

**INTERACTIVE EFFECTS OF PREDATION AND ASSEMBLY TIME ON
TROPICAL BUT NOT TEMPERATE MARINE INVASIONS**

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by
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ABSTRACT

Non-native species richness has been observed to peak at mid-temperate latitudes, shaping a pattern of richness and abundance that is distinct from native species patterns that peak in the tropics. Stronger species interactions, and therefore biotic resistance, may lower invasion success in the tropics and help explain the discrepancy between native and non-native richness and abundance. To test the hypothesis that strong predation and competition in the tropics could limit invasion success, we conducted a distributed experiment on sessile marine invertebrate communities in four regions spanning 47-degrees latitude of the eastern Pacific Ocean. We manipulated predator access and resource availability at 12 sites and sampled experimental communities in early and late stages of assembly. Overall, our results suggest that biogeographic location, assembly timescale, and predation interactively shape invasion success across latitude. Strong predation reduced richness of non-native species in the tropics at both assembly timescales but increased non-native species richness in the subtropics during early assembly. Predation also increased non-native abundance in the tropics by late-stage assembly and shaped non-native composition at both assembly stages. Effects of predation at higher latitudes were weak or undetectable, and increasing resource availability never had a positive impact on non-native richness or abundance at any latitude. Further, non-native richness was greater at early relative to late assembly stages at mid to low latitudes and was consistently low in our high latitude region at both timescales. In a complementary experiment, short-term predator exposure reduced non-native abundance in Panama, further confirming the influence of predation in this tropical region. Our results highlight important biogeographic differences in invasion dynamics and disentangle local mechanisms that can shape regional patterns.

I dedicate my thesis to my fiancé, Joseph Sheely, whose unwavering support, and love have been my anchor through this journey. To my two pups, Charlee and Zeke, whose companionship and boundless energy have brought me joy and comfort during the toughest times and latest nights. To my parents, Tracy and Tom Stevenson, for their endless encouragement, guidance, and sacrifices that have shaped me into the person I am today. And last, but certainly not least, to my sisters, Hannah and Brianna Stevenson, for their constant love, inspiration, and the shared laughter that kept me grounded.

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CHAPTER 1

INTRODUCTION

Patterns of native and non-native richness and abundance can vary across different latitudes, and understanding these patterns is important for predicting and managing global invasions (Lonsdale 1999, Sax 2002). The introduction of non-native species into new environments can change patterns of biodiversity, alter habitats, and possibly harm economies (Stachowicz et al. 2002). However, non-native species' patterns can vary from one another as some have limited ranges due to dispersal limitation, abiotic filters, and biotic resistance, while others have ranges that span from temperate to tropical regions (Sax and Gaines 2008). As the number of invasions increases globally, it is important to understand large-scale patterns in invasions dynamics (Ruiz et al. 2011).

The latitudinal diversity gradient, which describes the decline in species richness from the equator to the poles, is a well-established pattern for native species and has been shown for all major taxonomic groups (Hillebrand and Associate Editor: Chris 2004, Tittensor et al. 2010). In contrast, while native species richness peaks in tropical latitudes, non-native species richness can peak at mid-temperate latitudes, with lower richness in both tropical and high-latitude regions (Sax 2001, Fridley et al. 2007). This pattern across latitude has been observed for many non-native taxa, including terrestrial mammals, birds, and plants (Sax 2002). A decline in invasion success in the tropics could result from an under-sampling of tropical ecosystems as well as historical patterns of biotic exchange and propagule pressure (Lonsdale 1999, Fridley et al. 2007, Seebens et al. 2017).

Biogeographic differences in species interaction strength may further underlie these latitudinal patterns. One leading evolutionary hypothesis for the tropical peak in native biodiversity is the Biotic Interactions Hypothesis which suggests that strong species interactions in the tropics increase the rate of diversification, ultimately creating high tropical biodiversity (Schemske et al. 2009). Recent large-scale experiments support the prediction that species interactions, particularly predation, can indeed be intense in the tropics, and shape patterns of community diversity, biomass, and composition over ecological time (Freestone et al. 2011). Strong species interactions in the tropics, however, may also increase biotic resistance and limit invasion success (Freestone et al. 2013, Kimbro et al. 2013, Freestone et al. 2021), although we are at the early stages of understanding how these invasion processes unfold across broad biogeographic scales.

Predator-prey interactions play a crucial role in shaping ecosystem dynamics and the intensity and impact of predation on communities can be greater in the tropics (Freestone et al. 2011). The variation in predation strength across different latitudes likely has profound consequences for the structure of communities over ecological and evolutionary timescales worldwide (Silvestro et al. 2020). Furthermore, predation has the potential to exert a substantial influence on the fundamental processes of prey community assembly and stability. As a result, it actively shapes the patterns of prey composition and diversity at multiple scales (Jurgens et al. 2017). Predation can also act as a strong mechanism of biotic resistance to invasions (Sax 2001), with impacts that are stronger in the tropics, particularly in marine systems (Freestone et al. 2013, Kimbro et al 2013).

Standardized experimental comparisons of the impact of predation on non-native species success across latitude, however, are rare.

In addition to predation, competition can also serve as a strong agent of biotic resistance in communities (Santamaría et al. 2021), with effects that may also vary across latitude. The more diverse native ecosystems in the tropics may harbor stronger competitive dynamics, possibly increasing resistance to invasion (Fridley and Sax 2014). The prediction of stronger competition in the tropics aligns with the biotic interactions hypothesis and therefore has strong theoretical support (Schemske et al. 2009, Roslin et al. 2017). In contrast, hierarchical competitive structure that is common in polar environments may serve to resist invasion (Barnes 2002), suggesting that competition may also support biotic resistance at high latitudes. Few experimental studies have attempted to experimentally test the impacts of competition across latitude, however, and its role in structuring invasion outcomes.

We aimed to reveal the interactive effects of competition and predation on species invasion success across latitude during different assembly timescales using a large-scale experiment, spanning the subarctic to the tropics, in a nearshore marine ecosystem. We tested the hypotheses that (1) the changing relative influences of both competition and predation with latitude will result in latitudinal differences in invasions by non-native species. (2) Non-native species will have greater abundance and richness in mid-latitudes due to high biotic resistance in the tropics and harsh abiotic conditions at high latitudes. (3) Early timescales will harbor more non-native species due to their ability to colonize quickly. Understanding the mechanisms driving biogeographic patterns of invasion can help inform management strategies across different latitudes and regions (Sax 2002,

Pyšek et al. 2020). By integrating these ecological interactions and temporal dynamics, our research provides a comprehensive framework for predicting invasion success and formulating targeted interventions to mitigate the impact of invasive species.

Furthermore, this study underscores the importance of considering both biotic and abiotic factors in invasion biology, highlighting the complex interplay between ecological processes and environmental gradients.

CHAPTER 2

METHODS

2.1 Study System

To investigate how predation and competition impact marine invasions across latitudes, we conducted a large-scale distributed experiment across 47 degrees of latitude on the Pacific coast of North and Central America that focused on nearshore marine sessile invertebrate communities (Freestone et al. 2021). These diverse multiphyletic communities include bryozoans, ascidians, sponges, polychaetas, barnacles, hydroids, and bivalves. They are ideal systems for these questions given their fast growth and recruitment rates, their ability to colonize natural and artificial hard substrates, and their experimental tractability (Freestone et al. 2021). Furthermore, over 340 non-native marine species are established on the west coast of the continental US, which makes the Pacific Coast of North America an excellent model of nearshore invasion dynamics (2023, Guard 2023).

Experiments were conducted in four regions, spanning from the subarctic to the tropics (Appendix S1: Fig S1; (Freestone et al. 2021). Our focal regions were: (1) subarctic Ketchikan, Alaska (55° N, 131° W), mid-temperate San Francisco, California (37° N, 122° W), subtropical La Paz, Mexico (24° N, 110° W) and tropical Panama City, Panama (8° N, 79° W). To capture the variability in each region, experiments were conducted at three sites within each of the four regions, for a total of twelve study sites across the latitudinal gradient. Each site was a recreational marina in high salinity (mean > 20 ppt) nearshore habitat, and sites were separated by at least 10km to ensure

independence and limit among-site dispersal. To capture temporal changes in species interactions, experiments were conducted at two distinct stages of community development. Experiments focusing on early-assembly dynamics were conducted for three months and late-assembly experiments were conducted for 12 months. Experiments were initiated during the season of high productivity in each region based on seasonal climate and oceanographic dynamics. Experiments were deployed in Alaska in June 2015, California in May 2016, Mexico in June 2017, and Panama in December 2015. One site in Panama needed to be redeployed after the loss of panels due to storms in spring of 2016.

To standardize habitat among the distinct biogeographic regions, we used polyvinyl chloride (PVC) settlement panels ($14 \times 14 \times 0.95$ cm & sanded on one side) as model habitat for our focal prey communities of sessile marine invertebrates. Panels were deployed from floating docks at 1m depth and were hung upside down facing the sea floor to limit algal growth. By hanging the panels above the sea floor, we limited access to the prey communities by benthic predators to focus more directly on the contribution of fish to predation dynamics. All panels were deployed clean, and invertebrate larvae were allowed to undergo natural settlement and growth under randomly assigned experimental conditions for either three or twelve months.

2.2 Predator Exclusion & Competition Experiments

To test the effects of predation and competition on invasion dynamics, we conducted a factorial experiment that manipulated predator access and resource availability for our focal prey communities. To test the effect of predation, we used three predator exclusion treatments: (1) low predation treatment (caged), (2) ambient predation

control (no cage), and (3) ambient predation procedural control (partial cage). Cages and partial cages (18 cm × 18 cm × 7 cm) were made of marine grade plastic with a 6.35mm mesh to exclude macropredators. Cages fully enclosed the experimental panel, and partial cages had four sides but no front, which faced the seafloor when deployed. Partial cages were employed to control for shading and altered flow dynamics while allowing full access to the predator community. Cages were cleaned and maintained every two weeks to ensure their integrity and prevent overgrowth.

To test the effect of competition on invasion dynamics, we experimentally increased a primary limiting factor in this system, space, through standardized biomass removals (Bonfim et al. 2024). We employed three biomass removal treatments: (1) no removal (0% removed), (2) low biomass removal (18% of surface biomass was removed), and (3) high biomass removal (54% of surface biomass was removed). To remove biomass, we scraped random 2.54cm-wide vertical sections of the settlement panel (1 vertical section for the low biomass removal treatment; 3 vertical sections for the high biomass removal treatment), thereby removing any invertebrates in those areas and creating open space for new colonizers. Biomass removals occurred 1, 2, 6, 10, and 11 months after deployment of the experiment. Therefore, 3-month experimental panels were exposed to two biomass removal events, and 12-month panels experienced five scraping events.

We employed a factorial design, and therefore the three predation and three competition treatments were fully crossed yielding nine treatment combinations. These treatment combinations were randomly assigned to panels and were replicated five times at each of the 12 sites. In addition, two independent sets of these experimental panels

were deployed at each site to enable retrievals after three and twelve months. Due to constraints on field work in Mexico, however, we were not able to conduct a full factorial experiment in this region for the 12-month deployment; therefore, Mexico is included in 3-month analyses only. This experimental design included a total of 945 experimental units (panels) across the 12 sites and two timeframes.

Panels were then retrieved after three or twelve months, weighed for biomass measurements, and then sampled for their sessile invertebrate composition. Invertebrates were identified to the lowest taxonomic unit possible, usually species, using a dissecting microscope and commonly used external diagnostic characteristics. Specimens of each species were collected, and identifications were confirmed by taxonomic experts and DNA barcoding whenever possible. We then used the National Exotic Marine and Estuarine Species Information System (NEMESIS; (Fofonoff PW 2018) to assign status to confirmed species and complemented status information with published literature. Species were designated as native, introduced, or cryptogenic (species of unknown origin; (Carlton 1996)). For the purposes of our analyses, we pooled the cryptogenic with the native category to have a conservative estimate of invasions.

Richness of non-native species on each panel was recorded as the total number of non-native species identified after a complete census of invertebrates present on each panel. Abundance was calculated as the percent cover of each taxonomic group using a 50-point grid and accounting for multiple layers of species at each point. All taxa present at each of the 50 points were recorded as an observation. Given that overgrowth is common in these communities, the number of observations of taxa often exceeded 50. Abundance of non-native species on each panel was a percentage calculated by dividing

the total number of observations of non-native species by the total number of taxa observations on each panel.

2.3 Predator Exposure Experiment

As an additional experiment to test the hypothesis that predator impact on non-native species is stronger in the tropics, we conducted a short-term 3-day exposure experiment where mature communities were exposed to predation. This short-term experiment complemented the longer-term predator exclusion experiment that examined aggregate impacts of predation as communities assembled over time. Panels for the exposure experiment (>20 per site) were initially deployed in full predator exclusion cages, using the same cages as described above, to allow assembly under reduced predation. After the initial assembly period of 3 or 12 months, ten panels were retrieved per site, and measurements of biomass and species composition were recorded using non-destructive sampling of abundance on the 50-point grid. Panels were then redeployed in their initial locations to begin the 3-day exposure experiment. Five panels per site and per assembly time period were redeployed without cages to expose those communities to predation (no cage; n=120, while the remaining five panels were re-caged as controls (cage; n=120). At the conclusion of the 3-day exposure, communities were again retrieved and sampled for richness and composition following methods employed in the factorial experiment.

2.4 Data Analysis

2.4a Predator Exclusion & Competition Experiments

To examine how invasion dynamics varied across latitude within these communities, linear mixed models (LMM) were used to test the hypothesis that predation

and competition effects on introduced species richness and relative abundance would vary by region and assembly timescales. Richness and relative abundance of non-native species were modeled separately using the same predictor variables. We tested the fixed effects of region, treatment (predator exclusion [full cage, open, partial] and biomass removal [no removal, low, high]), assembly timescale (3 and 12 months), and all interactions. Site (nested within region) and its interactions with treatment and timescale were included as random factors. Four sets of models were constructed to test these interactive effects of predation and biomass removal over two different assembly timescales. The first model tested the effects on non-native richness after 3 months across all 4 regions, while the second model examined non-native abundance over the same period. The third model, like the first, assessed non-native richness but over 3 and 12 months in 3 regions, excluding Mexico due to incomplete data. The final model examined non-native abundance over 3 and 12 months in 3 regions, again excluding Mexico.

For the response variables of richness and abundance, we fit and compared a series of models: a zero-inflated gamma, zero-inflated Gaussian model, and a gaussian linear model without zero inflation. These three models were compared using corrected Akaike Information Criteria (AICc) values to select the most parsimonious model. Linear models with Gaussian distributions were selected when examining richness. Among the three models tested for abundance, the zero-inflated model with a Gaussian distribution was selected for the 3-month abundance model and the linear model with Gaussian distribution was selected for the 3- and 12-month abundance model.

To test for regional differences in the effects of predation and competition on invasion success, planned contrasts were conducted to compare introduced species richness and abundance under ambient levels of predation (experimental [no cage] and procedural [partial cage] controls) versus low predation (caged) as well as between high and low levels of biomass removal at the 3- and 12-month assembly timescale in each region using Holm tests. We also conducted planned contrasts to test for differences between the experimental (no cage) and procedural (partial cage) controls, but these treatments did not differ in any model ($p > 0.05$), and we therefore only report the predation contrasts. We used the Shapiro-Wilk test and Levene's test to check for normality and homoscedasticity of residuals, respectively. All analyses and visualizations were performed in R version 4.2.3 (R Development Core Team 2022) using the packages `glmmTMB` (Brooks et al. 2017) for GLMMs; `lme4` (Bates et al. 2015) and `lmerTest` (Kuznetsova et al. 2017) for LMMs; `emmeans` (Lenth 2022) for multiple comparison analysis; `car` (Fox and Weisberg 2019) for Levene's tests; and `DHARMA` (Hartig 2022) for overdispersion tests of residuals.

To test for regional differences in the effect of predation and competition on introduced species composition, we conducted multivariate analyses on introduced species abundances across the two assembly timescales for each region individually. We first calculated Bray–Curtis dissimilarity distances among communities based on relative abundances of introduced species. We then examined the fixed effects of predation treatment (3 levels), biomass removal treatment (3 levels), the random effect of site (nested in region), and all interactions, on community dissimilarity using permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001). To align with our

other analyses, we ran two versions of this model using: (1) 3-month data only for all four regions, and (2) 3- and 12-month data for three regions (without Mexico), which included a fixed factor of time. Monte Carlo (MC) tests were used to calculate p-values. We further performed pairwise comparisons to identify specific treatment and assembly timescale differences for each region. To explore the contribution of individual introduced species to the dissimilarities among communities, we used similarity percentage analysis (SIMPER) to compare levels of the factors of time and treatment. The analysis aimed to identify the key species contributing to the observed dissimilarity. All multivariate analyses were performed on PRIMER (Anderson, 2008).

2.4b Predator Exposure Experiment

In the predator exposure experiment, relative abundance of non-native species was modeled to test for regional and temporal variation in predator intensity and impact. We tested the fixed effects of region, predator exposure treatment (control: full cage, exposed: no cage), sampling interval (before and after exposure), assembly timescale (3 and 12 months), and all interactions. Site (nested within region) and its interactions with treatment and timescale were included as random factors. Two sets of models were constructed to test these interactive effects of predation over two different assembly timescales. The first model tested the effects on non-native abundance after 3 months across all 4 regions, while the second model examined non-native abundance over 3 and 12 months. To test for regional differences among the predator exposure treatments, planned contrasts were used to test for differences in abundance before and after redeployment (sampling interval) for each treatment and assembly timescale in each region.

We then conducted multivariate analyses on non-native species abundances across the two assembly timescales and sampling intervals to examine variation in species composition. We first calculated Bray–Curtis dissimilarity distances among communities based on relative abundances of introduced species. We then examined the fixed effects of = exposure treatment (controls and exposed), sampling interval (before and after), and assembly timescale (3- and 12-months), the random effect of site (nested in region), and all their interactions on community dissimilarity using permutational multivariate analysis of variance (PERMANOVA) in our tropical region of Panama. (Anderson, 2001). Carlo (MC) tests were used to calculate p-values.

CHAPTER 3

RESULTS

Across the 12 sites in our four study regions, we detected 193 sessile taxa representing Anthozoa, Ascidiacea, Bivalvia, Bryozoa, Cirripedia, Gastropoda, Hydrozoa, Porifera, Sabellidae, Serpulidae, and Spirorbidae. We observed 60 taxa in Alaska, 55 in California, 99 in Mexico, and 94 in Panama. Of these 193 taxa, 17 species were identified as non-native in Panama, 16 in Mexico, 18 in California, and 4 in Alaska. Therefore, as predicted, temperate California had the highest regional richness of non-native taxa, closely followed by our low latitude regions of Mexico and Panama, while subarctic Alaska had the fewest number of non-native taxa (Appendix S1: Fig S2). Furthermore, California had the highest proportion of non-natives identified compared to total taxa identified. As the overall biodiversity increased towards low latitudes, however, the number of unresolved taxa also increased due to taxonomic gaps and/or uncertainty. Only confirmed species identifications with non-native status were considered non-native species in our analyses, to ensure a conservative estimate of invasion. Our non-native species list nevertheless includes the most abundant non-natives and therefore still captures a strong signal of invasions across latitude.

3.1 Predator Exclusion & Competition Experiments

Predation impacted non-native invertebrate community richness at both early and late community assembly timescales, but only in lower latitude regions, with the strongest and most consistent effects in tropical Panama. Predator exclusion effects did not interact with resource availability in any model (interaction effect, $p > 0.05$), indicating predation had a strong and independent effect (Appendix S1: Table S1).

When examining early assembly invasion dynamics across all four study regions, predation decreased non-native species richness in Panama (Fig 1; Region \times Treatment: $F_{6,15.997} = 3.909$, $p = 0.013527$; contrasts: Panama: $t = -2.61$, $p = 0.045$) while increasing non-native species richness in Mexico ($t = 3.38$, $p = 0.015$) but had no effect in California or Alaska (Appendix S1: Table S1, Table S2). When testing for predation effects across both early and late assembly stages in three focal regions, predation again decreased non-native species richness in Panama (Region \times Treatment $F_{4,96.38} = 4.16$, $p = 0.0024$; contrasts: Panama: $t = -3.73$, $p = 0.028$) at both assembly timescales but had no effect on California or Alaska (Appendix S1: Fig S3).

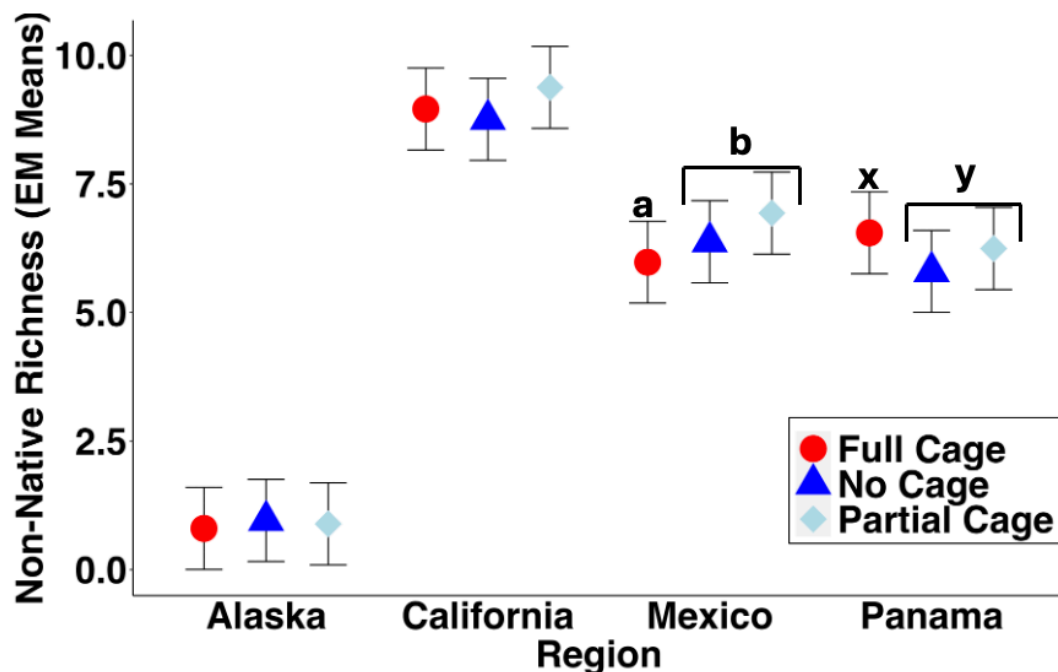


Figure 1. Effects of predator exclusion on non-native species richness at an early assembly timescale expressed as estimated marginal means from mixed models (+/ SE). Letters indicate significant treatment contrasts between treatment and controls ($\alpha = 0.05$). Brackets indicate combined contrast of procedural control and control treatment types

(partial caged and no caged). Refer to methods for details on process of grouping controls together.

In contrast to a decrease in non-native richness due to predation in Panama, predation increased non-native species abundance in Panama, but this pattern only emerged at the late assembly timescale (Fig 2; Region \times Treatment \times Assembly Timescales: $F_{4,71.595} = 4.38$, $p = 0.0032$ contrasts: Panama, 12 months: $t = 3.31$, $p = 0.016$). While predation also increased the abundance of non-native species in California at the early assembly timescale ($t = -2.96$, $p = 0.033$), this pattern was no longer present at late assembly. There were no predation effects observed in Alaska at either timescale (Fig 2; Appendix S1: Table S1, S2).

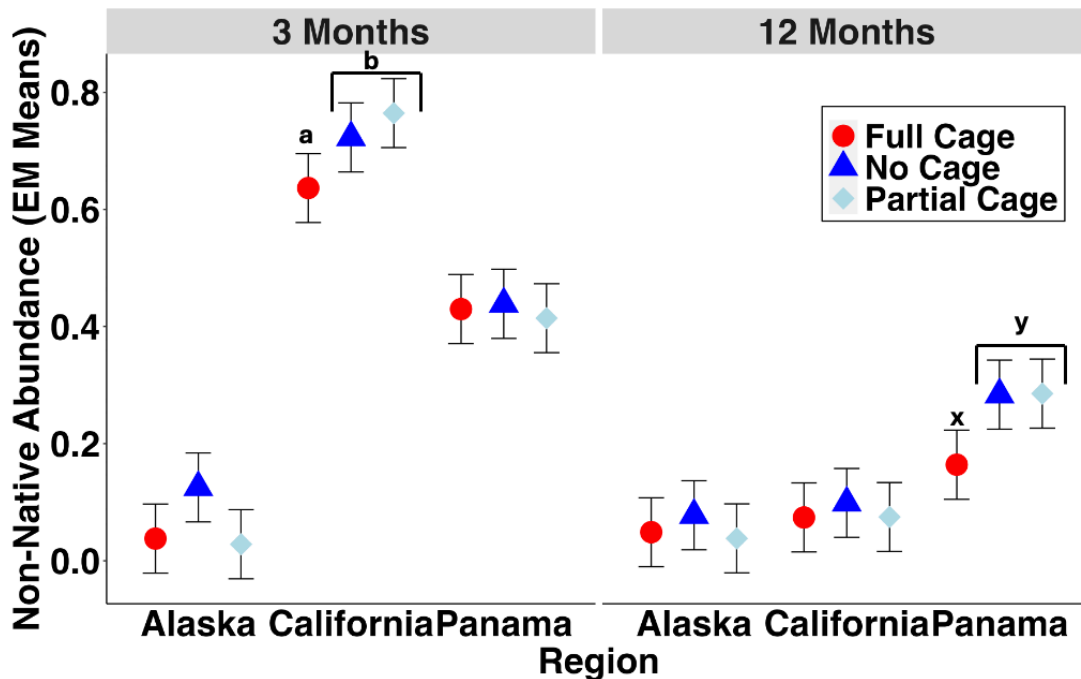


Figure 2. Effects of predator exclusion on non-native species abundance over an early (left side) and late (right side) assembly timescale expressed as estimated marginal means from mixed models (+/ SE). Letters indicate significant treatment contrasts ($\alpha = 0.05$).

Brackets indicate combined contrast of procedural control and control treatment types (partial caged and no caged). Refer to methods for details on process of grouping controls together.

Across both early and late assembly stages, predation shaped community composition of non-native species, but only in tropical Panama. At early assembly, predation had a strong effect on non-native composition in Panama (Fig 3; PERMANOVA: predator exclusion contrast: pseudo- $F_1 = 19.92$, $p = 0.003$; Appendix S1: Table S3) but not in Alaska, California, or Mexico. The top contributing species to non-native community dissimilarity between caged and control treatments in Panama was *Ascidia sydneyensis*, a soft-bodied solitary ascidian, accounting for 37% of the dissimilarity between treatments. *A. sydneyensis* was the dominant species when macropredators were excluded, with an average abundance of 47%, but was absent under ambient predation (Appendix S1: Table S4). In contrast, two calcified species, *Amphibalanus reticulatus*, a barnacle, and *Schizoporella pungens*, an encrusting bryozoan, were the dominant species in control communities that were open to ambient predation. Both species were over two to three times less abundant when macropredators were excluded, with a combined contribution of nearly 50% to the dissimilarity between treatments. At late assembly, predation continued to shape composition of non-natives in Panama (PERMANOVA: predator exclusion contrast: pseudo- $F_2 = 9.17$, $p = 0.001$; Appendix S1: Table S3). Interestingly, by 12 months, *S. pungens* had replaced *A. sydneyensis* as the dominant non-native species in both caged and control treatments, with the average abundance of *S. pungens* again being over two times higher under ambient predation, contributing 61% to treatment dissimilarity. The effect of predation was 1.83

times stronger on non-native composition at three months than 12 months (PERMANOVA; Predation treatment x Assembly Timescale: pseudo- $F_2 = 5.26$, $p = 0.001$; Appendix S1: Table S3), possibly due to the decline in overall abundance of the soft-bodied *A. sydeiensis* (Appendix S1: Table S4).

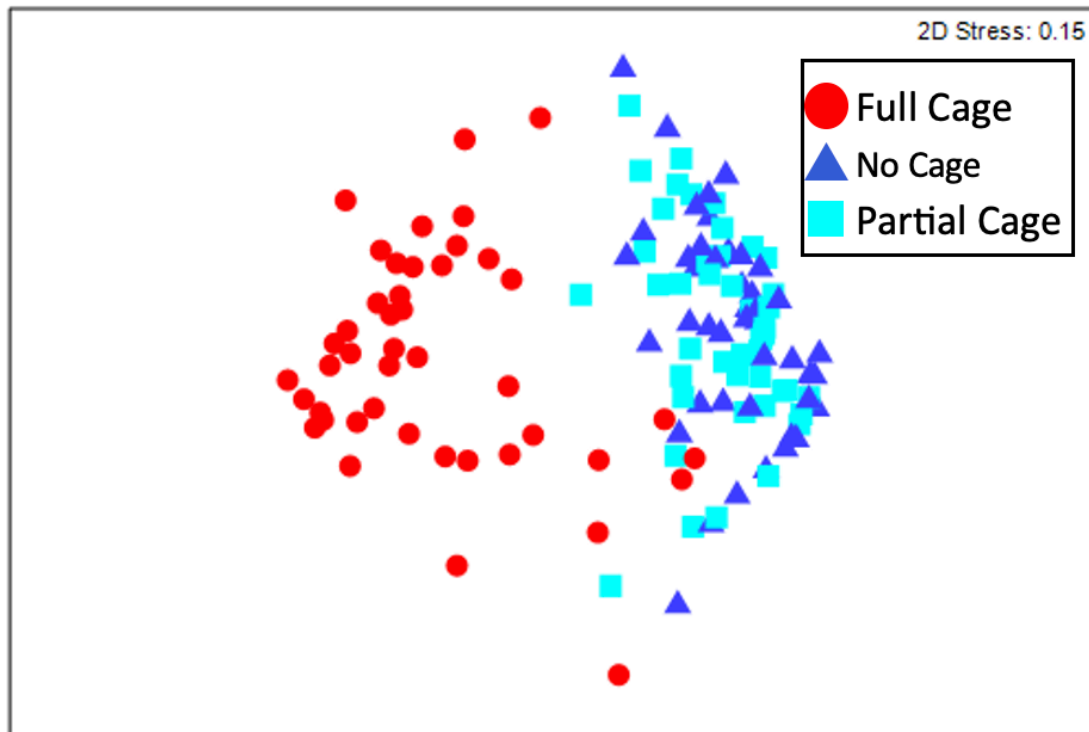


Figure 3. Multidimensional scaling plot for non-native communities in Panama after 3 months. Symbols indicate treatments. Communities across three sites are shown. Each point is a single community on a panel, and closer relative proximity among points indicates greater compositional similarity.

Although abundance did not vary significantly in subtropical Mexico, different species were contributing to the compositional change over predator exclusion treatments. The top contributing species to non-native community dissimilarity between caged and control treatments in Mexico was *C. inaudita*, an encrusting bryozoan,

accounting for 27% of the dissimilarity between treatments. *S. pungens* and *W.* were the two other species accounting for 14% and 11% of the dissimilarity, respectively (Appendix S1: Table S4).

Despite the substantial increase in resource availability provided by the biomass removals, these treatments had limited impacts on the non-native community. Biomass removals decreased non-native species abundance at the early assembly timescale in tropical Panama (3- month Assembly timescale: Region \times Competition: $F_{4,71.595} = 4.38$, $p = 0.029$ contrasts: Panama: $t = -4.13$, $p = 0.005$), but had no effect during late assembly in Panama, in other regions at either timescale, or on non-native species richness in any region ($p > 0.05$; Appendix S1: Table S1, Table S2; Fig S4).

Assembly timescale also had an independent effect on non-native richness at low and mid latitude regions. Non-native species richness was greater at 3 months relative to 12 months in Panama (Fig 4; Region \times Assembly Timescales $F_{2,6.001} = 16.99$, $p = 0.0034$; contrasts: Panama: $t = -3.67$, $p = 0.02$) and California ($t = -8.32$, $p = 0.0005$; Appendix S1: Table S1, S2). In Panama, striking compositional differences were apparent between the assembly timescales (Fig 5; Appendix S1: Table S3), and highlighted the decline in *Ascidia sydneinsis* and *Amphibalanus reticulatus* from three to twelve months, and the slight increase in *Schizoporella pungens* at twelve months that collectively contributed over 85% to the temporal dissimilarity (SIMPER; Appendix S1: Table S4).

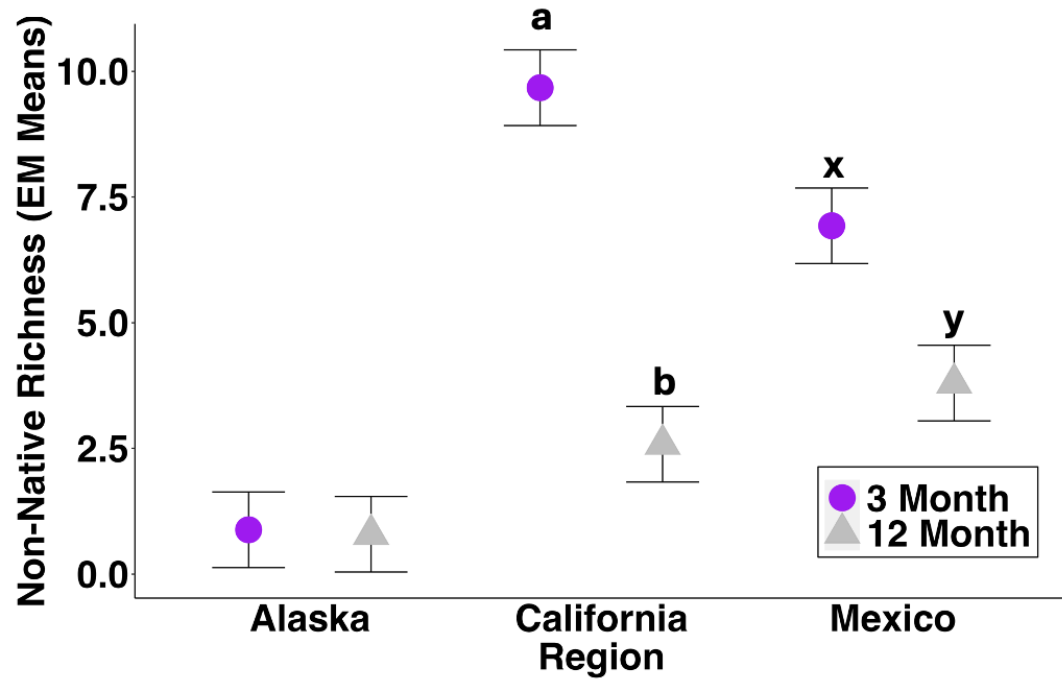


Figure 4. Effects of assembly timescales on non-native species richness expressed as estimated marginal means from mixed models (+/ SE). Asterisks indicate significant treatment contrasts ($\alpha = 0.05$).

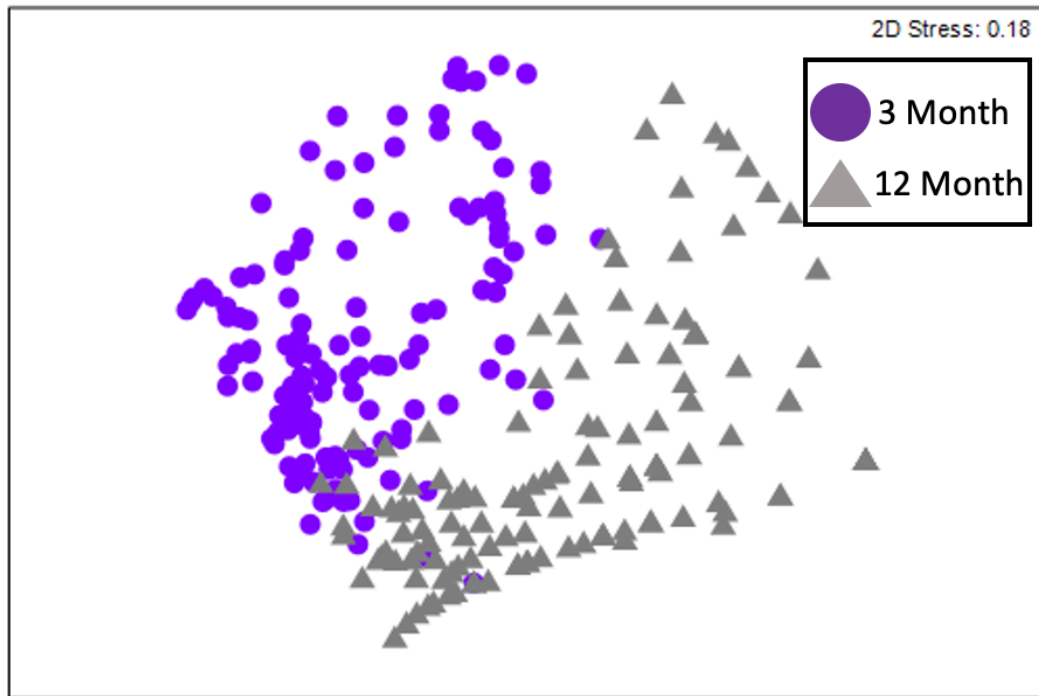


Figure 5. Multidimensional scaling plot for non-native communities in Panama over both assembly timescales. Symbols indicate assembly timescales. Communities across three sites are shown. Each point is a single community on a panel, and closer relative proximity among points indicates greater compositional similarity.

3.2 Predator Exposure Experiment

Short-term exposure to predation caused a clear reduction in non-native species abundance in the tropics, providing results that were consistent with the strong effects of predation observed in the predator exclusion experiment. Reductions were observed when the experimental community was at an early or a late assembly stage, demonstrating a consistent effect irrespective of community age. Predator exposure decreased non-native species abundance in Panama after three months (Fig 6; Region \times Treatment \times Pre/Post: $F_{1,104} = 12.47$, $p = 0.0062$ contrasts: Panama: $t = -7.02$, $p = 0.001$),

but had no effect in Mexico, California, or Alaska ($p > 0.05$; Appendix S1: Table S1, S2). Similarly, predator exposure decreased non-native species abundance in Panama at both timescales in the 3/12-month model (Region \times Treatment: $F_{2,7.59} = 6.71$, $p = 0.021$ contrasts: Panama: $t = -3.59$, $p = 0.035$), while having no effect on any other region ($p > 0.05$; Appendix S1: Fig S5), demonstrating a consistent impact of short-term predation at both community assembly timescales.

The PERMANOVA analysis reveals significant effects of site (pseudo-F = 25.64, $p = 0.0001$) and the interaction between site and predator exposure treatment (pseudo-F = 3.66, $p = 0.0033$; Appendix S1: Table S3) on the observed community structures in Panama over three and twelve months. However, neither the pre-post periods nor the predator exposure treatment alone showed significant effects (pre-post: pseudo-F = 4.10, $p = 0.1245$; predator exposure: pseudo-F = 2.35, $p = 0.2228$). These results suggest that site-specific factors and the interaction between site and predator presence are important in shaping community assembly, while the direct effects of predator exposure and temporal changes are less pronounced.

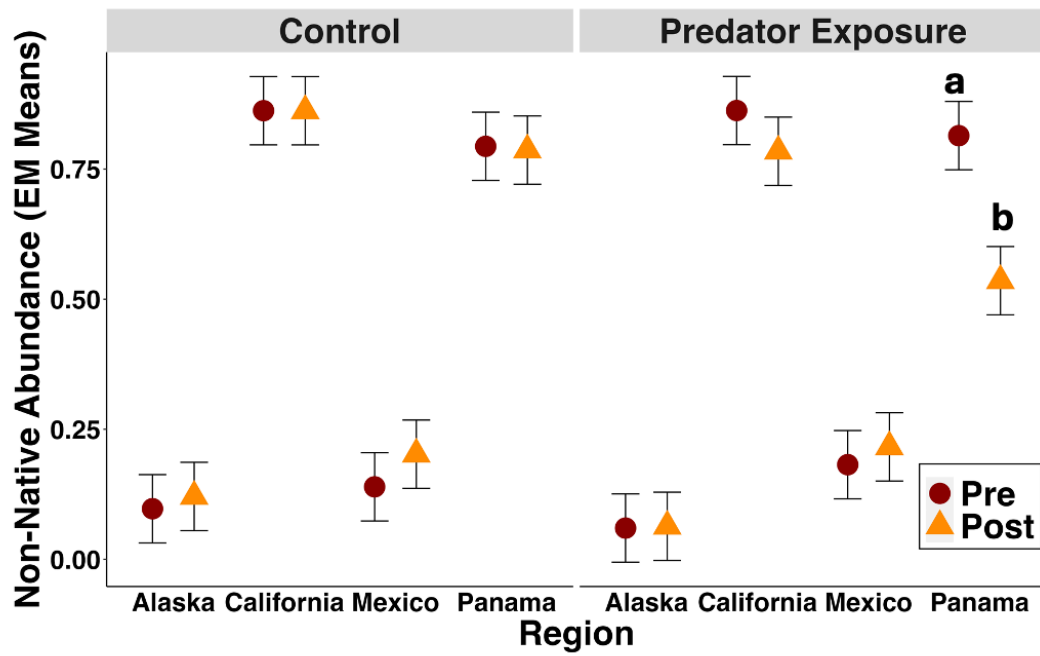


Figure 6. Effects of predator exposure on non-native species abundance expressed as estimated marginal means from mixed models (+/ SE). Asterisks indicate significant treatment contrasts ($\alpha = 0.05$). The effect in Panama was retained in the 3/12-month model (Appendix S1: Figure S5).

CHAPTER 4

DISCUSSION

The findings from this study provide valuable insights into the complex dynamics of non-native species invasions across different latitudes in marine ecosystems. Overall, the study supports the hypothesis that biogeographic location, assembly timescale, and predation interactively shape invasion success across latitude. No models showed a significant interaction between resource availability and predation, suggesting that these mechanisms operate independently with additive rather than interactive effects. These results underscore the importance of considering multiple ecological factors when developing management strategies to mitigate the impact of invasive species across diverse marine environments.

The study reveals that the impact of predation on non-native species varies across both latitude and assembly timescales. In the tropical region of Panama, strong predation reduced non-native species richness at early and late assembly timescales, a result that is consistent with both the biotic interactions hypothesis (Schemske et al. 2009) and stronger biotic resistance in the tropics (Carlton 1996, Freestone et al. 2013). The presence of native predators in Panama may have a significant influence on the successful establishment of non-native species, resulting in lower invasion success in this region. The most dominant non-native taxa in our control communities that were open to ambient predation were barnacles and encrusting bryozoans, both species that may be unpalatable or more difficult for predators to consume, thus dominating in communities with higher predation (Dias et al. 2020). In contrast, the most dominant non-native taxa in

the caged treatment communities were ascidians, a species that is more often preyed upon due to this soft bodied nature (Giachetti et al. 2022).

Conversely, in the subtropical region of Mexico, strong predation increased non-native species richness during early community assembly. This finding is intriguing and may be linked to differences in predator communities and their interactions with native and non-native species. The subtropical region may have a different predator composition, leading to different impacts on non-native species compared to the tropical region. Additionally, the availability of different resources and the timing of invasions may also contribute to the observed pattern. For instance, non-native species *Celleporaria inaudita*, *Schizoporella pungens* and *Amphibalanus reticulatus* were most abundant in Mexico and were driving the patterns there. Many of the non-natives in Mexico were hard-bodied bryozoans and barnacles that are less preferred by predators, as predation reduced better competitors like tunicates (Buckeridge and Reeves 2009).

Interestingly, predation increased non-native abundance in Panama, but this pattern was observed only at the late assembly timescale. This result suggests that predation may play a more significant role in shaping established communities rather than early colonization events (Lu et al. 2019). Established communities may be more stable but can be susceptible to predator impacts, leading to changes in non-native abundance. In contrast, early colonization events are likely influenced more by other factors such as propagule pressure and resource availability. Alternatively, this pattern suggests that abundance patterns took time to emerge, as communities in Panama matured over time. This delayed response suggests that the subtle, yet critical effects of predation may gradually influence the composition of non-native species in the

ecosystem. In contrast, richness patterns, which can capture the presence of rare species, responded more quickly. This nuanced interplay between abundance and richness patterns emphasizes the complexity of non-native species dynamics and highlights the importance of long-term ecological monitoring to fully grasp the subtle shifts occurring within ecosystems.

While competition is likely an important factor in community assembly and invasion dynamics, our experimental manipulations of resource availability did not support this prediction. Biomass removals never increased invasion success, as would be predicted if these removals were effective in reducing competition and releasing competitively inferior species. Biomass removals reduced non-native abundance in Panama in the 3-month model, but this effect was not observed for either assembly stage in the 3/12-month model, suggesting a weaker effect that was likely driven by the disturbance from the removals rather than competition per se. The lower richness of non-native species at late-stage assembly in California and Panama could indicate competitive exclusion by native species, however an increase in richness or abundance with biomass removals at 12 months in these regions was not observed. It is important to note that biomass removals were random, increasing the overall resource availability in the community rather than selectively reducing abundances of competitive dominants. Therefore, competition may be stronger at late-stage assembly (López and Freestone 2022) but the effects may be cumulative across the 12-month developmental time scale rather than operating within the monthly intervals of biomass removals. Furthermore, a greater diversity of non-native species at early assembly may also result from rapid colonization (Graebner et al. 2012). Therefore, non-native species may exploit early

colonization opportunities, while native species may become more resistant to invasion as they mature and develop stronger competitive interactions (Stachowicz et al. 2002).

When considering the higher non-native species richness in California and Panama relative to subarctic Alaska, several other factors beyond predation and competition may contribute to these regional patterns. First, propagule pressure and historical patterns of biotic exchange are critical factors influencing invasion dynamics. Both California and Panama have historically experienced higher levels of shipping and maritime traffic, which can serve as significant pathways for the introduction of non-native species (Seebens et al. 2013, Glon et al. 2020, Ashton et al. 2022). Furthermore, California is recognized as a highly invaded estuary (Cohen and Carlton 1998, Ruiz et al. 2011). The high human activity in these regions may have resulted in a higher frequency of introductions (Jurgens et al. 2018), but environmental filtering and predation pressure have been shown to reduce invasion risk over time (Bonfim et al.).

Abiotic factors and environmental conditions can also play a role in shaping non-native species richness. Differences in temperature, salinity, and other physical factors could limit the establishment and spread of non-native species in these regions. For example, abiotic seasonality can significantly influence the success of non-native species in new environments (Thomaz 2022). In regions with pronounced seasonal variations, such as subarctic and temperate zones, the changing abiotic conditions can pose challenges for non-native species to establish and persist (Kazanavičiūtė et al. 2024). Fluctuations in temperature, light availability, and nutrient levels can directly impact the survival and reproductive success of introduced species, as they might not be adapted to cope with the rapid shifts in environmental conditions. Additionally, the timing of species

introductions can also play a crucial role (Torres et al. 2022). Non-native species that arrive during favorable conditions may have a higher chance of establishment and subsequent population growth. Conversely, those introduced during unfavorable conditions may struggle to survive, limiting their ability to become established in the new ecosystem. Therefore, considering the interaction between abiotic seasonality and the timing of species introductions is essential when studying and managing non-native species invasions. Furthermore, El Niño effects caused high freshwater influx and low salinity in the California region during the period of deployment in 2016. This resulted in excess mortality in the region and could have impacted non-native species' abilities to establish. Additionally, the availability of suitable habitat and substrate for colonization may differ among regions, influencing the establishment success of non-native species. Finally, the biogeographic origin of non-native species introductions might also contribute to regional variations in non-native species richness. Some non-native species may have a greater affinity for temperate regions, while others might be more adapted to tropical conditions, depending on their origin (Kirk et al. 2021). Thus, the species pool available for introduction and establishment may vary with latitude, contributing to the observed patterns of non-native species richness. In summary, while species interactions and assembly time appear to be crucial factors influencing non-native species richness in these regions, it is essential to consider the interplay of multiple factors, including historical patterns of introduction, abiotic conditions, and species-specific preferences.

Lastly, the observed decline in non-native richness towards the poles may be attributed to the especially harsh abiotic conditions and slower growth rates in these regions, making them less favorable for non-native species establishment. In addition,

there is lower intensity and a shorter history of propagule pressure in Alaska (Bonfim et al. in press). However, this is changing with increased shipping in the Arctic, which is causing a northern expansion of invaders (Jurgens et al. 2018, Daly et al. 2023). Given this expanding source of propagule pressure, future studies on invasions in polar regions could reveal novel invasion dynamics.

Using this original exploration of non-native species richness and abundance in a standardized experiment across a latitudinal gradient, we demonstrate that invasion outcomes can vary with biogeographic region, exposure to predation, and assembly time. Our results highlight patterns in invasion dynamics and biotic resistance which can have significant implications for the management and conservation of marine ecosystems. Understanding the factors that influence the success of non-native species across different latitudes can help predict and inform control efforts for invasions, especially in vulnerable regions. Conservation efforts may need to focus on enhancing biotic resistance and promoting strong predator communities to limit the establishment and spread of non-native species, particularly in tropical ecosystems. Recognizing the variable impacts of predation and competition across latitudes enables more informed decision-making in invasive species control efforts. As global shipping and climate change continue to reshape marine environments, the ability to predict and manage non-native species invasions becomes increasingly vital.

In conclusion, our study provides valuable insights into the intricate dynamics of non-native species invasions across varying latitudes in marine ecosystems. By exploring the interactive roles of predation, competition, assembly timescales, and biogeographic factors, we have unveiled an intricate mosaic of invasion patterns. Our findings

emphasize the importance of considering both regional and temporal factors when assessing the success of non-native species. This research contributes to a deeper understanding of ecological invasions, shedding light on the mechanisms that shape community structure and biodiversity across different latitudes. By addressing questions central to invasions across latitudes, our study advances ecological theory and provides actionable insights for wildlife agencies tasked with preserving the delicate balance of marine ecosystems.

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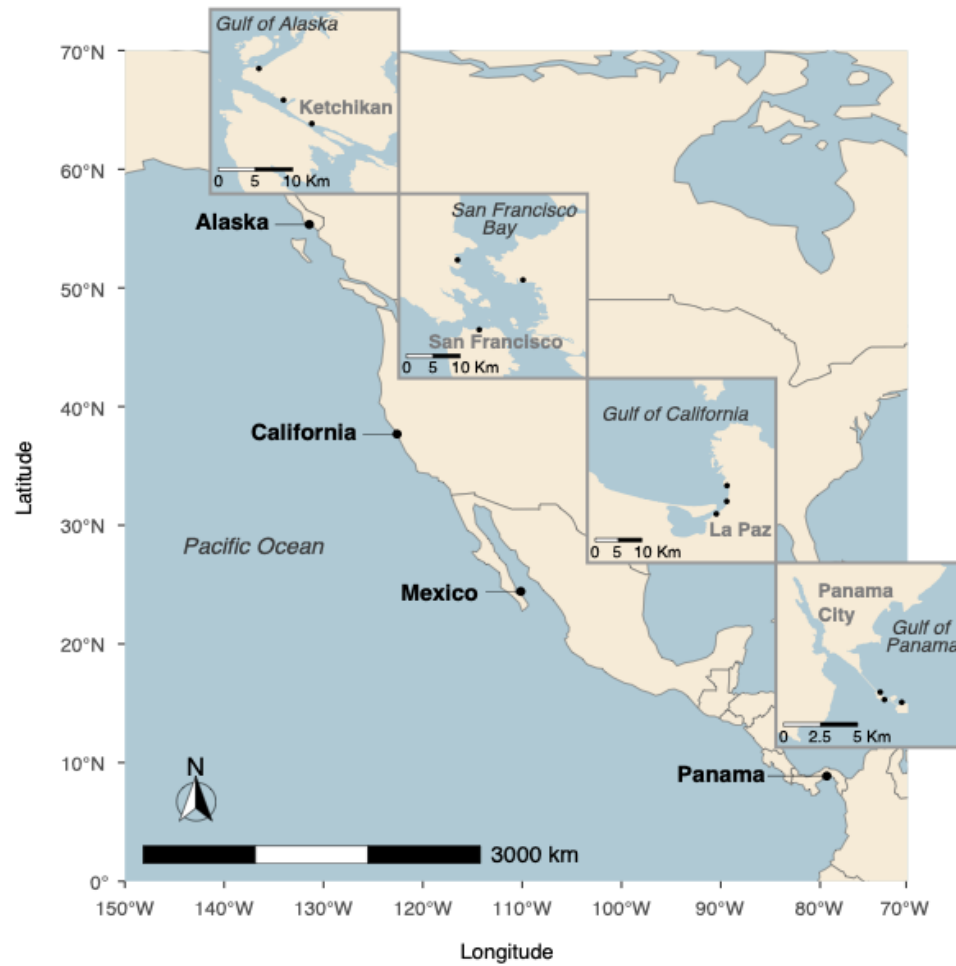
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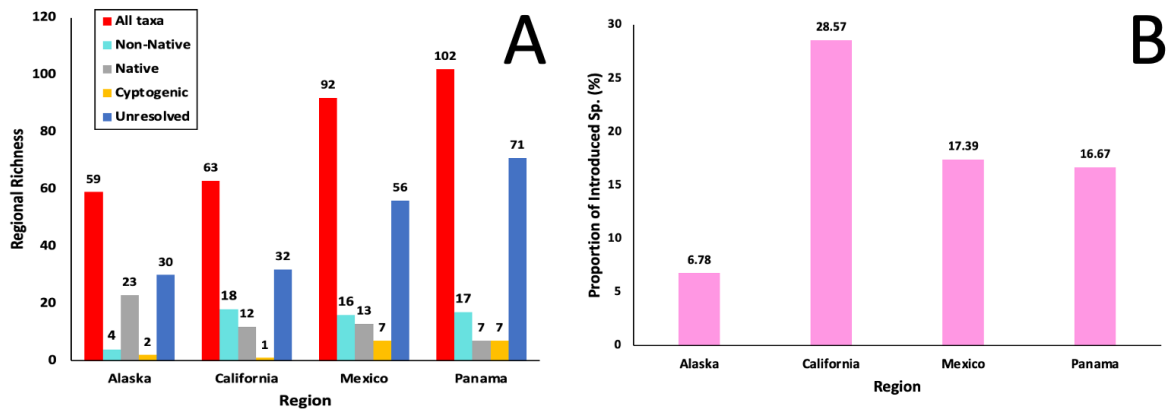
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APPENDIX A S1

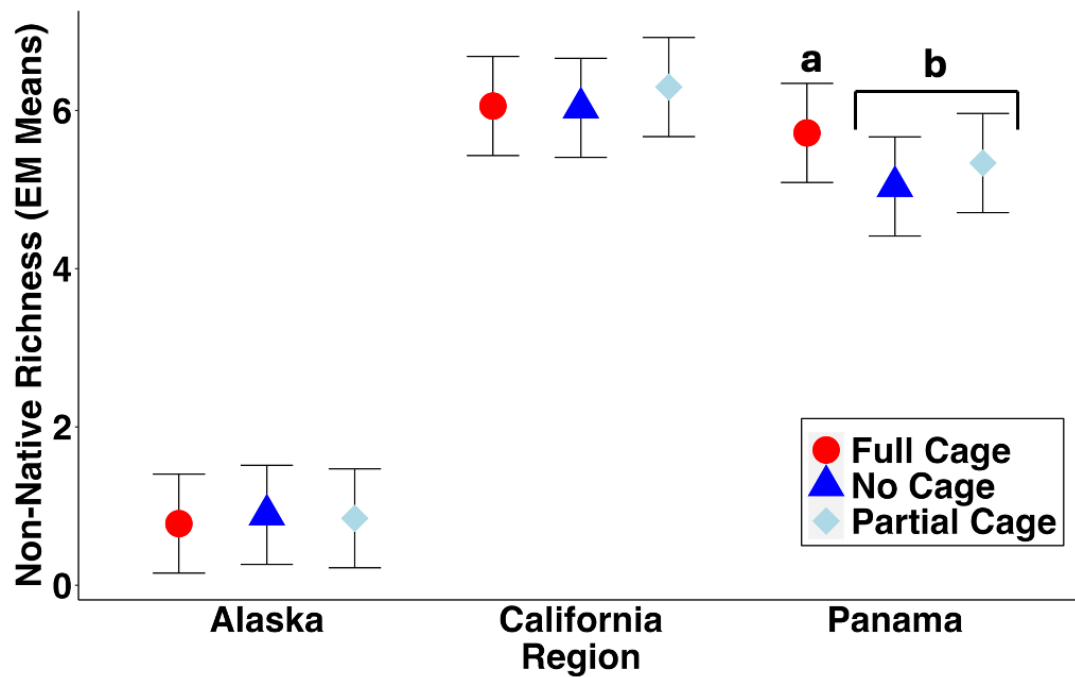


Appendix S1: **Figure S1.** Map of study sites, reproduced from Freestone et al. (2021).

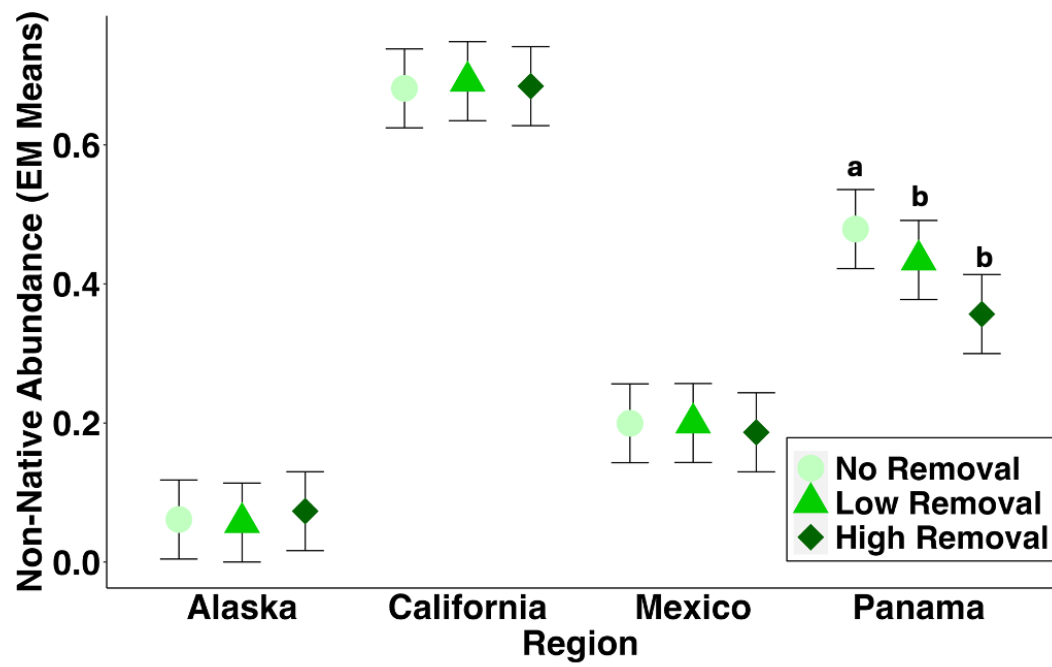
Experiments were conducted at three sites (shown as black dots) in each of four regions, for 12 study sites across the latitudinal gradient.



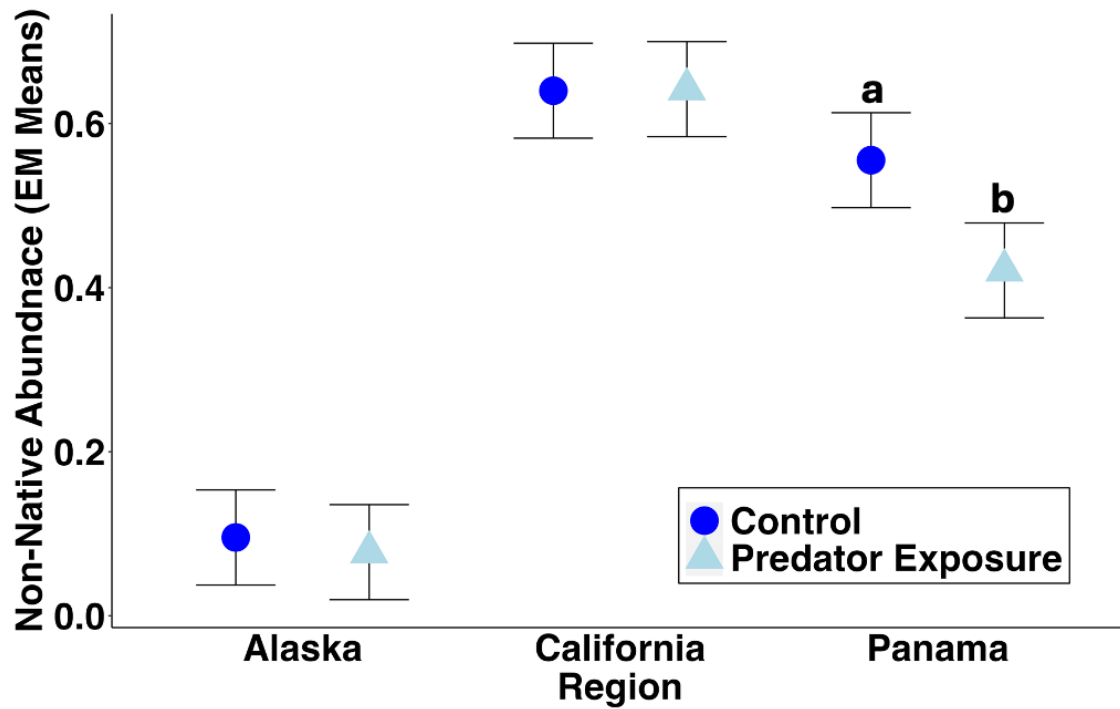
Appendix S1: **Figure S2.** A) Regional richness across 4 study regions. Panama had the greatest number of species identified and Alaska had the fewest. B) California had the greatest number of non-native species identified.



Appendix S1: **Figure S3.** Effects of predator exclusion on non-native species richness across both assembly timescales expressed as estimated marginal means from mixed models (+/ SE). Letters indicate significant treatment contrasts between treatment and controls ($\alpha = 0.05$). Brackets indicate combined contrast of procedural control and control treatment types (partial caged and no caged). Refer to methods for details on process of grouping controls together.



Appendix S1: **Figure S4.** Effects of biomass removals on non-native species abundance at an early assembly timescale expressed as estimated marginal means from mixed models (+/ SE). Asterisks indicate significant treatment contrasts ($\alpha = 0.05$).



Appendix S1: **Figure S5.** Effects of predator exposure on non-native species abundance across both assembly timescales expressed as estimated marginal means from mixed models (+/ SE). Asterisks indicate significant treatment contrasts ($\alpha = 0.05$).

Appendix S1: Table S1. Linear Model Results

Model type	Factor	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)
3 Month Predator Exclusion Richness							
	Region	68.405	22.802	3	8.000	18.941	0.0005
	Predator Exclusion	14.702	7.3512	2	15.998	6.107	0.0107
	Competition	1.021	0.5106	2	15.998	0.424	0.6615
	Region: Predator Exclusion	28.231	4.7052	6	15.997	3.909	0.0135
	Region: Competition	9.481	1.5802	6	15.997	1.313	0.3073
	Predator Exclusion: Competition	7.075	1.7687	4	31.993	1.469	0.2346
	Region: Predator Exclusion:Competition	12.53	1.0442	12	31.986	0.867	0.5859
3/12 Month Predator Exclusion Richness							
	Region	34.405	17.202	2	6.000	21.332	0.0019
	Predator Exclusion	4.394	2.197	2	96.379	2.725	0.0706
	Competition	2.323	1.161	2	96.402	1.440	0.2419
	Assembly Timescales	39.353	39.353	1	6.001	48.800	0.0004
	Region: Predator Exclusion	13.432	3.358	4	96.376	4.164	0.0024
	Region:Competition	3.789	0.947	4	96.399	1.175	0.3268
	Region:Assembly Timescales	27.394	13.697	2	6.001	16.985	0.0034
	Predator Exclusion:Assembly Timescales	3.904	1.952	2	96.379	2.421	0.0942
	Competition:Assembly Timescales	3.099	1.55	2	96.402	1.922	0.1519
	Predator Exclusion:Competition	5.018	1.254	4	96.375	1.556	0.1924
	Region:Predator Exclusion:Competition	5.778	0.722	8	96.369	0.896	0.5233
	Region:Predator Exclusion:Assembly Timescales	3.035	0.759	4	96.376	0.941	0.4437
	Region:Competition:Assembly Timescales	0.506	0.126	4	96.399	0.157	0.9594
	Predator Exclusion:Competition:Assembly Timescales	2.198	0.549	4	96.375	0.681	0.6066
	Region:Predator Exclusion:Competition:Assembly Timescales	2.484	0.31	8	96.369	0.385	0.9262

Appendix S1: Table S1. (continued)

Model type	Factor	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)
3/12 Month Predator Exclusion Abundance							
	Region	0.59571	0.29785	2	14.367	20.5426	6.12E-05
	Predator Exclusion	0.13327	0.06663	2	12.184	4.5957	0.0325695
	Competition	0.05203	0.02602	2	12.251	1.7943	0.2072791
	Assembly Timescales	0.61316	0.61316	1	10.372	42.2888	5.80E-05
	Region:Predator Exclusion	0.05347	0.01337	4	12.184	0.922	0.4823772
	Region:Competition	0.07637	0.01909	4	12.251	1.3168	0.3178102
	Region:Assembly Timescales	0.5563	0.27815	2	10.372	19.1835	0.0003273
	Predator Exclusion:Assembly Timescales	0.00069	0.00034	2	71.597	0.0236	0.9766568
	Competition:Assembly Timescales	0.00654	0.00327	2	71.613	0.2256	0.7985892
	Predator Exclusion:Competition	0.01289	0.00322	4	71.608	0.2223	0.9251477
	Region:Predator Exclusion:Competition	0.04891	0.00611	8	71.605	0.4217	0.9043737
	Region:Predator Exclusion:Assembly Timescales	0.25394	0.06348	4	71.595	4.3785	0.0031834
	Region:Competition:Assembly Timescales	0.03776	0.00944	4	71.611	0.651	0.6280105
	Predator Exclusion:Competition:Assembly Timescales	0.02359	0.0059	4	71.6	0.4067	0.8032156
	Region:Predator Exclusion:Competition:Assembly Timescales	0.06133	0.00767	8	71.597	0.5287	0.8311242
Model Type	Factor	Chisq	Df	Pr(>Chisq)			
3 Month Predator Exclusion Abundance							
	Region	76.2082	3	< 2.2e-16			
	Predator Exclusion	10.7325	2	0.004672			
	Competition	4.2658	2	0.11849			
	Region: Predator Exclusion	8.2196	6	0.222454			
	Region: Competition	14.0175	6	0.029441			
	Predator Exclusion: Competition	3.4443	4	0.486395			
	Region: Predator Exclusion: Competition	8.697	12	0.72857			

Appendix S1:Table S1. (continued)

Model Type	Factor	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)
3 Month Predator Exposure Abundance							
	Region	1.60061	0.53354	3	8	44.7723	2.40E-05
	Predator Exposure	0.03388	0.03388	1	8	2.8429	0.1302653
	Pre Post	0.05401	0.05401	1	8	4.5327	0.0658934
	Region:Predator Exposure	0.04691	0.01564	3	8	1.3121	0.3360062
	Region:Pre Post	0.3133	0.10443	3	8	8.7635	0.0065733
	Predator Exposure:Pre Post	0.14864	0.14864	1	104	12.4732	0.0006169
	Region:Predator Exposure:Pre Post	0.15517	0.05172	3	104	4.3405	
3/12 Month Predator Exposure Abundance							
Model Type	Factor	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)
	Region	0.5007	0.25035	2	6	27.331	0.0009676
	Predator Exposure	0.07845	0.078446	1	7.457	8.564	0.0206297
	Assembly Timescales	0.2014	0.201404	1	6	21.9875	0.003364
	Pre Post	0.16498	0.164979	1	5.999	18.011	0.0054177
	Region:Predator Exposure	0.12282	0.061409	2	7.598	6.7041	0.0209973
	Region:Assembly Timescales	0.10491	0.052453	2	6	5.7264	0.0406311
	Predator Exposure:Assembly Timescales	0.01935	0.019354	1	191.293	2.1129	0.1477034
	Region:Pre Post	0.16647	0.083235	2	5.999	9.0868	0.0152955
	Predator Exposure :Pre Post	0.00972	0.00972	1	162.004	1.0612	0.3044853
	Assembly Timescales:Pre Post	0.01576	0.015759	1	161.68	1.7204	0.1914992
	Region:Predator Exposure :Pre Post	0.00985	0.004926	2	162.265	0.5378	0.585055
	Predator Exposure :Assembly Timescales:Pre Post	0.0033	0.003301	1	161.081	0.3604	0.549146
	Region:Predator Exposure :Assembly Timescales	0.00063	0.000313	2	214.125	0.0342	0.9663709
	Region:Predator Exposure :Assembly Timescales:Pre Post	0.08463	0.021159	4	161.672	2.3099	0.0600977

Appendix S1: Table S2. Planned Contrast Results *all control contrasts were not sig.

Model Type	Contrast	Estimate	SE	df	t.ratio	p.value
3 Month Predator Exclusion Richness: Richness x Predator Exclusion						
	Panama caged vs. controls	-0.5272327	0.2019644	16.49472	-2.6105225	0.04522622
	Mexico caged vs. controls	0.6777778	0.2003168	15.99209	3.3835287	0.01516725
	California caged vs. controls	0.2176878	0.3979419	15.54506	0.5470342	1
	Alaska caged vs. controls	0.2444444	0.4006337	15.99209	0.6101445	1
3 Month Predator Exclusion Abundance: Region x Competition						
	Panama control vs. low	-0.04443699	0.0293960 ₉	498	-1.5116632	1
	Panama low vs. high	-0.07783307	0.0296159	498	-2.62808341	0.097369639
	Panama control vs. high	-0.12227006	0.0296159	498	-4.12852693	0.000513663
	California control vs. low	0.01026663 ₄	0.0293960 ₉	498	0.34925164	1
	California low vs. high	-0.00708066	0.0293088 ₁	498	-0.24158814	1
	California control vs. high	0.00318597 ₃	0.0293088 ₁	498	0.10870361	1
	Mexico control vs. low	0.00034698 ₄	0.0293960 ₉	498	0.01180374	1
	Mexico low vs. high	-0.01332214	0.0293960 ₉	498	-0.45319409	1
	Mexico control vs. high	-0.01297515	0.0293960 ₉	498	-0.44139036	1
	Alaska control vs. low	-0.0044089	0.0293960 ₉	498	-0.14998267	1
	Alaska low vs. high	0.01641901 ₃	0.0293960 ₉	498	0.55854406	1
	Alaska control vs. high	0.01201010 ₉	0.0293960 ₉	498	0.40856139	1
3/12 Month Predator Exclusion Richness: Region x Predator Exclusion						
	Panama caged vs. controls	-0.52835412	0.1416261	6.130078	-3.7306266	0.02806998
	California caged vs. controls	0.10908138	0.1404326	5.928702	0.7767527	0.93430778

Appendix S1: Table S2. (continued)

Model Type	Contrast	Estimate	SE	df	t.ratio	p.value
	Alaska caged vs. controls	0.0888889	0.1406579	5.96777	0.631951	0.93430778
3/12 Month Predator Exclusion Richness: Region x Assembly Timesales						
	Panama 3 vs. 12 mo	-3.12935185	0.852181	6.001787	-3.672168	0.020843625
	California 3 vs. 12 mo	-7.09203848	0.8520862	5.999182	-8.3231467	0.000490023
	Alaska 3 vs. 12 mo	-0.0888889	0.8520797	5.999011	-0.1043199	0.920315799
3/12 Month Predator Exclusion Abundance: Region x Predator Exclusion x Assembly Timesales						
	Panama controls 3 mo vs. caged 3 mo	-0.00326096	0.0364604	26.45071	-0.08943839	1
	Panama controls 12 mo vs. caged 12 mo	0.12060826 ₈	0.0364454	26.40359	3.30928645	0.01624903
	California controls 3 mo vs. caged 3 mo	-0.107157	0.0362292	25.79007	-2.95774618	0.0327624
	California controls 12 mo vs. caged 12 mo	-0.01285769	0.0363440	26.12076	-0.35377681	1
	Alaska controls 3 mo vs. caged 3 mo	-0.03893848	0.0363151	26.03928	-1.07223874	1
	Alaska controls 12 mo vs. caged 12 mo	-0.00917669	0.0363151	26.03928	-0.25269621	1
3 Month Predator Exposure Abundance: Region x Predator Exposure x PrePost						
	Panama control pre vs. control post	-0.00718195	0.0398608	29.71429	-0.18017571	1.00E+00
	Panama predator exposure pre vs. predator exposure post	-0.27866741	0.0398608	29.71429	-6.9910092	7.66E-07
	Mexico control pre vs. control post	0.06260646	0.0398608	29.71429	1.57062621	5
	Mexico predator exposure pre vs. predator exposure post	0.03429348	0.0398608	29.71429	0.86033056	5
	California control pre vs. control post	-5.1007E-05	0.0398608	29.71429	-0.00127963	1.00E+00
	California predator exposure pre vs. predator exposure post	-0.07814608	0.0398608	29.71429	-1.96047319	4.16E-01
	Alaska control pre vs. control post	0.02370020	0.0398608	29.71429	0.59457381	8

Appendix S1: Table S2. (continued)

Model Type	Contrast	Estimate	SE	df	t.ratio	p.value
3/12 Month Predator Exposure Abundance: Region x Predator Exposure x Assembly Timescale						
Panama	3 mo control pre vs. control post	0.007182	0.034947	71.52106	0.205507	1.00E+0 2.14E-10
Panama	3 mo predator exposure pre vs predator exposure post	0.278667	0.034947	71.52106	7.973909	1.00E+0
Panama	12 mo control pre vs. control post	0.031529	0.034947	71.52106	0.902198	1.00E+0 3.23E-01
Panama	12 mo predator exposure pre vs. predator exposure post	0.077971	0.035749	76.44118	2.181061	1.00E+0
California	3 mo control pre vs. control post	5.1E-05	0.034947	71.52106	0.00146	1.00E+0 3.13E-01
California	3 mo predator exposure pre vs. predator exposure post	0.078146	0.034947	71.52106	2.236106	1.00E+0
California	12 mo control pre vs. control post	0.015756	0.034947	71.52106	0.450844	1.00E+0
California	12 mo predator exposure pre vs. predator exposure post	0.050188	0.034947	71.52106	1.436088	1.00E+0
Alaska	3 mo control pre vs. control post	-0.0237	0.034947	71.52106	-0.67817	1.00E+0
Alaska	3 mo predator exposure pre vs. predator exposure post	-0.00341	0.034947	71.52106	-0.09767	1.00E+0
Alaska	12 mo control pre vs. control post	0.012032	0.034947	71.52106	0.344286	1.00E+0
Alaska	12 mo predator exposure pre vs. predator exposure post	-0.00964	0.034947	71.52106	-0.27582	1.00E+0

Appendix S1: Table S3. PERMANOVA results *all control contrasts were not sig.

Model Type	Source of Variation	df	SS	MS	Pseudo-F	P(perm)	Unique perms	P(MC)
Panama Predator Exclusion 3 Months								
	Site	2	32518	16259	22.863	0.0001	9948	0.0001
	Predation	2	90546	45273	14.118	0.0368	9684	0.0003
	Predator Exclusion Contrast: Procedural control vs. Control	1	117.88	117.88	0.06278 ₃	0.9831	170	0.938
	Predator Exclusion Contrast: Caged vs. Controls	1	90333	90333	19.915	0.0823	360	0.0026
	Competition	2	5178.7	2589.3	2.5673	0.0476	9403	0.0499
	SitexPredator Exclusion	4	12830	3207.6	4.5105	0.0001	9924	0.0001
	SitexControls	2	3755.5	1877.8	2.8265	0.0099	9940	0.0124
	SitexCaged	2	9073.8	4536.9	6.3005	0.0001	9935	0.0001
	SitexCompetition	4	4034.5	1008.6	1.4183	0.1268	9907	0.1257
	Predator ExclusionxCompetition	4	4726.6	1181.7	1.1853	0.3264	9924	0.33
	ControlxCompetition	2	534.03	267.01	0.34255	0.8778	9965	0.8943
	CagedxCompetition	2	4191	2095.5	1.6977	0.1819	9947	0.1723
	SitexPredator ExclusionxCompetition	8	7976.9	997.11	1.4021	0.0708	9872	0.0754
	SitexControlxCompetition	4	3118.1	779.53	1.1734	0.302	9922	0.3149
	SitexCagedxCompetition	4	4938.4	1234.6	1.7145	0.0351	9927	0.0405
	Residuals	106	75380	711.13				
	Total	132	2.35E+0					
California Predator Exclusion 3 Months								
	Site	2	1.64E+0 ₅	82234	96.393	0.0001	9933	0.0001
	Predation	2	23261	11630	2.5671	0.0612	9396	0.04
	Predator Exclusion Contrast: Procedural control vs. Control	1	21481	21481	2.6419	0.0871	180	0.0869
	Predator Exclusion Contrast: Caged vs. Controls	1	1779.5	1779.5	1.914	0.3514	60	0.1974

Appendix S1: Table S3. (continued)

Model Type	Source of Variation	df	SS	MS	Pseudo-F	P(perm)	Unique perms	P(MC)
	SitexPredator Exclusion	4	18124	4530.9	5.311	0.0001	9910	0.0001
	SitexControls	2	16264	8132.1	9.3376	0.0001	9924	0.0001
	SitexCaged	2	1859.4	929.71	1.3073	0.231	9941	0.2357
	SitexCompetition	4	9350.3	2337.6	2.7401	0.0004	9920	0.0006
	Predator ExclusionxCompetition	4	3034.1	758.52	0.67429	0.7603	9923	0.8147
	ControlxCompetition	2	1081	540.5	0.44905	0.853	9952	0.9026
	CagedxCompetition	2	1953.1	976.54	0.93343	0.4934	9951	0.5044
	SitexPredator ExclusionxCompetition	8	8999.7	1125	1.3187	0.1075	9887	0.102
	SitexControlxCompetition	4	4815	1203.7	1.3822	0.1337	9927	0.1291
	SitexCagedxCompetition	4	4184.8	1046.2	1.4711	0.1241	9891	0.1236
	Residuals	109	92989	853.11				
	Total	135	3.23E+0					
Mexico Predator Exclusion 3 Months								
	Site	2	1.40E+0	69812	41.624	0.0001	9925	0.0001
	Predation	2	30485	15243	2.5934	0.0504	9689	0.0214
	Predator Exclusion Contrast: Procedural control vs. Control	1	23053	23053	2.691	0.1096	360	0.0674
	Predator Exclusion Contrast: Caged vs. Controls Competition	1	7522.6	7522.6	2.3192	0.2624	180	0.1008
	SitexPredator Exclusion	2	3941.9	1971	1.1207	0.5087	9659	0.3767
	SitexControls	4	23514	5878.6	3.505	0.0001	9904	0.0001
	SitexCaged	2	17137	8568.6	4.6726	0.0001	9930	0.0001
	SitexCompetition	2	6488	3244	1.8572	0.0464	9926	0.0459
	Predator ExclusionxCompetition	4	7035.1	1758.8	1.0486	0.3856	9895	0.3827
	ControlxCompetition	4	6704.2	1676.1	0.62829	0.8273	9923	0.8872
	CagedxCompetition	2	2635.1	1317.5	0.8762	0.5441	9960	0.5725
	Total	2	4079.8	2039.9	0.52976	0.7793	9947	0.8697

Appendix S1: Table S3. (continued)

Model Type	Source of Variation	df	SS	MS	Pseudo-F	P(perm)	Unique perms	P(MC)
	SitexPredator ExclusionxCompetition	8	21346	2668.2	1.5909	0.0113	9864	0.0108
	SitexControlxCompetition	4	6014	1503.5	0.81988	0.7137	9882	0.7039
	SitexCagedxCompetition	4	15405	3851.4	2.2049	0.0027	9885	0.0036
	Residuals	106	1.78E+0	1677.2				
	Total	132	4.10E+0					
Panama Predator Exclusion 3/12 Months								
	Site	2	24499	12249	10.402	0.001	999	0.001
	Predation Exclusion	2	88000	44000	9.1681	0.003	997	0.001
	Competition	2	6326.3	3163.2	0.97327	0.501	998	0.479
	Assembly Timescales	1	1.28E+0	1.28E+0 ₅	13.1	0.049	179	0.002
	Sitex Predation Exclusion	4	19199	4799.7	4.0759	0.001	999	0.001
	SitexCompetition	4	13002	3250.5	2.7603	0.001	997	0.001
	SitexAssembly Timescales	2	19537	9768.7	8.2955	0.001	998	0.001
	Predator Exclusionx Competition	4	4621.3	1155.3	0.70258	0.72	999	0.781
	Predator ExclusionxAssembly Timescales	2	28361	14180	5.2575	0.001	998	0.001
	CompetitionxAssembly Timescales	2	5618	2809	1.3584	0.34	999	0.269
	SitexPredator ExclusionxCompetition	8	13157	1644.6	1.3966	0.058	998	0.061
	SitexPredator ExclusionxAssembly Timescales	4	10789	2697.4	2.2906	0.001	999	0.003
	SitexCompetitionxAssembly Timescales	4	8272	2068	1.7561	0.022	999	0.033
	Predator Exclusion xCompetitionxAssembly Timescales	4	6393.6	1598.4	1.1903	0.344	998	0.29
	SitexPredator ExclusionxCompetitionxAssembly Timescales	8	10744	1343	1.1404	0.251	998	0.257
	Residuals	213	2.51E+0	1177.6				
	Total	266	6.42E+0					
Panama Predator Exposure 3/12 Months								
	Pre Post	1	8071.4	8071.4	4.1047	0.1245	38	0.0692

Contrast: Pre vs. Post Site	1	8071.4	8071.4	4.1047	0.1136	38	0.0735
Predator Exposure Treatment	2	42872	21436	25.64	0.0001	9948	0.0001
Contrast: Predator Exposure vs. Control	1	7200.9	7200.9	2.3511	0.2228	38	0.1754
Pre Post:Site	1	7200.9	7200.9	2.3511	0.2056	38	0.173
Contrast: Pre post vs. Site	2	3932.7	1966.4	2.352	0.0319	9939	0.0385
Assembly Timescale: Predator Exposure Treatment	2	3932.7	1966.4	2.352	0.0336	9949	0.0347
Contrast: Pre Post vs. Assembly timescale	1	5959.5	5959.5	4.1967	0.1138	2115	0.0715
Contrast: Assembly timescale vs. Predator Exposure	1	5959.5	5959.5	4.1967	0.1111	2090	0.07
Site:Predator Exposure Treatment	1	5959.5	5959.5	4.1967	0.1147	2049	0.0758
Contrast: Site vs. Predator Exposure	2	6125.6	3062.8	3.6634	0.0033	9941	0.0041
Assembly timescale: Site: Predator Exposure Treatment	2	6125.6	3062.8	3.6634	0.0028	9952	0.0036
Contrast: Pre post vs. Site vs. Predator Exposure	2	2840.1	1420	1.6985	0.1249	9946	0.1335
Assembly timescale vs. Site vs. Predator Exposure	2	2840.1	1420	1.6985	0.1243	9962	0.13
Residuals	48	40130	836.05	1.6985	0.1251	9954	0.1316
Total	59	1.17E+0					

Appendix S1: Table S4. SIMPER Results

Model Type									
Panama Predator Exclusion 3 Months									
Group control (open, partial)									
Average similarity: 59.94									
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%				
Amphibalanus_reticulatus	0.43	40.07	2.26	66.85	66.85				
Schizoporella_pungens	0.26	15.94	1.08	26.58	93.43				
Group caged									
Average similarity: 51.61									
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%				
Ascidia_sydneyensis	0.47	32.21	1.46	62.42	62.42				
Amphibalanus_reticulatus	0.13	vc8.86	1.02	17.17	79.59				
Groups control (open, partial) & caged									
Average dissimilarity = 72.38									
Species	Group control Av.Abund	Group caged Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%			
Ascidia_sydneyensis	0	0.47	27.03	1.72	37.34	37.34			
Amphibalanus_reticulatus	0.44	0.13	20.98	1.63	28.98	66.32			
Schizoporella_pungens	0.26	0.1	16.43	1.41	20.17	86.49			
Model Type									
Panama Predator Exclusion 12 Months									
Group control (open, partial)									
Average similarity: 46.85									
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%				
Schizoporella_pungens	0.27	30.39	1.15	64.86	64.86				
Hippoporina_indica	0.02	8.72	1.07	18.6	83.46				^

Appendix S1: Table S4. (continued)

Model Type									
Group caged									
Average similarity: 36.79									
Species		Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%			
Schizoporella_pungens		0.12	15.62	0.72	42.45	42.45			
Hippoporina_indica		0.02	12.21	1.66	33.19	75.64			
Groups control (open, partial) & caged									
Average dissimilarity = 64.37									
		Group control		Group caged					
Species		Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%		
Schizoporella_pungens		0.27	0.12	39.45	1.62	61.28	61.28		
Amphibalanus_reticulatus		0.07	0.02	11.04	0.97	17.15	78.43		

Model Type									
Panama Predator Exclusion Assembly Timescales 3/12 Months									
Group 3 month									
Average similarity: 44.62									
Species		Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%			
Amphibalanus_reticulatus		0.33	25.6	1.27	57.37	57.37			
Schizoporella_pungens		0.21	11.81	0.94	26.46	83.82			
Ascidia_sydneyensis		0.16	3.74	0.3	8.39	92.21			

Appendix S1: Table S4. (continued)

Model Type	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Species					
Schizoporella_pungens	0.22	24.62	0.96	60.33	60.33
Hippoporina_indica	0.02	9.82	1.19	24.06	84.4
Amphibalanus_reticulatus	0.05	5.64	0.61	13.82	98.22
Groups 3 month & 12 month					
Average dissimilarity = 73.63					
	Group 3	Group 12			
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%
Amphibalanus_reticulatus	0.33	0.05	28.57	1.34	38.8
Schizoporella_pungens	0.21	0.22	20.29	1.3	27.56
Ascidia_sydneyensis	0.16	0.02	13.99	0.65	19
Hippoporina_indica	0.04	0.02	3.78	0.75	5.13
					Cum.%
					38.8
					66.36
					85.36
					90.5

Model Type

California Predator Exclusion 3 Months

Group caged					
Average similarity: 35.86					
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Botryllus_schlosseri	0.16	13.29	1.12	37.06	37.06
Ciona_savignyi	0.11	6.02	0.72	16.78	53.84
Bugula_neritina	0.07	3.64	0.73	10.14	63.98
Bugula_stolonifera	0.06	3.53	0.61	9.84	73.83

Appendix S1: Table S4. (continued)

Model Type									
Group control (open, partial)									
Average similarity: 37.13									
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%				
Bugula_neritina	0.4	14.78	0.77	39.81	39.81				
Botryllus_schlosseri	0.09	6.03	1.03	16.24	56.05				
Bugula_stolonifera	0.11	5.11	0.71	13.76	69.81				
Ciona_savignyi	0.09	2.73	0.63	7.34	77.16				
Groups caged & control (open, partial)									
Average dissimilarity = 69.64									
	Group caged	Group control							
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%			
Bugula_neritina	0.07	0.4	19.21	1.15	27.59	27.59			
Botryllus_schlosseri	0.16	0.09	7.49	0.89	10.76	38.35			
Diplosoma_listerianum	0.07	0.09	7.01	0.82	10.07	48.42			
Ciona_savignyi	0.11	0.09	6.84	1.04	9.83	58.25			
Bugula_stolonifera	0.06	0.11	6.43	0.95	9.24	67.49			
Molgula_manhattensis	0.03	0.06	5.13	0.75	7.37	74.85			
Model Type									
Mexico Predator Exclusion 3 Months									
Group caged									
Average similarity: 29.69									
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%				
Celleporaria_inaudita	0.09	16.78	0.83	56.51	56.51				
Watersipora_subtorquata	0.05	9.6	0.59	32.35	88.86				

Appendix S1: Table S4. (continued)

Model Type		Group control (open, partial)		Group caged		Group control	
Group control (open, partial)		Average similarity: 25.63					
Species		Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%	
Celleporaria_inaudita		0.15	14.23	0.71	55.52	55.52	
Schizoporella_pungens		0.09	5.25	0.41	20.49	76	
Groups caged & control (open, partial)		Average dissimilarity = 77.76					
Species		Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Celleporaria_inaudita		0.09	0.15	27.22	1.27	35	35
Schizoporella_pungens		0.01	0.09	13.95	0.76	17.94	52.94
Watersipora_subtorquata		0.05	0.01	11.12	0.88	14.3	67.25
Amphibalanus_reticulatus		0.01	0.03	7.65	0.69	9.84	77.08
Model Type		Group caged		Group control			
Panama Predator Exposure 3 Months							
Group Control (open, partial)		Average similarity: 51.98					
Species		Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%	
Ascidia_sydneyensis		27.33	29.26	0.91	56.3	56.3	
Bugula_neritina		17.33	18.75	1.08	36.07	92.37	
Group Predator Exposure		Average similarity: 35.08					

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Bugula_neritina	14.6	14.14	0.95	40.31	40.31
Ascidia_sydneyensis	17.53	11.35	0.53	32.35	72.66

Groups Control (open, partial) &
Predator Exposure

Average dissimilarity = 59.99

Species	Group Control	Group Predator	Av.Diss	Diss/SD	Contrib%	Cum.%
	Av.Abund	Exposure Av.Abund				
Ascidia_sydneyensis	27.33	17.53	27.9	1.17	46.5	46.5
Bugula_neritina	17.33	14.6	19.89	1.1	33.16	79.67