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104:501–528.
- Jeanne, R. L. 1979. A latitudinal gradient in rates of ant predation. *Ecology* 60:1211–1224.
- MacArthur, R. H. 1969. Patterns of communities in the tropics. *Biological Journal of the Linnean Society* 1:19–30.
- Menge, B. A. 1991. Relative importance of recruitment and other causes of variation in rocky intertidal community structure. *Journal of Experimental Marine Biology and Ecology* 146:69–100.
- Menge, B. A., and J. Lubchenco. 1981. Community organization in temperate and tropical rocky inter-tidal habitats: prey refuges in relation to consumer pressure gradients. *Ecological Monographs* 51:429–450.
- Mittelbach, G. G., et al. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters* 10:315–331.
- Nydam, M., and J. J. Stachowicz. 2007. Predator effects on fouling community development. *Marine Ecology Progress Series* 337:93–101.
- Osman, R. W., R. B. Whitlatch, and R. J. Malatesta. 1992. Potential role of micropredators in determining recruitment into a marine community. *Marine Ecology Progress Series* 83:35–43.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* 100:65–75.
- Pennings, S. C., and B. R. Silliman. 2005. Linking biogeography and community ecology: latitudinal variation in plant–herbivore interaction strength. *Ecology* 86:2310–2319.
- Peterson, B. J., K. R. Thompson, J. H. Cowan, and K. L. Heck. 2001. Comparison of predation pressure in temperate and subtropical seagrass habitats based on chronographic tethering. *Marine Ecology Progress Series* 224:77–85.
- Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. *American Naturalist* 100:33–46.
- Ruzicka, R., and D. F. Gleason. 2008. Latitudinal variation in spongivorous fishes and the effectiveness of sponge chemical defenses. *Oecologia* 154:785–794.
- Sanford, E., M. S. Roth, G. C. Johns, J. P. Wares, and G. N. Somero. 2003. Local selection and latitudinal variation in a marine predator-prey interaction. *Science* 300:1135–1137.
- Sax, D. F. 2001. Latitudinal gradients and geographic ranges of exotic species: implications for biogeography. *Journal of Biogeography* 28:139–150.
- Schemske, D. W. 2002. Ecological and evolutionary perspectives on the origins of tropical diversity. Pages 163–173 in R. L. Chazdon and T. C. Whitmore, editors. *Foundations of tropical forest biology*. University of Chicago Press, Chicago, Illinois, USA.
- Schemske, D. W., G. G. Mittelbach, H. V. Cornell, J. M. Sobel, and K. Roy. 2009. Is there a latitudinal gradient in the importance of biotic interactions. *Annual Review of Ecology, Evolution, and Systematics* 40:245–269.
- Stachowicz, J. J., R. B. Whitlatch, and R. W. Osman. 1999. Species diversity and invasion resistance in a marine ecosystem. *Science* 286:1577–1579.
- Vermeij, G. J. 1978. *Biogeography and adaptation: patterns of marine life*. Harvard University Press, Cambridge, UK.
- Waycott, M., et al. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences USA* 106:12377–12381.
- Whitlatch, R. B., and R. W. Osman. 2009. Post-settlement predation on ascidian recruits: predator responses to changing prey density. *Aquatic Invasions* 4:121–131.
- Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution and Systematics* 34:273–309.
- Witman, J. D., R. J. Etter, and F. Smith. 2004. The relationship between regional and local species diversity in marine benthic communities: A global perspective. *Proceedings of the National Academy of Sciences USA* 101:15664–15669.
- Witman, J. D., and K. P. Sebens. 1992. Regional variation in fish predation intensity: a historical perspective in the Gulf of Maine. *Oecologia* 90:305–315.
- Wulff, J. L. 2005. Trade-offs in resistance to competitors and predators, and their effects on the diversity of tropical marine sponges. *Journal of Animal Ecology* 74:313–321.