­Environmental heterogeneity and conserved community architecture drive spatial patterns of diversity across the Gulf of Alaska large marine ecosystem

**Abstract**  
  
**Introduction**The effects of biodiversity on ecosystem stability and the mechanisms structuring communities are fascinating questions of ecological study. This is evidenced by the substantial efforts dedicated to understanding diversity-stability relationships and the processes underlying species co-existence. However, there is increasing recognition that our knowledge of these concepts stems mostly from local ecological systems. Much less is known about the stabilizing effect of biodiversity at large scales, and especially in a spatial context. Spatial stability in ecosystem properties and processes can be dependent on the spatial structure of biodiversity (Leibold et al. 2004, Wang and Loreau 2014, Wang and Loreau 2016), which can occur across multiple scales, from between organisms to between ecosystems. Species richness is one of the most fundamental metrics of diversity and measures the number of species in a given space (habitat, ecosystem, etc.). However, in a more explicit spatial context, biodiversity can be examined within local scale communities (alpha diversity), between local scale communities (beta diversity), and within regional scale communities (gamma diversity) (Jost 2007).  When multiplicatively examining stability at the regional scale, gamma diversity is the product of alpha and beta diversity, which confer stability through asynchronous variation within local communities and through asynchronous variation in biomass and community composition among local communities, respectively (Wang and Loreau 2014). A key mechanism linking the local and regional scales is dispersal, which supports stability at the regional scale by permitting local species coexistence through enabling locally extirpated species to recolonize from neighboring local communities (cite original ref for the concept of dispersal in metacommunities, also Leibold et al. 2004). Environmental heterogeneity is also a key mechanism underpinning patterns of diversity over space (Tamme et al. 2010), and variation in the relative importance of dispersal and environmental heterogeneity leads to a suite of spatial patterns in local community structure (Leibold et al. 2004). Lower dispersal levels maximize diversity and provide compensatory species dynamics, thus maximizing regional stability and creating the portfolio effect (cite). While numerous theories have been advanced to explain patterns of community composition, no single unifying construct seems adequate to explain observed patterns of species co-existence (Wilson 2011), but see (citation).  Most studies of co-existence occur in terrestrial systems where factors governing co-existence can be carefully controlled and monitored. In marine ecosystems, identifying opportunities for comparative studies is difficult and thus few studies compare patterns and mechanisms of differences in community composition and species co-existence in these systems (Smith, Orvos, and Cairns Jr. 1993).  However, recent studies have supported the theory that community composition influences stability of ecosystem functions in marine ecosystems through response redundancy, because compensation among species or functional groups leads to more consistent ecosystem properties (Schindler, Armstrong, and Reed 2015, Blake and Duffy 2010, Schindler et al. 2010).  Recent reviews also indicate that dispersal supports local coexistence of species via the spatial storage effect, where species disperse across an ecosystem in order to maintain optimal environmental conditions despite spatial variation (Snyder and Chesson 2004, others).  The mechanisms underlying co-existence and composition effects, response and functional redundancy and dispersal, also influence the portfolio effect across larger spatial scales.  The portfolio effect is one explanation for stability in multi-species communities. It ensures that ecosystems function more reliably because multi-species assemblages increase the likelihood that some species can maintain functioning in the face of perturbations (Loreau 2010, others).  This occurs when species have asynchronous responses to environmental perturbations, but when summed across the whole assemblage the responses average out statistically leading to greater stability with greater diversity (citations). In a spatial context, regional ecosystems and communities function more reliably because variation between local communities increases the likelihood of compensatory fluctuations in the face of environmental heterogeneity. Thus, we expect biodiversity to increase both local and regional stability by buffering against variability in functioning and enhancing biomass production.  The specific mechanisms that underlie these effects locally are species’ intrinsic responses to perturbations, the speed of those responses, and a reduction in interspecific competition (Loreau and de Mazancourt 2013, others).  At the regional scale, these effects are driven by mechanisms such as spatial environmental heterogeneity, which begets spatial heterogeneity in local community responses to environmental conditions (by virtue of spatial turnover in species composition), interspecific interactions (both trophic and non-trophic), and dispersal (Loreau, Mouquet, and Holt 2003, Loreau and de Mazancourt 2013, Wang and Loreau 2014).  The Gulf of Alaska (GOA) provides an excellent region to examine mechanisms governing the portfolio effect and community composition.  This continental shelf ecosystem exhibits spatial heterogeneity and complex topography that is punctuated by submarine troughs and canyons which act to steer currents, creating several relatively distinct areas of similar conditions that can be compared (﻿Lagerloef 1983).  Previous studies have utilized this complex topography for natural experiments comparing responses of selected fish species to natural or anthropogenic disturbance (﻿Hollowed et al. 2007, ﻿Logerwell et al. 2007, ﻿Walline et al. 2012).  This spatial heterogeneity can also lead to locally heterogeneous environmental conditions such as variation in primary production and freshwater inputs that can influence ecosystem processes and functions.  The GOA and other boreal marine systems also experience high seasonal, interannual, decadal, and multi-decadal climate-driven variability that can impact marine species (﻿Anderson and Piatt 1999, ﻿Hollowed et al. 2001, ﻿Stachura et al. 2014), however the responses of diverse marine communities are less understood. These climate-driven perturbations can impact communities at multiple spatial scales,and can create heterogeneity (e.g. freshwater inputs, sea surface temperatures, primary production) or homogeneity (e.g. atmospheric forcing, the Pacific Decadal Oscillation, Alaska Coastal Current) across this large marine ecosystem. Anthropogenic perturbations including oil spills can also impact marine ecosystems at multiple spatial scales.  One of the largest marine oil spills on record, the 1989 Exxon Valdez oil spill (EVOS) impacted shoreline and continental shelf areas in a large portion of the GOA region, and threatened rich cultural and fisheries resources. The groundfish assemblage in the GOA is a model community in which to examine changes in diversity, community composition, and the role of diversity in stabilizing a large marine ecosystem. The groundfish community is well-studied, widely distributed across the GOA, and most species are known to respond to climate and human-induced perturbations (Anderson & Piatt 1996, Hollowed papers, others). In this paper, we evaluated spatial patterns of diversity and community composition among the 55 most common groundfish species across the Gulf of Alaska over a period of large natural (e.g., climate regime shifts) and anthropogenic (e.g., EVOS) environmental perturbations, and considered whether we can identify mechanisms underlying these spatial patterns. Specifically, we addressed the following questions: 1) Are local communities more variable than regional communities?  2) Are species diversity and functional diversity associated with stability across this large marine ecosystem?  3) Does community composition alter community stability?  We show that while diversity varies remarkably little across the region, community composition does vary perhaps driven by biomass dominant species, and there is evidence to support the portfolio effect.   
   
**Methods**

*Data*  
Since 1984, the Alaska Fisheries Science Center (AFSC) has conducted comprehensive bottom trawl surveys in the GOA to monitor trends in the distribution and abundance of groundfish populations. The surveys were run triennially from 1984 to 1999 and biannually thereafter (14 years total). The full survey area includes the continental shelf and upper continental slope (to 1,000 m depth) in the GOA and extends from the Islands of Four Mountains (170° W) 2,300 km east to Dixon Entrance (54° N). The AFSC contracts three commercial trawlers from May through August and samples the standard 320,000 km 2 survey area with approximately 820 survey stations. The catch data result in observations of catch-per-unit-area (CPUE), which are averaged and expanded by survey area to estimate the relative abundance of important groundfish species. This multi-species survey is based upon a stratified-random design and the area-swept method of estimating abundance (von Szalay et al. 2010).  The net used in this survey is a four-seam, high-opening Poly Nor’Eastern trawl featuring a 27.2 m headrope and a 36.7 m footrope equipped with rubber bobbin roller gear. The net is deployed from the vessel while the vessel steams ahead at three knots.  Once on the seafloor, the net is towed for 30 minutes (prior to 1992) or 15 minutes (1992 - present).  In most years the net was equipped with a bottom contact sensor on the footrope, and a Seabird SBE-39 bathythermograph on the headrope. The catch was processed by the scientific crew who identified all living organisms, weighed, and counted the catch of each species.  It should be noted that because species exhibit different vulnerability to the survey trawl, these data reflect the demersal fish community on the continental shelf.  
       To assess species diversity across the GOA, we used smoothed estimates of species occurrence and densities that were generated from AFSC survey data by Shelton et al. (). The authors constructed separate spatio-temporal statistical models for 55 groundfish species to identify their patterns of occurrence and abundance in the GOA. The 55 species groups represent species that were observed in at least 3% of the survey tows (>230 tows). Briefly, the spatio-temporal models used CPUE (kg∙hectare-1) observed on each trawl as the response variable and the explanatory variables included both linear and quadratic terms for log(bottom depth) at each trawl location (Shelton et al. 2014, Tolimieri et al. 2015). Because most species were absent from a large number of observed trawls, the presence and distribution of species density were modeled separately, analogous to a delta-GLM approach with two sub-models (Pennington et al. 1983, Maunder and Punt 2004, Shelton et al. 2014). The first sub-model (‘occurrence model’) described the probability of occurrence of individual species in each year and at each trawl location and the second sub-model (‘positive model’) described the CPUE of species in each year and at each location conditional on the occurrence of at least one individual. Both sub-models model included spatial random effects that follow a first-order autoregressive process and account for variation not explicitly included in the model. Once the sub-models were estimated, model estimates were projected to the center of 2x2 km grid cells created for the entire GOA. Shelton et al. () generated 1,000 Markov Chain Monte Carlo (MCMC) samples from the joint approximate posterior density for each species and for each MCMC sample predicted a density for each sub-model to the 2x2km grid. Unconditional expectations for CPUE (kg∙hectare-1) of species in each year and at each location were then calculated by multiplying each MCMC sample from the occurrence and positive model. These predicted CPUEs for each 2x2 km grid cell were combined to generate index-standardized mean estimates (and standard deviations) of CPUE for each species in each year within discrete study areas (see *Study areas* below) (Shelton et al. 2012, 2014, Ward et al. 2015). Details on model structures, formulations and projections can be found in Shelton et al. () and in Supplementary Appendix A1. To assess functional diversity, we selected functional traits representing orthogonal components of community structure. These included body size, longevity, trophic structure, use of benthic vs. pelagic resources, and habitat. We assembled functional trait data for a subset of GOA groundfish species (44 of the 55) using the AFSC’s life history database (http://access.afsc.noaa.gov/reem/LHWeb/Index.php), 2015 Stock Assessment reports (www.afsc.noaa.gov/REFM/Stocks/assessments.htm, accessed…), and Fishbase (http://www.fishbase.org/search.php, accessed…).  We also included diet information from the AFSC’s Resource Ecology and Ecosystem Monitoring diet database (www.afsc.noaa.gov/REFM/REEM/DBDefault.htm, accessed…), as well as estimates of trophic position based on Aydin et al. (2007).  Where possible we used trait data from the Gulf of Alaska, however, when these were not available we used all available data from other regions.  The subset of species for which trait data were available was not biased towards any particular functional groups or traits. Functional trait data is provided in Supplementary Appendix A2.

*Study areas*We mapped the extent of both the trawl survey data and the EVOS over the shelf region of the central GOA.  We then selected study areas on the shelf across a gradient of expected oil exposure and different bottom depths: 9 contiguous areas of depth 50 - 150 m (’shallow areas’), 5 additional contiguous areas of depths 151 - 300 m (’deep areas’) (Figure 1). Study areas were separated by canyons or areas of shallower depth and thus represent discrete replicate areas.   This provided us with an area East of the spill that likely did not receive oil (shallow area 1), areas that were likely oiled (shallow areas 2 - 6, deep areas 10, 11), and areas West of the spill extent that were also likely unoiled (shallow areas 7 - 9, deep areas 12 - 14) (Figure 1).  Study areas were located between 145° W and 159° W and ranged in size from 1,352 – 15,136 km (see Supplementary Table S1 for more information on study areas).  We note that an artifact of the spatio-temporal statistical model is that some information is shared between study areas due to the spatial range of correlations, however in most species/study area cases the distances between the 14 regions exceeded the species range. Species with higher frequencies of occurrence tended to have lower spatial ranges with the dominant species (e.g. cod, halibut, sablefish, and pollock) being less than 60 km.  [*The estimated range at which the spatial correlation in the spatial field falls to 0.05 after accounting for depth ranged from 10 km – 500 km with most species exhibiting a range of 65 km*. – include in model description above or in Appendix A1?]

*Analysis*  
Since diversity often confers stability (here spatial stability), we calculated several diversity metrics for the GOA groundfish community: alpha, beta, and gamma diversity, species richness, and functional diversity.  In the context of our work, alpha diversity is the effective number of species in a study area, beta diversity is the effective number of distinct communities and represents differences in species composition between the shallow or deep study areas, and gamma diversity is the effective number of species across all shallow or deep areas. To estimate alpha and gamma, we calculated the exponent of the Shannon-Wiener index using the predicted densities of species within study areas and across shallow and deep areas, respectively, and used a multiplicative relationship between alpha and beta (alpha \* beta = gamma) to estimate beta diversity for each study area ([Jost 2007](https://www.authorea.com/users/93870/articles/114080/_show_article#jost_partitioning_2007), [Shannon 1948](https://www.authorea.com/users/93870/articles/114080/_show_article#shannon_mathematical_1948)). Species richness was estimated summing the predicted occurrence of all species within each shallow and deep study area (Dorazio et al. 2006). To correct for uncertainty in the model predictions that we are using to estimate species diversity metrics, we resampled the expected distributions of species occurrence and densities within each study area 1000 times using bootstrap methods and calculated the mean and variance of the diversity metrics. The R code for the bootstrap analysis is provided in Supplementary Appendix A3. Diversity metrics were calculated using the vegan package in R (Oksanen et al. 2016).   
       We examined functional diversity in the 14 study areas using Rao’s index of quadratic entropy (henceforth Rao’s Q) (Rao 1982), which represents functional richness and functional divergence (Mouchet et al. 2010).  We used a square-root corrected species-by-species Gower distance matrix for functional traits and the predicted mean densities from the spatio-temporal model for the species-by-species abundance matrix. Continuous traits were log-transformed prior to analysis and we used only uncorrelated traits (Botta-Dukát 2005). We did not correct Rao’s Q for the effect of species richness because richness did not vary significantly between local areas (Mouchet et al. 2008).  To test for differences in Rao’s Q between study areas, we used a one-way ANOVA followed by a Tukey post-hoc test.  Functional diversity analyses were conducted using the FD package in R (Laliberté et al. 2015).   
       To assess spatial variation in community composition between local study areas, we used non-metric multidimensional scaling (NMDS) with Bray-Curtis dissimilarities.  The predicted mean densities of individual species varied by eight orders of magnitude between local study areas and years.  Therefore, to allow the result to be driven equally by rare and abundant species, we standardized the data using a Wisconsin-style double transformation of square-root transformed data.  We used permutational multivariate analysis of variance (PERMANOVA) to evaluate the significance of between-area differences in community composition (Anderson 2001).  To evaluate whether PERMANOVA results were driven by between- or within-area differences in (temporal) replicates, we evaluated the homogeneity of within-region dispersions (Anderson 2006). Multivariate analyses were computed using the vegan package in R (Oksanen et al. 2016).  
       To evaluate evidence for a spatial portfolio effect, we calculated the coefficient of variation (CV) of total groundfish densities for each local community (i.e. study areas) and for the regional community (i.e. study areas combined), for both shallow areas and deep areas. We calculated an index of the strength of the spatial portfolio effect from the ratio of local / regional CV, where ratios > 1 indicate a stabilizing (portfolio) effect (after Anderson, Cooper, and Dulvy 2013).   
     

**Results**  
*Diversity*We examined five diversity metrics within each of the 9 shallow areas and 5 deep study areas in the GOA to understand how diversity varies across this large marine ecosystem.  Species richness at each study area was relatively low, and ranged from approximately 9 - 13 in shallow areas and 11 - 14 in deep areas (Figure 2a,b).  The western-most shallow areas (8, 9) had higher species richness (add stats), and those areas east of Kodiak Island had lower richness.  Alpha diversity (within area diversity) varied little between study areas, and averaged approximately 9 species across both shallow and deep sites (Figure 2a,b).  Shallow areas had slightly higher alpha diversity on average, but also had higher variability (add stats), while deep site 13, at the western end of Kodiak Island, had the lowest alpha diversity (add stats here).  Beta diversity (between area diversity) was also remarkably similar across both shallow and deep areas, and averaged approximately 9 in shallow areas and 5 in deep areas (Figure 2a,b). Given the invariance of diversity both within and between study areas, we examined functional diversity to better understand the groundfish community.  Rao’s Q, our measure of functional diversity, showed little variation across most shallow and deep local communities with few exceptions (Figure 3): Local communities in shallow area 6 differed significantly from those in areas 1, 2, and 4, and areas 2 and 9 also differed significantly (Tukey test, p < 0.05).  Deep areas did not differ significantly in functional diversity (ANOVA, p = 0.071).  Overall, species richness and diversity as well as functional diversity of the groundfish community were conserved across the central GOA over a 31-year period.  
  
*Community composition*Because functional diversity depends to a large extent on species identity, we also examined community composition. Xx, xx and xx were the most abundant species (XX% of total biomass).  Composition varied across a longitudinal gradient, with shallow areas 8 and 9 showing no overlap with the rest of the shallow areas (Figure 4).  Despite areas 1 - 7 showing some overlap, all shallow areas were significantly different in composition from each other (PERMANOVA, p = 0.005, R2= 0.22).  Likewise, the deep areas West of Kodiak Island also showed no overlap with those to the East, and though the distinction was less pronounced, all deep sites differed significantly in composition (PERMANOVA, p = 0.005, R2= 0.23) (Figure 3).  These results were confirmed by a homogeneity test of within-area dispersions, which indicates that differences are attributed to real between-area differences in community composition (shallow p = 0.94, deep p = 0.89).  Therefore, between both deep and shallow areas, the groundfish community composition varied across space with distinct groups of species in the individual study areas.  In shallow areas 1-7 east of Kodiak (and to a lesser degree in deep areas 1-4), compositional turnover was driven by rare and intermediate-density species. Community composition with respect to the most abundant species did not show spatial turnover: compositional turnover was not apparent when data were transformed to emphasize the influence of the most abundant species (i.e. Hellinger transformation; Supplementary Figure S1); instead, turnover was only apparent when data were transformed to allow subdominant species equal chance of explaining community structure (i.e. Wisconsin - Square root transformation; Figure 3).  
*Portfolio Effect*While our diversity metrics point at a stabilizing effect across the GOA, we also explicitly tested whether there was more variation among individual study areas as compared to the regional community (the portfolio effect).  Coefficients of variation (CV) for local communities were greater than regional community CV by a factor of 2.34 for shallow sites and a factor of 1.35 for deep sites.  Mean CV for shallow local communities (0.171 +/- 0.043) were greater than that of the regional shallow community (0.073; Figure 4).  Similarly, in deep study areas, local community CV (0.253 +/- 0.077) were greater than the regional community CV (0.187; Figure 4).  Therefore, the portfolio effect is evident because the regional GOA groundfish community (across approx. 2,000 km) is significantly less variable than local communities.  
  
**Discussion** Our results support species sorting (environmental heterogeneity) and conserved community architecture hypotheses for spatial patterns of diversity. In both shallow and deep areas we documented variation in species richness (Fig. X - *shallow areas 8 and 9, and deep areas 13 and 14 had greater diversity than remaining communities, not sure if this was statistically significant?)* and spatial turnover in community composition (Fig. Y). Additionally, beta diversity was high (local communities held 1/5th to 1/10th of the regional species pool in shallow and deep areas respectively *)* in all local communities, reflecting compositional turnover. Variation in species richness and species identity (compositional turnover) followed the longitudinal gradient with the exception of shallow community 7 . Despite the presence of conditions which should facilitate strong dispersal (an open system, mobile species, and the strong Alaska Coastal Current), we observed strong compositional turnover between local communities along the longitudinal gradient. While compositional turnover has been observed in open marine systems along latitudinal gradients (e.g. coral-associated fish: Mellin et al. 2014, fish assemblages of the North Sea prior to warming: Magurran et al. 2015), … Species richness was greatest in local communities west of Kodiak Island (shallow communities 8 and 9, deep communities 13 and 14), where primary production (re. intensity and annual duration of the Chl a ‘bloom’; Figs. 6a and 4 in Waite & Mueter 2013), total community abundance, and top predator abundance (Shelton et al. in prep.) were lowest. Like other recent work (e.g. Adler et al. 2010 Science, Grace et al. 2014 Funct. Ecol.), our result stands in contrast to longstanding theory, which predicts that species richness should exhibit a unimodal relationship (rise and then fall) with productivity (Grimes 1973, 1979). Because predator abundance is positively related to predation intensity, the result also stands in contrast to classical predation-diversity theory, which predicts that prey diversity should increase with predator abundance and predation pressure (cite Paine, Menge, Sutherland papers). This result may arise from a spatial predation refugia – although predator: prey ratios were similar between local communities, the reduction in absolute predator abundance was likely associated with reduced predation pressure … *our result* *would occur if generalist predators consume prey items in proportion to their relative abundance, causing local extirpations of less abundant species; cite Hixon & Beets (1993 Ecol. Monogr.) for* n*egative relationship between predator abundance and prey diversity among coral reef-associated fish.* ***Can you guys think of other factors which could drive this low productivity – high diversity result? We used the presence/absence model output for species richness – how would this influence the result?***

Despite variation in species richness and community composition across local communities, our metrics of community architecture / organization (*you guys might prefer another term here?)* also supported a conserved community architecture hypothesis. Functional diversity, computed from traits representing multiple independent (uncorrelated) elements of community structure, was invariant among both shallow and deep areas, indicating that local communities were structured similarly with respect to functional roles. For both shallow and deep areas we documented statistically invariant indices of alpha diversity (evenness) – within shallow and deep suites of communities, local communities had a similar degree of skew in relative abundance among those species present in the community. This result is corroborated by our metric of community structure *(either Ole’s triangle figure (so far only for shallow areas) or we could plot ratios of predator:prey abundance for each local community),* which indicated that local communities are consistently dominated by apex predators, with similar ratios of predator : prey abundance. Intriguingly, among local communities situated adjacent and to the east of Kodiak Island (local communities 1-7 and 10-13), we documented that spatial turnover occurs among subdominant (Fig. Z c, d) but not dominant (Fig. Z a, b) species. The same was observed among westernmost sites (8, 9, 13, & 14), albeit to a lesser degree, as evidenced by reduced distances between centroids following the Hellinger transformation. In other words, identity and community composition of numerically dominant species was invariant among eastern sites (and less variable than subdominant species among westernmost sites), and turnover occurred instead among subdominant species along the longitudinal (environmental) gradient. This result, combined with invariance in functional diversity and predator-prey ratios, suggests that there was functional redundancy among the subgroup of sub-dominant species as they were sequentially replaced along the longitudinal (environmental) gradient – subdominant species were replaced along the longitudinal gradient in such a way that they filled the same community roles in each local community.

*Consider citing evidence from the literature for conserved community structure (with or without conserved species identity) across environmental gradients: e.g. Sprules’ (2008) conserved biomass size spectra (conserved zooplankton community structure over time in Lakes Erie and Ontario, and conserved whole-food-web structure across an environmental gradient between 4 lakes). Other studies?*

The high beta diversity and spatial turnover in community composition we observed may help buffer the regional Gulf of Alaska groundfish community against perturbations. We documented evidence for a spatial portfolio effect: greater temporal instability in local vs regional communities was associated with lower diversity (exp H’) in local vs regional communities (*I think we can say 'associated with' because we see this pattern in both our shallow & deep areas, kind of like having 2 replicates*). A primary mechanism underlying the spatial portfolio effect is species’ differential responses to environmental conditions and perturbations (Wang & Loreau 2014, definitely cite other lit too). In the GoA groundfish community, the importance of environmental heterogeneity (species sorting) and functional complementarity mechanisms underlying spatial patterns of diversity which we document may contribute to the spatial portfolio effect ...

Insert brief text about perturbations in GOA 1984 - 2015  
Despite all of these perturbations, overall, across space (between local areas) the community does not show signals  
EVOS in the context of other perturbations (climate change, etc)

*A few more thoughts:*

1. We could consider framing our shallow / deep results as replicate suites of communities across depth types (ie 1 replicate in shallow communities, 1 replicate in deep communities)

2. We could consider comparing patterns in shallow vs deep areas, which differed in gamma (ie we could make a comparison of spatial patterns in diversity in shallow areas with higher gamma vs deeper areas with lower gamma). For example, species richness was greater in deep vs shallow areas, even though gamma was greater in deeper areas … seems counterintuitive, does it tell us something interesting about processes structuring our communities?  
**Bootstrapped gamma (expected gamma) for shallow areas = 56.4-81.6  
Bootstrapped gamma for deep areas = 27.4-39.5**Piacenza et al. 2015 showed that groundfish species richness was maximized at ~200m depth (the continental shelf break) in the contiguous US west coast (corresponds to our deep areas …).

3. Comparisons to the literature:   
a. We should compare to Mueter’s GoA diversity papers.  
b. Could also compare to spatial patterns of diversity on the contiguous US west coast (Piacenza et al. 2015) … but they looked at diversity hotspots … diversity hotspots were ephemeral, usually lasting no more than ~3 years (note they had a 10-year dataset of annual samples)

**Supplementary Materials**  
Supplement Table S1: Information of study areas (size, mean depth, bottom temp, # of modeled grid cells, etc.)  
Supplement Appendix A1: geostatistical model details  
Supplement Appendix A2: functional trait data  
Supplement Appendix A3: code for the bootstrapping analysis  
Supplement Figure 1: NMDS. To evaluate whether spatial turnover was driven by dominant or subdominant species, we simultaneously ran nMDS using a Hellinger transformation, which yields a result driven by only the most dominant species.  
Supplement Figures 2-4: Time series of diversity metrics and species richness?

## Data and Code Availability Trawl data, spatio-temporal model code and output, and code used for study analyses are publicly available at (insert URL).

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