



Epifaunal diversity patterns among eelgrass meadows suggest metacommunity structure

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Epifaunal diversity patterns among eelgrass meadows suggest metacommunity structure

Running head: Epifaunal diversity in seagrass

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ABSTRACT

In coastal seascapes, spatial habitat structure can support high animal diversity and secondary productivity. Still, seascape-scale connectivity among eelgrass meadows is an often-overlooked dimension of their ecological and conservation value. We tested whether eelgrass-associated biodiversity patterns are consistent with spatial processes such as abiotic habitat filtering or metacommunity dynamics. In Barkley Sound, British Columbia, we quantified epifaunal biodiversity on eelgrass (*Zostera marina*) among nine meadows to test three hypotheses: taxonomic diversity and composition i) vary randomly within meadows but ii) vary systematically among meadows reflecting seascape position and metacommunity dynamics, and iii) patterns are stable over time. We sampled epifaunal invertebrate biodiversity in a systematic spatial grid within 9 eelgrass meadows along a spatial gradient. We used univariate and multivariate diversity metrics to test for spatial and temporal diversity patterns. Though we identified two high-diversity meadows, epifaunal diversity varied as much over a few meters within the same meadow as among meadows separated by kilometers and of different sizes and exposures. This variation was not clearly explained by seascape position. Community similarity increased from May to August. These findings leave open the possibility that seascape scale metacommunity dynamics influence eelgrass-associated epifaunal biodiversity and its persistence in spatially patchy seascapes.

Key words: biodiversity; estuary; foundation species; grazer; invertebrate; metacommunity; seagrass; seascape ecology; *Zostera marina*.

INTRODUCTION

Understanding species' distribution and abundance is essential to understanding ecological communities and to making informed decisions about seascape management and biodiversity conservation. In highly diverse coastal marine habitats, understanding can be limited by a lack of basic information about where and when species occur and the spatial scales over which dominant diversity-influencing processes operate (Gaston 2000, Boström et al. 2006). Coastal foundation species such as seagrass and kelp are often targeted for conservation for the biodiversity they harbor and the ecosystem services they provide. Yet, how exactly these habitats support the high and productive animal assemblages, and the role of spatial arrangement of habitats, remains poorly understood.

While a spatially discrete habitat patch such as a seagrass meadow or a kelp bed may appear to host a complete or representative local faunal community, habitat provision by foundation species is just one of several processes that influence biodiversity of a patch: population dynamics and species interactions structure species assemblages at finer (within meadow) and broader (seascape) spatial scales in spatially structured 'metacommunities' (Leibold et al. 2004, Boström et al. 2006, Pillai et al. 2011). Rates of colonization and rescue effects from source-sink dynamics can play a major role in maintaining the species composition and functional integrity of an ecosystem, and understanding these dynamics is critical for successful management (Gerber et al. 2014, Furrer and Pasinelli 2016).

The purpose of this study is to explore potential metacommunity structure among eelgrass-associated epifaunal species as a first step to assess the most informative spatial scale

for understanding how eelgrass meadows support biodiversity and its associated ecosystem functions. Specifically, our aim was to target epifaunal biodiversity among spatial scales in a seagrass meadow seascape to determine whether individual meadows, or a set of meadows, are representative spatial units for biodiversity (i.e. – groupings of habitat that reflect regional patterns of diversity). Spatial variation in biodiversity is influenced by the spatial scales of ecological processes (e.g.- local predation pressure vs. regional dispersal patterns) that affect species' relative abundance and presence or absence (Leibold et al. 2004, Ricklefs 2004, Boström et al. 2006). Across a region, evolutionary and colonization history produce a shared regional species pool (*gamma diversity*). At finer scales, meadow- or host plant-scale biotic interactions (predation, competition, facilitation, resource provision) and abiotic conditions (temperature, salinity, etc.) filter species from the regional pool to a subset of regional diversity, called *alpha diversity* (DeTroch et al. 2001, Crist and Veech 2006, Sanders et al. 2007). Between local and regional scales, dispersal and colonization dynamics connect populations among habitat patches to produce metacommunities. In metacommunities, abundance and diversity vary among local sites, producing patterns of spatial turnover or variation, forms of *beta diversity* (Anderson et al 2011), that are jointly influenced by local and regional process (Leibold and Mikkelsen 2002, Leibold et al. 2004, Crist and Veech 2006, Henriques-Silva et al. 2013).

Eelgrass-associated epifauna are the critical links in the food web that connect high eelgrass related algal primary production to fish production in the food chain (Hemminga and Duarte 2000). Biogeographic variation in eelgrass-associated epifaunal diversity influences the strength of top down control in eelgrass meadows, and is central to many of the ecosystem services provided by these systems (Duffy et al. 2003, 2015, Amundrud et al. 2015).

Epifaunal diversity can vary substantially within and among meadows (Hemminga and Duarte 2000, Boström et al. 2006, Yamada et al. 2007, Carr et al. 2011, Barnes and Ellwood 2012, Barnes 2013). Within meadows, alpha diversity at fine scales ($0.5 - 1 \text{ m}^2$) is typically relatively consistent among patches within the same meadow and much lower than meadow-scale species diversity (Carr et al. 2011, Barnes and Ellwood 2012, Barnes 2013). This pattern suggests that compositional differences, one form of beta diversity, should be high and a relatively important component of seagrass associated biodiversity within meadows. Though studies of variation in species distribution have reported high turnover at moderate spatial scales ($< 150 \text{ m}$, Barnes and Ellwood 2012), few studies specifically assess beta diversity at the same scale. Among meadows, variation in species composition and diversity is in some cases explained partially by wave energy or exposure (e.g., fetch; Boström et al. 2006, Robinson et al. 2011) or salinity (Yamada et al. 2007, Boström et al. 2014, Barnes and Ellwood 2013). Still, in some cases diversity patterns are not readily explained by abiotic attributes (e.g., Carr et al. 2011, Barnes and Elwood 2012).

Here, we test the hypothesis that non-random spatial patterns in species composition and turnover within and among meadows distinguish meadows within a seascape and provide insight as to potential importance of abiotic factors and community dynamics in driving regional-scale epifaunal diversity patterns. Specifically, we hypothesize that 1) alpha (quadrat-scale) epifaunal diversity is the same among meadows, but within-meadow species composition varies in space to produce patterns of beta diversity that also vary among eelgrass meadows, and 2) spatial variation in species composition is consistent with i) local filtering of species based on abiotic conditions, or ii) metacommunity-scale processes that involve dispersal among meadows. We

also tested 3) whether patterns of diversity vary over time, and whether variation over time could provide insight to possible drivers of diversity patterns. To test these hypotheses, we used a nested sampling design to quantify spatial structure in seagrass-associated epifaunal biodiversity among nine meadows in British Columbia, Canada.

METHODS

Study system

We sampled epifaunal biodiversity in eelgrass *Zostera marina* meadows in summer of 2012 in Trevor Channel, Barkley Sound, where *Z. marina* is the only meadow-forming seagrass species (Figure 1A). In this region, *Z. marina* forms primarily subtidal, perennial meadows that range in size from $< 10 \text{ m}^2$ to $> 25,000 \text{ m}^2$ (Mason et al. 2015). A rich epifaunal assemblage of gastropods, crustaceans and other taxa live on and among eelgrass blades. Epifauna consume epiphytic algae growing on seagrass, detritus and each other, forming the base of a highly productive food web (Hemminga and Duarte 2000, Heck Jr. and Valentine 2006).

Structure and abiotic conditions

We quantified several biotic attributes of eelgrass meadows that could explain variation in eelgrass associated invertebrate biodiversity: shoot density, leaf area, epiphyte load, and meadow area. Shoot density and leaf area were estimated from three or four 0.28 m^2 quadrats collected outside each corner of a $4 \times 4 \text{ m}$ grid demarcated for community sampling (described below) at each site concurrent with epifaunal sampling. For all meadows in all time periods, we

removed a shoot from each corner quadrat, dried and weighed eelgrass and its associated epiphytes, and standardized epiphyte dry mass to eelgrass dry mass. Additionally, we sampled epiphytes more thoroughly at three sites during low-tide periods (< 0.5 m) in mid and late summer, by collecting 15 shoots per meadow from three tidal heights. We separated bladed epiphytes from periphyton and again standardized epiphyte mass to eelgrass mass. We estimated leaf area using methods described by Borg et al., 2010. We did not estimate quadrat-level density or leaf area for the same quadrats from which we sampled epifaunal biodiversity.

To quantify meadow-scale abiotic conditions, we measured temperature and salinity using a hand-held temperature/salinity sensor (YSI Inc., OH USA). Measurements were taken throughout the tidal cycle on biodiversity sampling days, and opportunistically on other days. We represented the estuarine abiotic gradient of salinity and temperature by quantifying the geographic position from the nearest freshwater input of each meadow. Position was estimated as linear distance in kilometers from the nearest freshwater source (Sarita River or Alberni inlet, Figure 1A). We estimated exposure to wave energy (using fetch as a proxy) by calculating the distance to nearest land from the eelgrass meadow in 10 degree increments around a centroid point and summed the distance.

Biodiversity sampling

To estimate epifaunal biodiversity and characterize variation within meadows, we used a 4 x 4 m grid of 16 standard quadrats (0.28 m^2), each separated by 1 m, in each meadow (Figure 1B; after Sanders et al. 2007, Duffy et al. 2015). Repeated sampling within meadows was rotated 90° around a central reference point at a distance of 1-2 m so that seagrass removed at one time

period would not impact the density of seagrass and associated epifaunal at subsequent samplings. This sampling design allowed for comparison of diversity among quadrats and meadows while standardizing for total area sampled and the spatial arrangement of samples. We placed sampling grids within contiguous meadows at least 2 m from any meadow edge. In each quadrat, we cut away eelgrass at the sediment-water interface and placed it into a 250 μ m mesh bag, collecting all eelgrass and epifauna. All sampled areas were at least 1 m below lower low water large tide (LLWLT) but not deeper than 3 m below LLWLT. Samples were then transported back to the lab in seawater, where all invertebrates were removed and preserved in 70% EtOH within 24 hours of collection.

To estimate variation in diversity among meadows, we sampled nine meadows between the open coast and Alberni Inlet in Trevor Channel (Figure 1; Table 1). We chose these meadows among the subset of known meadows in Trevor Channel ($n \sim 20$) because they are evenly distributed along the channel, they are large meadows (i.e., 0.12 – 11.33 ha), and they represent many of the shallow areas where eelgrass might occur. To determine whether spatial biodiversity patterns varied through time, we sampled five of these meadows three times, in May (early summer, time A), June/July (midsummer, time B) and August (late summer, time C) of 2012.

We identified every invertebrate > 1 mm to the lowest taxonomic resolution possible using light microscopy. Though many of our identifications are to species level, many other taxa are identified to higher levels (Family or Order). Consequently, our taxonomic diversity estimates should be considered minimum estimates. We classified invertebrate species to broad

175 trophic groups (grazer, predator, filter feeder, detritivore) based on our observations and
176 published information (Light and Carlton 2007, Macdonald et al. 2010).

178 *Biodiversity estimation*

179 To estimate diversity within and among meadows, we created species-quadrat and
180 species-site matrices with abundance data using information on every individual collected from
181 each quadrat (Gotelli and Colwell 2011). We estimated multiple biodiversity metrics: species
182 richness (number of species observed), their relative abundance, and the likelihood that
183 additional taxa were present but unobserved in estimating and comparing biodiversity among
184 samples and meadows. We estimated alpha (quadrat-scale) diversity by rarifying (ENS) and
185 using species richness values (R), Shannon diversity (H'), and Simpson evenness (S). The
186 effective number of species (ENS) is derived from the probability of an interspecific encounter
187 (PIE; Dauby and Hardy 2012). ENS is a standard metric that can help distinguish changes in
188 diversity from changes in abundance and can be interpreted as the number of equally-abundant
189 species that would exist in a sample of a given diversity value (Jost 2006). We used the R
190 package vegan (Oksanen et al. 2007, R Core Team 2016).

191 We quantified beta diversity in two ways. First, we estimated beta diversity (β_{BC}) *within*
192 each meadow using the Bray-Curtis dissimilarity metric, which accounts for relative abundance
193 of species and estimates differences among samples as their average distance from a group
194 (meadow-level) centroid (Tuomisto 2010, Anderson et al. 2011). This allows comparison of
195 quadrats to all other quadrats within the meadow. Second, we used a null model approach
196 developed by Chase et al. (2011) to evaluate possible mechanisms that influence community

similarity *among* meadows and to distinguish differences in beta diversity that reflect underlying patterns of community structure rather than random differences in alpha diversity among sites. The model uses the Raup-Crick beta diversity metric, β_{RC} , to compare pairwise dissimilarities between samples with a null expectation. This metric uses presence/absence of species and their relative occurrence among samples to assign probabilities that community samples are less similar (>0), more similar (<0) or no different ($=0$) than expected by chance. We analyzed patterns in community composition among all nine sites sampled at all time periods for both intra-meadow and inter-meadow variation.

Statistical diversity analyses

To test our first hypothesis that alpha diversity (quadrat-level species diversity) does not vary among quadrats we used one-way ANOVA on univariate diversity metrics among nine meadows sampled in July (midsummer, time B). To explore possible explanations for variation in diversity within and among meadows, we tested whether spatial patterns in grazer diversity varied with season, distance from each other, and meadow attributes. We conducted linear regression analyses using sampling date, distance among quadrats, meadow area, fetch and distance from freshwater inputs as predictors. We tested for correlations among these variables. Abundance and ENS were log-transformed to meet the assumption of homoscedasticity.

To test our second hypotheses that beta diversity within meadows varies among meadows, we compared beta diversity estimates with null expectations as described above. Beta and alpha diversity patterns can differ if species are aggregated within meadows (as opposed to

randomly distributed throughout the meadow), or if aggregation varies among species and dominance varies among meadows. We estimated aggregation within meadows using standardized Morisita's index (I), and then compared aggregation scores for species in each meadow with their rank. We specifically tested for aggregation within meadows, whether it is driven by the most abundant species, and whether the most abundant species are the same among meadows.

For all model comparisons, we ranked models using AICc, and compared them using likelihood ratio tests, δ_{aic} and Akaike weights (w). Models with a $\delta_{\text{aic}} < 2$ can be considered equivalent to the best model (Burnham and Anderson 2003). In the case of multiple highly ranked models, we selected the set of models that produced a cumulative $w > 0.95$, representing our confidence (95%) that the set includes the best model, and we averaged these models to produce coefficients of effects (Burnham and Anderson 2003). We examined residual plots for deviations from the assumptions of linearity or homoscedasticity (with the exception of parallel lines in a plot of the models' fitted values vs. residuals). This phenomenon resulted from including repeated values of position in the estuary in the model (Searle 1988). We tested hypotheses on a subset of our full dataset - the meadows sampled at all three time points - to conservatively test for an effect of temporal variation.

Elements of metacommunity methods

To test whether biodiversity patterns among meadows are consistent with metacommunity processes operating at the seascape scale, we applied the elements of metacommunity (EMS) framework (Leibold and Mikkelsen 2002, Presley et al. 2010). This

analysis first tests for coherence in species distributions among meadows by comparing observed species distributions with expected distributions based on a null model. If positive coherence is identified, spatial patterns can be further tested to identify patterns consistent with individualistic species distributions across the seascape (a Gleasonian model of species distributions), or clumped species distributions (Clementsian structure), or random, providing insight to possible types of community structure (Leibold and Mikkelsen 2002, Presley et al. 2010, Henriques-Silva et al. 2013). We analyzed metacommunity structure for the nine meadows sampled in July 2012 using the R package Metacom (Dallas 2014). We used a null model that fixed species richness within sites (‘fixed row’) but allowed composition to vary based on their marginal probabilities (method = “R1”).

RESULTS

Meadow attributes

We collected 71 samples for seagrass structural metrics. Meadows increased in shoot densities (+0.27 shoots/km) and associated leaf area (+240.73 cm²/km) with increasing proximity to the Pacific Ocean (Table S1). Shoot density and leaf area increased between May and August at meadows near freshwater but remained relatively high all summer at the seaward meadows (Table S1). Distance from fresh water input captured correlations with other variables: temperature, salinity, shoot density (Table S2). Salinity increased and temperature declined with distance from freshwater inputs, though these changes were relatively small in magnitude (Table S3). Epiphyte load was highly variable between meadows, uncorrelated with position in the

estuary and epiphyte abundances and the type of epiphytes present (periphyton vs. bladed algae) varied spatially and temporally (Table S4). The bladed brown epiphyte *Punctaria* sp. was abundant at two of the marine sites (DC and WI), and absent from the fresher NB.

Epifauna summary

We collected 304 seagrass samples with associated epifauna and identified approximately 81,500 invertebrates (47 taxa in 42 families). Of these, 30 taxa are considered epifaunal, meaning they regularly or always occur on the blades of eelgrass (rather than associated with sediment) (Table 2). We observed between 0 and 1200 individuals per 0.28 m² of seagrass meadow. Mean total abundance of all taxa at the quadrat scale did not vary among meadows in May, but did increase over the summer such that by August abundance was 2-3 times higher in seaward meadows (DC, WI, RP) compared to meadows nearer Alberni Inlet in which abundance was relatively stable over time (CB, NB; Table S5). The seasonal abundance increase in seaward meadows is clear in small (1-2 mm) and large (>2 mm) size fractions.

Of the 30 epifaunal taxa observed, 17 taxa are herbivorous or omnivorous consumers of epiphytic algae, classified as “grazers”. These comprised approximately 72% of all individuals. On average, in each meadow 6.0 (\pm 0.15) grazer taxa (isopods, harpacticoid copepods, amphipods, and gastropods) were detected. Among all samples, epifaunal assemblages were dominated by small (1-2 mm) invertebrates, which made up ~83% of individuals, whereas large invertebrates (> 8 mm) such as crabs, sea stars and urchins made up less than 3% of individuals.

Spatial biodiversity patterns

Between 10 and 22 epifaunal taxa (of the 30 observed) occurred in each meadow. Thus, there was substantial variation in observed diversity among meadows (Tables 1, 2, S5). We found that alpha diversity did not vary systematically among meadows with any predictor we tested (Figure 2, Table S5). Quadrat-level species richness [R] varied as much within meadows as among meadows (Figure 2A), with the exception of high species richness (alpha diversity) at RP and BI ($F = 8.9$, $df = 8$, 136 , $P < 0.001$). We observed similar patterns in Shannon diversity ($F = 4.6$, $df = 8$, 136 , $P < 0.001$) and Simpson diversity ($F = 3.8$, $df = 8$, 136 , $P < 0.001$), though for these metrics BI is not different, and DC has lower within-quadrat evenness than other meadows (Figure 2D). Rarified diversity estimates were more variable among meadows (Figure 2B; $F = 3.62$, $df = 8$, 120 , $P = 0.002$). The higher diversity of RP, lower S of DC, and differences in ENS were not explained by meadow-scale predictors such as distance from fresh water input, shoot density, meadow area or fetch (Table S5).

Beta diversity within meadows, reflecting similarity in relative abundance and composition of species from each of the 16 sampled quadrats, varied substantially among meadows (Figure 3E-F, Table S6). Comparison with the null model showed that both inter- and intra- meadow beta diversity (β_{RC}) was always less than expected by chance indicating that meadow epifauna were more similar than would be expected if species were distributed among meadows randomly (Figure 4A, Figure S7). A permutation test of multivariate homogeneity of group dispersions showed that within-meadow beta diversity varied among meadows, but beta diversity did not vary predictably by distance from fresh water input or with other abiotic and

biotic factors. Finally, analyses of aggregation indicated that individuals within species were spatially aggregated within meadows for most species (>80% in 7 of 9 meadows, Table 1).

Spatial variation in species composition was consistent with metacommunity-scale processes structuring biodiversity patterns. Among all nine meadows in July, elements of metacommunity structure (EMS) analysis based on presence/absence data suggested a checkerboard pattern of species distribution among meadows, indicating differences among meadows that were non-random. For all epifaunal taxa (30 taxa), EMS suggested negative spatial coherence (86 embedded absences relative to 56.17 ± 6.53 expected by the null model, $z = -4.57$, $P < 0.01$). For grazers (17 taxa), we observed a similar pattern of negative coherence (29 embedded absences relative to 16.42 ± 3.76 expected by the null model, $z = -3.35$, $P < 0.01$).

Temporal biodiversity patterns

Over time, quadrat-scale (alpha) richness increased, primarily between July and August, except at RP where richness spiked mid-summer (Figure 3A). Shannon diversity and Simpson's evenness did not vary systematically over time (Figure 3C-D), while ENS declined slightly overall between May and June (Figure 3B). By August, there was a trend toward lower quadrat-scale observed richness and lower ENS, which increased from marine to fresher meadows (Figure 3B).

Beta diversity as gamma/alpha and mean Bray-Curtis dissimilarity generally decreased over the summer, meaning quadrats within the same meadow became more similar. However, Bray-Curtis beta spiked at RP and CB in midsummer, likely due to a numerical increase in *Caprella* spp. and *Phyllaplysia taylori* at RP, and *Mytilus trossulus* at CB. These decreases in

beta diversity over the course of the summer are reflected in comparisons to null predictions (Figure 4), which found that among- and within-meadow beta diversity exhibited less dissimilarity than predicted values, a trend that strengthened on both scales over the course of the summer. This indicates that meadows were becoming more similar across small (<1 m) and large (>10 km) scales simultaneously. This trend can be attributed to the observed recruitment events by increasingly common mesograzers that occurred as the summer progressed.

Patterns in composition and dominance

Increasing similarity within and among meadows over time co-occurred with increases in abundance in common taxa, rather than by changes in their presence in meadows (Table 2, Figure 3). For example, *Caprella* spp. abundance increased more than ten-fold (from an average of 16 individuals/quadrate to 237 individuals/quadrate) from early to mid-summer, but by late summer a recruitment event of *Phyllaplysia taylori* led this species to outnumber *Caprella* spp. at RP and DC. However, changes in abundance were not consistently observed among sites. For example, the *P. taylori* recruitment event occurred at two sites, while a major mussel recruitment event occurred at other sites including NB and CB later during the same period, causing the species composition of these two sites to diverge from the others. Many species were rare but present at most sites and times, yet no species was common everywhere at all times (Table 2). Nearly half of epifaunal taxa analyzed (12) were common – five taxa were detected at every site and sampling time.

Meadow-scale patterns in species number and compositional variation were more similar among meadows than expected by chance, even though we observed different numbers and

combinations of species in each meadow. For example, samples collected within meadows mid-summer were typically more similar to samples from the same meadow than to samples from other meadows. These distinctive meadow species compositions reflected differences in numerically dominant species, rather than less striking differences in species presence or absence. However, while dissimilarity was greater among sites than within sites at the beginning of the summer compared to null expectations, the reverse was true by the end of the summer (Figure 4A).

Among all meadows, five taxa accounted for > 80% of invertebrates collected: the caprellid amphipods *Caprella* spp. (*C. laeviuscula* and *C. californica*), the sea hare *Phyllaplysia taylori* (primarily juveniles), the mussel *Mytilus trossulus* (primarily juveniles), the polychaete worm *Platynereis bicanaliculata*, and the sea spider *Pycnogonum* sp. However, abundances of these species were not consistently high among all meadows and all sampling periods.

DISCUSSION

Seagrass meadows host vast biodiversity, and this biodiversity is part of the immense ecological and economic value associated with seagrass ecosystems (Hemminga and Duarte 2000, Duffy et al. 2015, Heck and Williams 2000). Generalities and drivers of spatial patterns in eelgrass associated fauna are not well documented or understood (Boström et al. 2006). In an unprecedented spatially explicit description of the epifaunal biodiversity of British Columbia seagrass meadows over a summer season, we found that non-random spatial patterns in species composition and turnover distinguished meadows within the Trevor Channel seascape. In contrast, alpha diversity (species richness and ENS) was varied little over space and time.

Differences in meadow area, fetch and distance from freshwater input did not explain variation in diversity. These patterns suggest that species interactions and population dynamics are playing out across meadows in this region, and seagrass meadow communities may form larger metacommunities linked by dispersal.

Spatial patterns in epifauna suggest possible metacommunity structure, indicating that biodiversity may be maintained at the seascape scale rather than the meadow scale. Among meadows, species exhibited patterns consistent with a checkerboard distribution. Checkerboard patterns have been interpreted to reflect negative species interactions such that pairs of species do not occur together. Although this pattern could also reflect shared environmental affinities among groups of species (Leibold and Mikkelsen 2002, Presley et al. 2010, Henriques-Silva et al. 2013), the metacommunity analysis found no evidence for spatially nested or clumped community patterns that would have been more consistent with groups of species sharing environmental affiliations. This suggestion is also supported by the lack of an observed effect of meadow area or other abiotic predictors in this study. Absence of a signal of meadow area on diversity could indicate high connectivity (low isolation) among meadows. However, we only surveyed a small proportion of the larger meadows, so it is possible that higher diversity may be found in the larger meadows if sampled more extensively. Average quadrat scale diversity (7-20 species, Figure 3) and meadow-scale gamma diversity (Chao2 index estimate: 16 species per meadow + sd 3.39) was in all cases much lower than regional species diversity (47 observed taxa). Together, these patterns suggest that some processes limit the presence of regional taxa in all meadows, and that within-meadow communities may be maintained by a balance between habitat filtering and biological connectivity that maintains population connections among nearby

meadows. Such connectivity could maintain higher diversity in smaller meadows than expected based only on their size.

Contrary to some studies in other regions (Yamada et al. 2007, Barnes and Ellwood 2012), we did not observe a clear signal of continuous species turnover along the biotic and abiotic gradients associated with distance from fresh water input (Figure 2, Figure 3A-C), until, possibly, late summer (Figure 3D). We observed only weak, trends in invertebrate abundance and diversity with estuarine position (correlated with salinity and eelgrass structure). This may be indicative of the salinity regime of the sites sampled by Barnes (2013) and Yamada et al. (2007), which spanned a greater range in salinity ($< 5 - 35$ ppt and $6.2 - 32.2$ ppt, respectively) than did ours ($\sim 14 - 28$ ppt), and may have captured physiologically stressful, low-salinity conditions with a stronger influence on invertebrate assemblages.

Our findings are consistent with other studies that suggest that species compositional turnover in space is the main component of biodiversity in these systems. Quadrat-scale diversity seems to be quite constrained to a small number of species, regardless of meadow biotic or abiotic attributes. Thus, the processes that underlie spatial turnover are the ones that facilitate the high diversity of this system. Our study reveals spatial aggregation of most species within meadows. Aggregation can indicate micro-habitat variation, species interactions such as competition, predation or facilitation, or historical effects such as recovery from disturbance or stochastic events. We also observed turnover in composition among meadows that suggests a role for seascape-scale dispersal (>10 km), asynchronous community trajectories, or historical events such as disturbance and associated recovery.

Our study contributes to a limited number of existing beta diversity estimates for seagrass-associated epifauna. These studies have typically focused on turnover, i.e., directional change in beta diversity along some gradient, finding that beta diversity in seagrass beds can be driven by variation in salinity, seagrass species, tidal height, and sub-habitat type (e.g., seagrass shoots or sediment; De Troch et al. 2001, 2003, Barnes and Ellwood 2012, Knight et al. 2015). However, we know very little about non-directional variation in beta diversity within seagrass meadows, and (to our knowledge) no study has attempted to distinguish observed patterns in beta diversity from null expectations (Kraft et al. 2011). The comparison of null expectations to empirical datasets allowed us to infer whether random processes such as chance colonization and extinction, or deterministic processes like environmental filtering or competition are likely causes of observed patterns in community composition (Chase and Myers 2011).

Over the summer season, species turnover within and among meadows declined, reflecting demographic changes that increased the abundance and prevalence of several numerically dominant species. These demographic changes were driven by very different specific processes: annual recruitment pulses by the weakly-dispersing seagrass specialist *Phyllaplysia taylori* in RP and DC in August, recruitment by the pelagic dispersing and cosmopolitan mussel *Mytilus trossulus* at other sites, and population increases by benthic eelgrass-dwelling caprellid amphipods. These increases were similar among quadrats, but each reflects a temporary increase that is expected to change over time with juvenile mortality and population dynamics. Grazer taxa such as amphipods and isopods with continuous population dynamics and overlapping generations increased between May and July at all sites except NB. This latter pattern suggests some site-level factors such as food availability, seasonal warming,

or reduction in predation between May and July that was then reversed in DC, CB and NB by August. Despite this variation in univariate metrics and the identities of dominant species, multivariate metrics suggested composition overall was relatively stable through time, suggesting that the differences in abundance and richness are reflecting changes in dominance, consistent with observations in other systems (Douglass et al. 2010, Thom et al. 1995, Best and Stachowicz 2014). Still, the potential role of species interactions such as competition or predation in the temporal dynamics of these communities is not well understood.

CONCLUSIONS

Seagrass communities are known for their high epifaunal diversity and productivity, and fine-scale variation in species composition appears to be a critical component of this diversity. Understanding spatial and temporal variation is essential to linking the abiotic and biotic features of a marine seascape to the ecosystem functions that promote biodiversity as well as secondary productivity that emerges at higher trophic levels including fish, wading birds, and marine mammals. As anthropogenic pressure on valuable coastal ecosystems continues to accelerate at local and regional scales, it is more important than ever that we develop a baseline understanding of how biodiversity in seagrass meadows is maintained across ecologically relevant scales.

In this comprehensive assessment of eelgrass-associated biodiversity, we have shown that species diversity and abundance vary among seagrass meadows within a region, and that the variation is not clearly predictable from an estuarine gradient and related biotic and abiotic predictors. Although *Z. marina* provides relatively homogenous habitat, each *Z. marina* meadow appears to host a subset of epifaunal species observed in the larger region. These patterns are

indicative of a metacommunity system, and suggest that processes that maintain diversity in eelgrass communities may reflect a seascape of many meadows connected through dispersal. If true, the conservation of eelgrass systems will require a network approach that preserves numerous meadows within the region. Examining biodiversity patterns across a seascape has expanded our view of seagrass biodiversity, and additional research is required to address the challenges of understanding how spatial turnover in diversity is related to the function and resilience of these ecosystems.

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Table 1: Landscape attributes, diversity and aggregation estimates for epifaunal taxa in nine eelgrass meadows in Barkley Sound. Fetch was estimated by calculating the distance to nearest land from the eelgrass meadow in 10 degree increments around a centroid point and summing the distances. Diversity at the site level is reported as the number of epifaunal species (30 possible taxa, Table 2) observed in each meadow (γ_{site}) and diversity (R_{site}) estimated from extrapolated rarified estimates to 2x minimum following Chao et al (2014). Estimates of spatial aggregation (I_m) for epifaunal species (mean \pm se) with significant aggregation across species are indicated in bold (95% CIs do not include 0.5). The proportion of species in meadows with significant I based on X^2 tests is given.

Site name	Abbr.	Fetch (km)	Diversity (γ_{site})	Aggregation (I_m)	Diversity R_{site}	Proportion of species with significant I
Dodger Channel	DC	32.05	17	0.47 (0.34 – 0.59)	18.2 (10.0, 26.4)	91
Wizard Islet	WI	50.53	18	0.41 (0.25 – 0.57)	19.8 (11.5, 27.8)	83
Bald Eagle Cove	BE	58.97	17	0.5 (0.34 – 0.65)	22.2 (4.78, 39.7)	90
Ellis Island	EI	97.17	13	0.44 (0.28 – 0.60)	12.3 (7.6, 16.9)	82
Robber's Passage	RP	50.55	22	0.57 (0.51 – 0.64)	29.4 (19.6, 39.2)	93
Numukamis Bay	NB	68.72	16	0.46 (0.28 – 0.64)	19 (10.7, 27.3)	88
Crickitt Bay	CB	24.85	14	0.53 (0.37 – 0.69)	14 (9.0, 20.0)	89
Boyson Islands	BI	51.59	17	0.38 (0.21 – 0.55)	17 (12.4, 21.6)	77
Crow Cove	CC	29.41	10	0.23 (0.03 – 0.40)	9 (8.0, 10.9)	67

Table 2: Relative abundance of epifaunal taxa in meadows sampled at multiple times (May [M], June/July [J], and August [A], first panel), and once (June/July [J], second panel). Numbers indicate the rank of abundances relative to other species observed in that meadow at that time. T is overall rank for each species considering all meadows. Species with significant spatial intraspecific aggregation within the meadow, estimated as Morisita’s Index, are indicated in bold. Significance determined by chi-squared tests and $P < 0.05$. Grazers indicated with *.

Species	T	DC			WI			RP			NB			CB		
		M	J	A	M	J	A	M	J	A	M	J	A	M	J	A
Crustacean																
<i>Caprella</i> spp.*	1	1	1	2	9	5	2	1	1	2	11	11	6	3	6	4
<i>Aoroides columbiae</i> *	7	2	2	3	5	11	7	3	8	5	--	7	8	--	7	13
<i>Pentidotea resecata</i>	8	4	4	5	7	3	5	6	9	8	1	3	4	2	5	8
<i>Leptochelia dubia</i>	9	--	16	10	10	--	--	5	5	7	7	5	12	5	4	2
<i>Photis brevipes</i> *	12	5	3	8	4	7	6	9	6	9	5	8	3	8	8	5
<i>Monocorophium achersicum</i> *	13	6	6	6	14	9	14	--	18	--	9	--	9	12	9	6
Unknown amphipod	15	--	8	--	18	15	--	10	--	--	--	--	--	7	--	--
<i>Pontogeneia rostrata</i> *	16	9	5	--	2	--	8	--	15	--	8	15	15	10	13	--
<i>Harpacticoid copepod</i> *	17	12	13	16	11	12	18	--	11	12	3	--	5	13	--	10
<i>Eogammarus confervicolus</i>	18	7	12	--	12	--	16	--	--	--	13	12	--	--	--	--
<i>Ampithoe</i> spp.*	19	11	--	15	13	14	13	--	16	--	14	9	10	--	--	--
<i>Balanus</i> spp.	21	--	--	18	--	--	15	--	20	16	16	14	14	--	--	17
<i>Cirolana harfordi</i>	23	--	15	--	8	13	17	--	21	--	--	--	--	--	--	--
<i>Pugettia richii</i>	24	13	11	11	--	--	21	--	--	15	--	--	--	--	--	--
<i>Pandalidae</i>	26	--	--	14	--	--	20	--	17	10	--	--	--	--	--	--
<i>Pagurus quaylei</i>	29	14	--	--	16	--	22	--	--	--	--	--	--	--	--	--
<i>Nebalia</i> sp.	30	--	--	--	--	--	--	--	--	--	15	--	--	--	--	15
Gastropod																
<i>Phyllaplysia taylori</i> *	2	3	10	1	15	--	9	4	2	1	--	13	--	--	--	--
<i>Mytilus trossulus</i>	3	--	14	7	--	1	1	--	3	4	4	2	1	14	1	1

<i>Lacuna</i> spp.*	14	10	9	--	6	2	11	8	12	11	10	10	13	15	10	12
<i>Margarites helycinus</i> *	20	--	--	12	--	--	10	--	--	--	--	--	--	--	--	--
<i>Lottia pelta</i> *	22	--	--	9	17	--	19	--	--	--	--	--	--	11	--	--
<i>Haminoea</i> spp.*	27	--	--	--	--	--	--	--	19	13	--	--	--	--	--	16
<i>Alia carinata</i> *	28	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
<hr/>																
Annelid																
<i>Platynereis bicanaliculata</i>	4	8	7	4	1	4	4	2	4	3	6	6	7	4	12	7
<i>Janua pagastecheri</i>	10	--	--	--	--	8	3	7	7	6	--	--	--	9	--	--
<hr/>																
Other																
<i>Nematode</i>	5	--	--	13	3	15	--	--	10	--	12	1	2	--	2	3
<i>Pycnogonum</i> sp.	6	--	--	17	--	6	--	--	14	14	--	--	--	1	11	9
<i>Halacard mite</i>	11	--	--	--	--	10	--	--	13	--	2	4	--	6	3	11
<i>Nemertea</i>	25	--	--	--	--	--	--	--	--	17	17	--	11	--	--	14

Species	BE J	EI J	BI J	CC J
Crustacean				
<i>Caprella</i> spp.*	1	4	14	4
<i>Aoroides columbiae</i> *	10	6	8	--
<i>Pentidotea resecata</i>	3	11	6	5
<i>Leptochelia dubia</i>	16	--	4	7
<i>Photis brevipes</i> *	5	7	--	--
<i>Monocorophium achersicum</i> *	--	--	12	9
Unknown amphipod	2	--	5	3
<i>Pontogeneia rostrata</i> *	14	12	10	--
<i>Harpacticoid copepod</i> *	--	--	--	--
<i>Eogammarus confervicolus</i>	8	9	--	--
<i>Ampithoe</i> spp.*	--	--	15	--
<i>Balanus</i> spp.	--	10	--	--

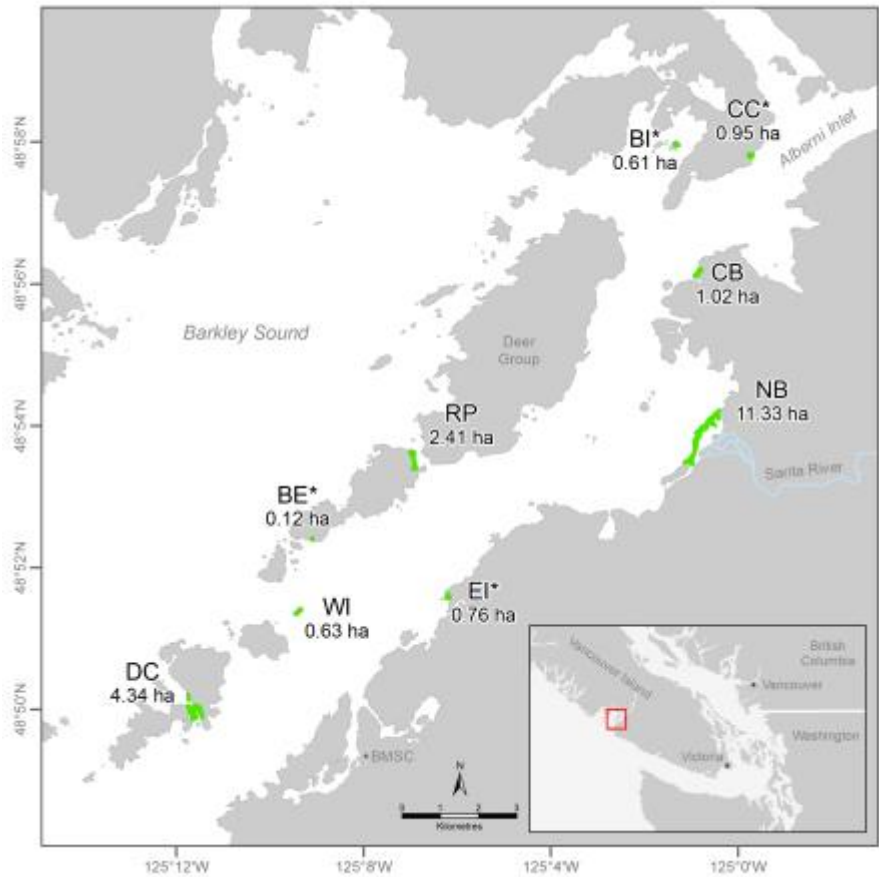
<i>Cirolana harfordi</i>	15	--	--	--
<i>Pugettia richii</i>	--	--	--	--
<i>Pandalidae</i>	17	--	--	--
<i>Pagurus quaylei</i>	--	--	16	--
<i>Nebalia</i> sp.	--	--	--	--
<i>Gastropod</i>				
<i>Phyllaplysia taylori</i> *	9	3	--	--
<i>Mytilus trossulus</i>	7	1	2	1
<i>Lacuna</i> spp.*	4	--	7	--
<i>Margarites helycinus</i> *	--	--	--	--
<i>Lottia pelta</i> *	--	--	13	--
<i>Haminoea</i> spp.*	--	--	--	--
<i>Alia carinata</i> *	--	--	9	--
<i>Annelid</i>				
<i>Platynereis bicanaliculata</i>	6	5	11	--
<i>Janua pagastecheri</i>	12	--	--	--
<i>Other</i>				
<i>Nematode</i>	--	--	1	6
<i>Pycnogonum</i> sp.	13	2		8
<i>Halacard mite</i>	11	8	3	2
<i>Nemertea</i>	--	--	--	--

Table 3: Comparisons of univariate diversity metrics over time using two-way ANOVA with site and sampling time as main effects. *P < 0.01, **P < 0.001

Model	Main Effect	df	Sum Sq	Mean Sq	F
Alpha	Site	4	58.57	14.64	**2.99x10-4
	Time	2	53.5	26.75	**6.47x10-5
	Site*time	8	122.92	15.37	**1.15x10-5
	Residuals	191	503.41	2.64	--
H'	Site	4	4.41	1.1	**3.48x10-5
	Time	2	0.16	0.08	0.6
	Site*time	8	5.43	0.68	**1.06x10-4
	Residuals	191	30.65	0.16	--
S	Site	4	1.91	0.3	**4.42x10-5
	Time	2	0.09	0.05	0.36
	Site*time	8	1.23	0.15	**9.55x10-4
	Residuals	191	8.51	0.04	--
ENS	Site	4	3.23	0.81	**1.70x10-5
	Time	2	1.91	0.96	*1.18 x10-3
	Site*time	8	3.65	0.46	*1.38x10-3
	Residuals	191	26.18	0.14	--

Figure 1: A) Seagrass is found at the coastal margins of Trevor Channel (approximately 200m deep), one of three channels in Barkley Sound that connect freshwater sources in Alberni Inlet and Numukamis Bay with the open Pacific Ocean. Eelgrass meadows sampled during summer 2012 between Alberni Inlet and the Pacific Ocean southwest of Dodger Channel (DC). Five meadows were sampled in May, July and August, while four additional meadows were sampled once in midsummer (asterisk). Site names as in Table 1. BMSC = Bamfield Marine Sciences Centre. **B)** In each meadow, 16 plots were sampled in a grid, at least two meters from the meadow edge, and >1 m depth. Samples were cut at the substrate (dashed line, inset).

A)



B)

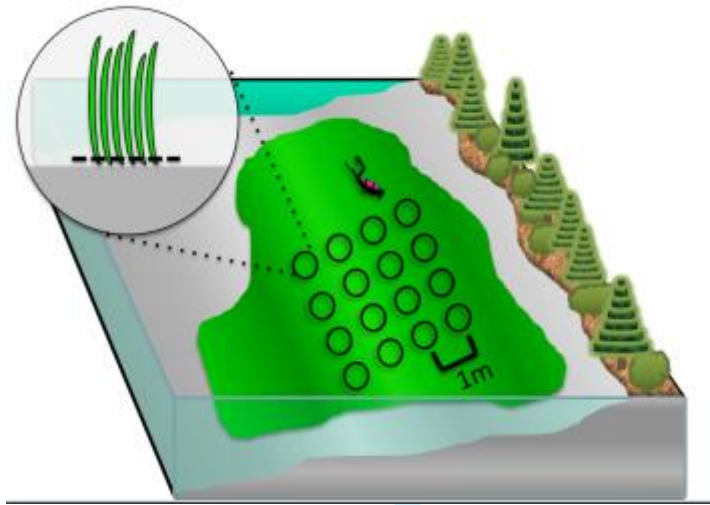


Figure 2: Fine-scale epifaunal diversity estimated from sampled plots (0.28 m², n = 16) in nine eelgrass meadows in Trevor Channel, British Columbia, in midsummer 2012. Asterisks indicate significant differences ($P < 0.01$) among sites, based on a one-way ANOVA. Sites are arranged left to right in terms distance from a freshwater source, with DC being the most marine and farthest from a freshwater source (Figure 1).

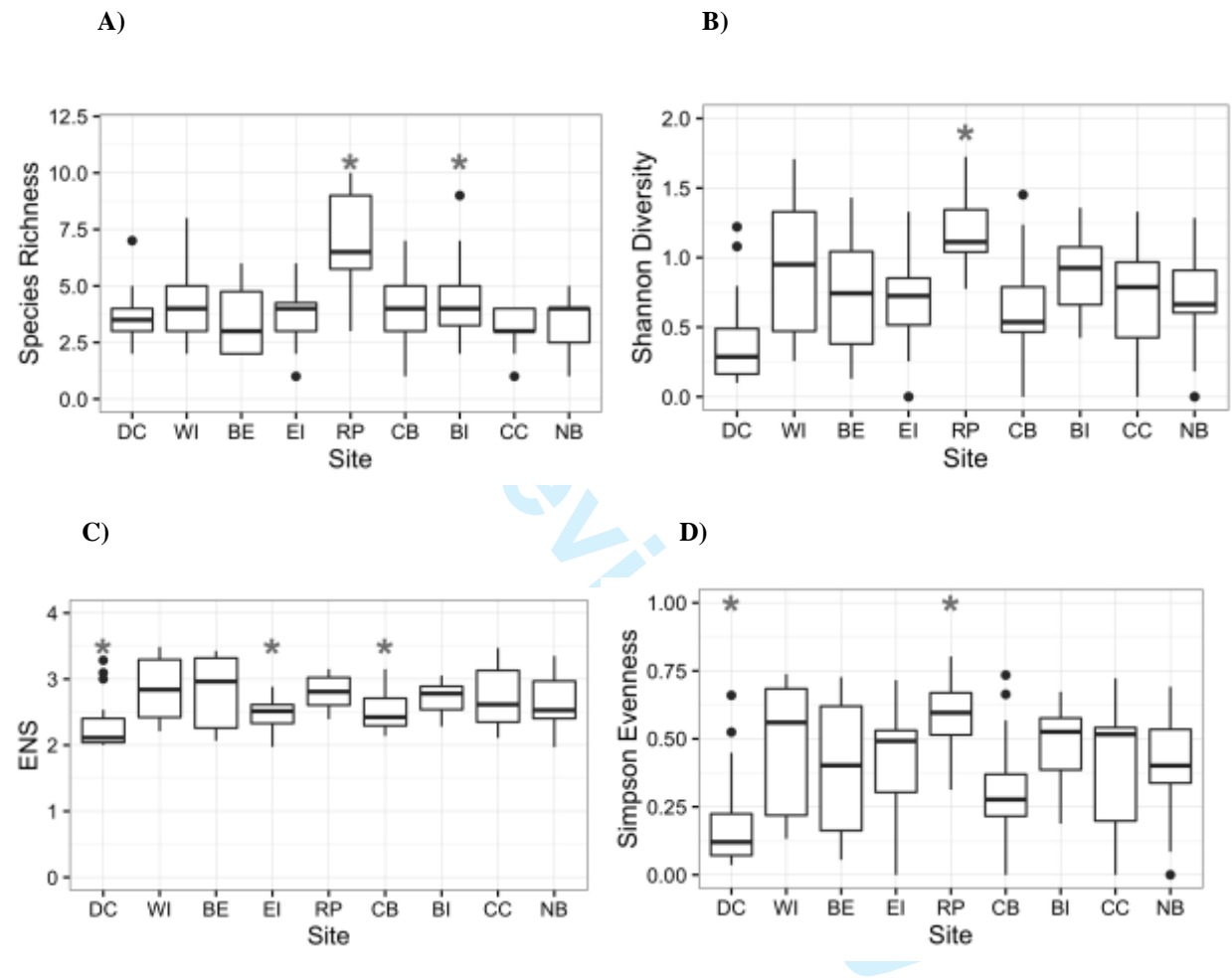
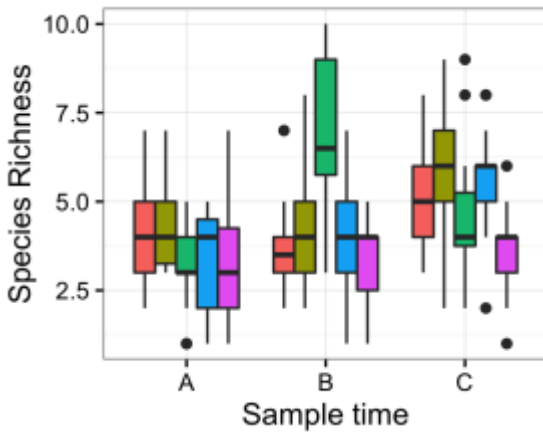
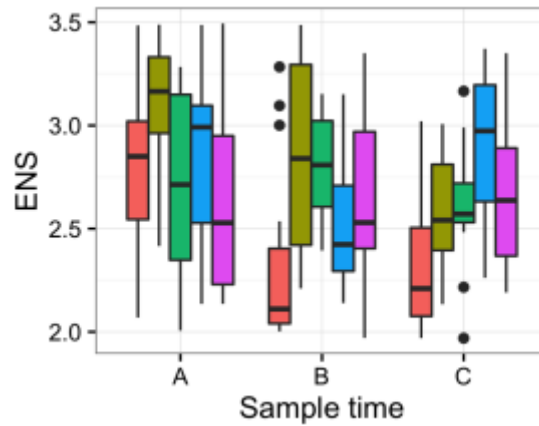


Figure 3: Temporal trends in rarified richness (A), effective number of species (B), shannon diversity (C), simpson evenness (D), and beta diversity as gamma/alpha (E) and mean Bray-Curtis distance (F) within all sites and time periods in May (“A”), June/July (“B”), and August (“C”). Site abbreviations as in Table 1.

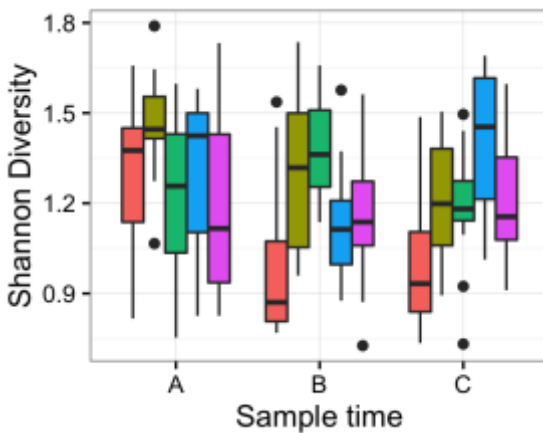
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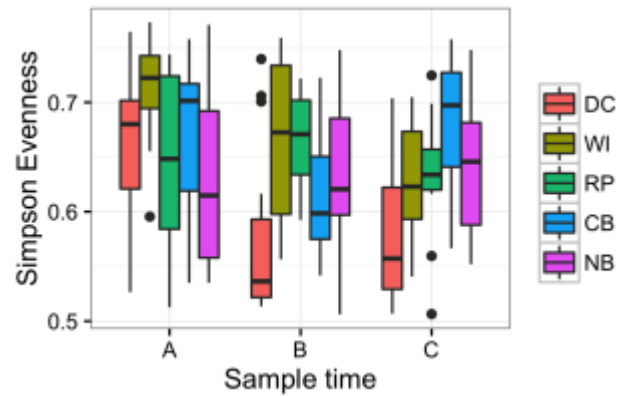
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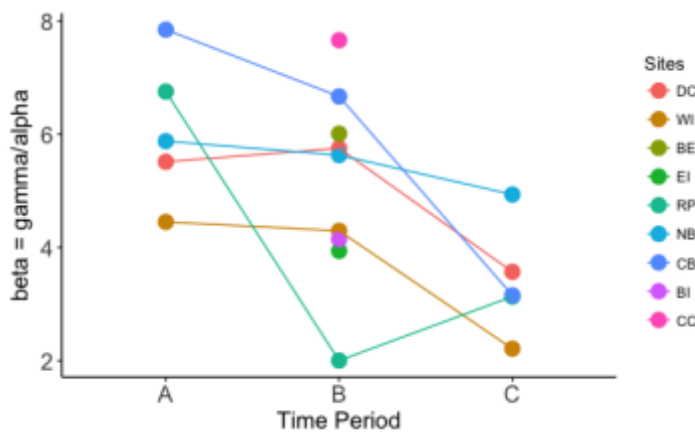
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D)



E)



F)

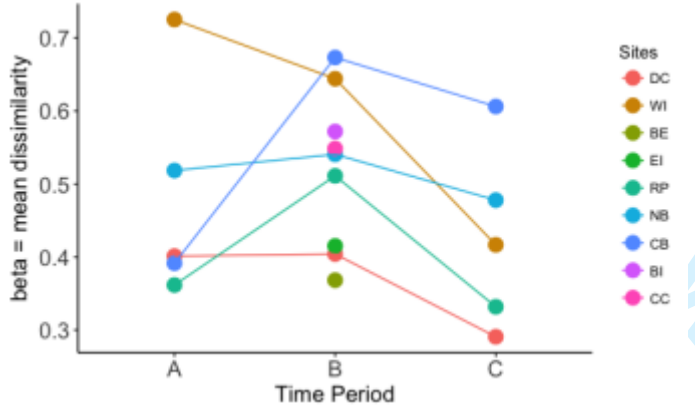
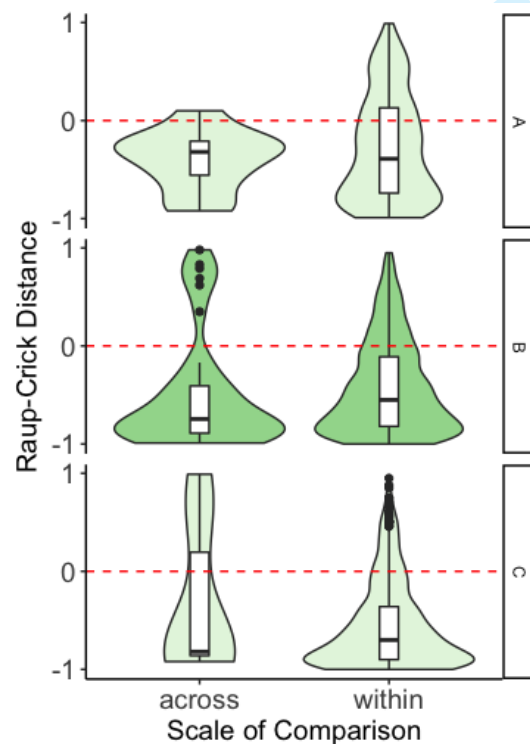
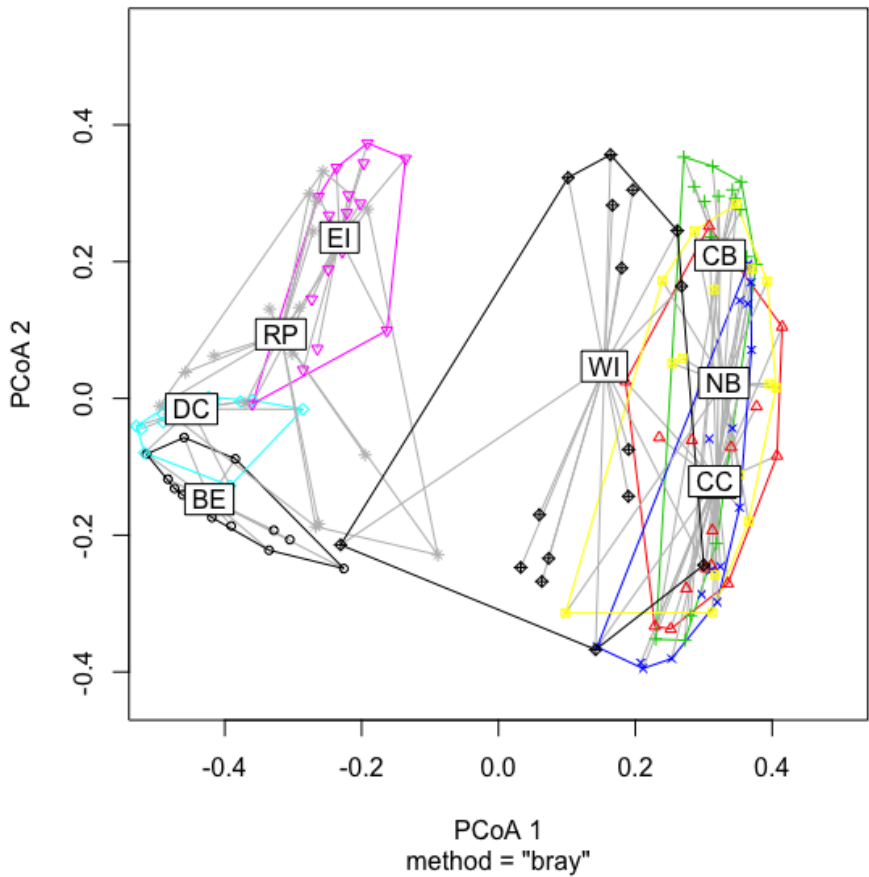


Figure 4: A) Beta diversity (species composition) within and among meadows varied less than expected. Expected beta diversity (rescaled Raup-Crick Probabilities, B_{RC}) = 0, values approaching 1 show greater dissimilarity than null predictions, values approaching -1 show less dissimilarity than null predictions, with values at 0 being no different from the null predictions. Comparisons show among- and within-site probabilities for 5 (light green) and 9 (dark green) meadows. Comparisons across meadows pool all meadows within each sampling time, comparisons within meadows are pooled within each individual meadow. Box plots embedded with violin plots show median and quartiles, and width of violin plots show kernel probability density of those variables, with wider portions being more likely than narrower portions. **B)** nMDS of community composition and abundance in mid-summer across all sites using Bray-Curtis metric. 2-D stress = 0.23.

A)



B)



Appendix

Table S1: Mean shoot density and leaf area (cm²) with standard error (SE), and mean epiphyte load standardized as grams of epiphyte per gram of seagrass (dried weight) for patches of eelgrass meadow (0.28m²) sampled in May, July, and August 2012.

Month	Site	Mean Shoot Density	SE Shoot Density	Mean Leaf Area	SE Leaf Area	Mean Epiphyte Load
May	DC	12.3	±1.4	8037	±2229	0.02
	WI	8	±2.3	3928	±1866	0.11
	RP	7.7	±1.5	2245	±5	0.16
	NB	6.5	±0.3	1593	±476	0.09
	CB	4	±1.0	1903	±704	0.05
July	DC	14.8	±2.0	9257	±1493	0.07
	WI	12.5	±1.8	5608	±1223	0.15
	BE	7	±1.5	2542	±787	0.04
	EI	12.5	±1.2	6246	±1078	0.03
	RP	10.3	±1.8	4372	±1576	0.04
	NB	8.3	±3.1	5062	±2285	0.09
	CB	6.5	±0.9	2885	±381	0.04
	BI	5.5	±1.4	2811	±1315	0.05
	CC	6	±2.2	3576	±1736	0.02
August	DC	12.7	±1.9	7902	±1213	0.01
	WI	7.8	±1.8	4611	±392	0.08
	RP	8	±1.8	4514	±781	0.03
	NB	9.5	±0.6	4302	±1216	0.06
	CB	7.3	±1.1	3562	±537	0.02

Table S2: Model results for tests of relationships between abiotic and biotic meadow attributes. In all models, intercepts were allowed to vary randomly among meadows: dfw – distance from fresh water input.

Model	df	logLik	AICc	Delta	Wt
Salinity					
Y ~ dfw	4	-418.12	844.5	0	0.629
Y ~ temp+dfw	5	-417.64	845.7	1.18	0.343
Y ~ temp*dfw	6	-419.04	850.7	6.17	0.028
Y ~ temp	4	-422.87	854.0	9.50	0.005
Y ~ 1	3	-424.32	854.8	10.27	0.004
Y ~ temp+dfw+fetch	6	-428.54	869.7	25.16	0.000
Y ~ fetch	4	-434.09	876.5	31.94	0.000
Temperature					
Y ~ dfw	4	-328.31	664.9	0	0.434
Y ~ 1	3	-329.69	665.5	0.64	0.315
Y ~ Sal	4	-329.23	666.7	1.84	0.173
Y ~ Sal + dfw	5	-328.97	668.4	3.47	0.076
Y ~ Sal*dfw	6	-332.06	676.7	11.83	0.001
Y ~ fetch	4	-340.49	689.3	24.35	0.000
Y ~ Sal+dfw+fetch	6	-340.05	692.7	27.80	0.000
Shoot Density					
Y ~ dfw	4	-92.90	195.2	0	1.000
Y ~ 1	3	-105.79	218.3	23.15	0.000
Leaf Area					
Y ~ dfw	4	-306.82	623.0	0	0.998
Y ~ 1	3	-314.42	635.6	12.62	0.002
Epiphytes					
Y ~ 1	3	6.87	-2.9	0	0.999
Y ~ dfw	4	3.01	12.0	14.92	0.001

Table S3: Mean summer temperature and salinity values (May – August 2012) with standard error (SE).

Site	Mean Temperature	SE Temperature	Mean Salinity	SE Salinity
DC	12.6	±0.2	25.7	±0.6
WI	13.7	±0.2	21.7	±0.5
RP	14.1	±0.3	22.4	±0.4
NB	14.9	±0.4	16.6	±0.5
CB	14.8	±0.5	17.3	±0.5

Table S4: Mean epiphyte loads \pm standard error at the three sites in June (period B) and August (period C) 2012.

Epiphyte load is standardized to seagrass dry weight in grams. Bladed epiphytes are *Punctaria* sp.

Site	Bladed epiphyte load		Periphyton load	
	<u>Jun</u>	<u>Aug</u>	<u>Jun</u>	<u>Aug</u>
DC	0.45 \pm 0.05 (14)	0.15 (1)	0.56 \pm 0.06 (15)	0.56 \pm 0.05 (15)
WI	0.04 \pm 0.03 (7)	0.43 \pm 0.12 (13)	0.61 \pm 0.07 (15)	0.57 \pm 0.04 (15)
NB	--	0.12 (1)	0.87 \pm 0.08 (15)	1.05 \pm 0.12 (15)

Table S5: Model selection results for a set of candidate models predicting plot-level ($n = 9$) univariate richness indices across nine eelgrass meadows in July 2011. The top-ranked model is listed first in each group; models with $\Delta > 2$ are considered to have little support by the data.

Model		df	logLik	AICc	Delta	Wt
Alpha						
G	Y ~ site	10	-234.49	490.8	0	1
D	Y ~ 1	2	-262.61	529.3	38.46	0
.	Y ~ area	3	-261.96	530.1	39.26	0
B	Y ~ dfw	3	-262.25	530.7	39.83	0
A	Y ~ fetch	3	-262.6	531.4	40.54	0
C	Y ~ dfw*fetch	5	-262.23	534.9	44.1	0
F	Y ~ area*fetch	5	-262.35	535.2	44.33	0
H'						
G	Y ~ site	10	-51.28	124.4	0	0.999
C	Y ~ dfw*fetch	5	-64.17	138.8	14.39	0.001
B	Y ~ dfw	3	-67.36	140.9	16.48	0
F	Y ~ area*fetch	5	-65.66	141.8	17.37	0
A	Y ~ fetch	3	-68.52	143.2	18.8	0
D	Y ~ 1	2	-69.96	144	19.58	0
.	Y ~ area	3	-69.69	145.6	21.15	0
S						
G	Y ~ site	10	27.76	-33.7	0	0.945
C	Y ~ dfw*fetch	5	18.67	-26.9	6.81	0.031
F	Y ~ area*fetch	5	17.93	-25.4	8.29	0.015
B	Y ~ dfw	3	14.96	-23.7	9.94	0.007
A	Y ~ fetch	3	13.35	-20.5	13.16	0.001
D	Y ~ 1	2	11.63	-19.2	14.5	0.001
.	Y ~ area	3	12.21	-18.2	15.45	0
ENS						
G	Y ~ site	10	-52.19	126.2	0	0.628
C	Y ~ dfw*fetch	5	-59.21	128.9	2.66	0.166
F	Y ~ area*fetch	5	-59.78	130	3.8	0.094
.	Y ~ area	3	-62.56	131.3	5.07	0.05
B	Y ~ dfw	3	-63.13	132.4	6.2	0.022

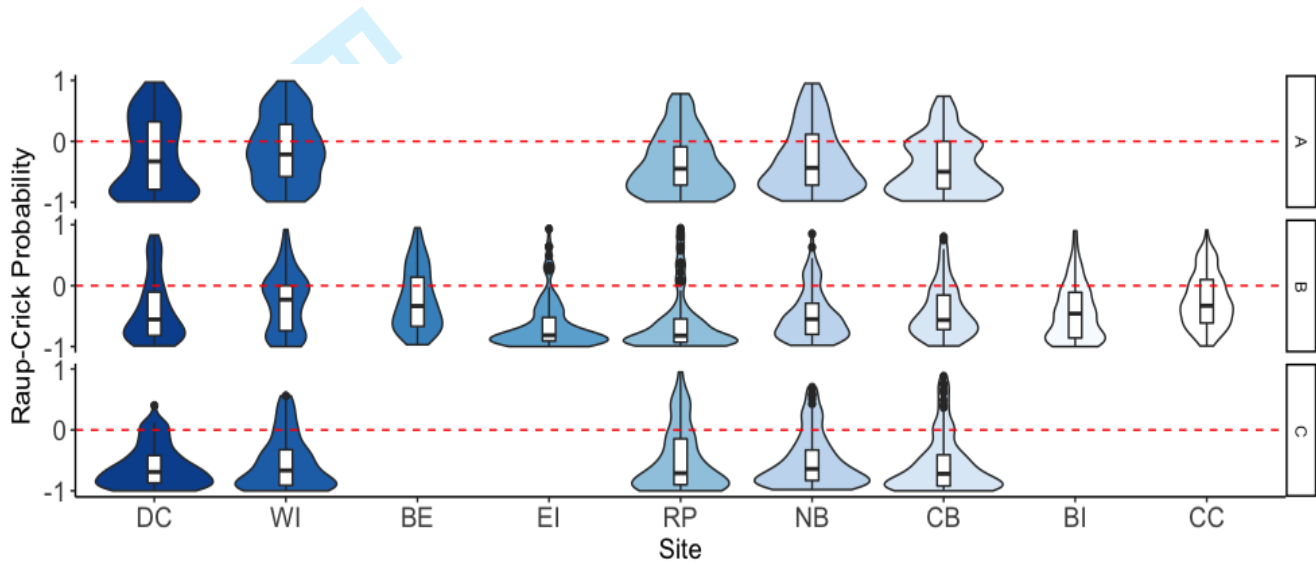
A	Y ~ fetch	3	-63.13	133.1	6.8	0.016
D	Y ~ 1	2	-64.88	133.9	7.62	0.011

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Table S6: Values of beta diversity within each site per time period expressed as gamma/mean alpha, and mean Bray-Curtis dissimilarity

Site	Beta (gamma/alpha)			Beta (Bray-Curtis)		
	<u>A</u>	<u>B</u>	<u>C</u>	<u>A</u>	<u>B</u>	<u>C</u>
DC	5.5133	5.7523	3.5714	0.4012	0.4041	0.2908
WI	4.4519	4.295	2.214	0.7253	0.6442	0.4167
BE	NA	6.0095	NA	NA	0.3683	NA
EI	NA	3.9396	NA	NA	0.4152	NA
RP	6.7528	2.0041	3.1348	0.3616	0.5112	0.3318
NB	5.8785	5.6306	4.9355	0.5185	0.5407	0.4779
CB	7.8462	6.6667	3.1566	0.3915	0.6733	0.6062
BI	NA	4.1469	NA	NA	0.5719	NA
CC	NA	7.6588	NA	NA	0.5486	NA

FIGURE S7: Beta diversity (species composition) within and among meadows varied less than expected. Expected beta diversity (rescaled Raup-Crick Probabilities, B_{RC}) = 0, values approaching 1 show greater dissimilarity than null predictions, values approaching -1 show less dissimilarity than null predictions, with values at 0 being no different from the null predictions. Comparisons show among-site probabilities for 9 meadows over the course of summer 2012 (May = A, June/July = B, August = C). Box plots embedded with violin plots show median and quartiles, and width of violin plots show kernel probability density of those variables, with wider portions being more likely than narrower portions.



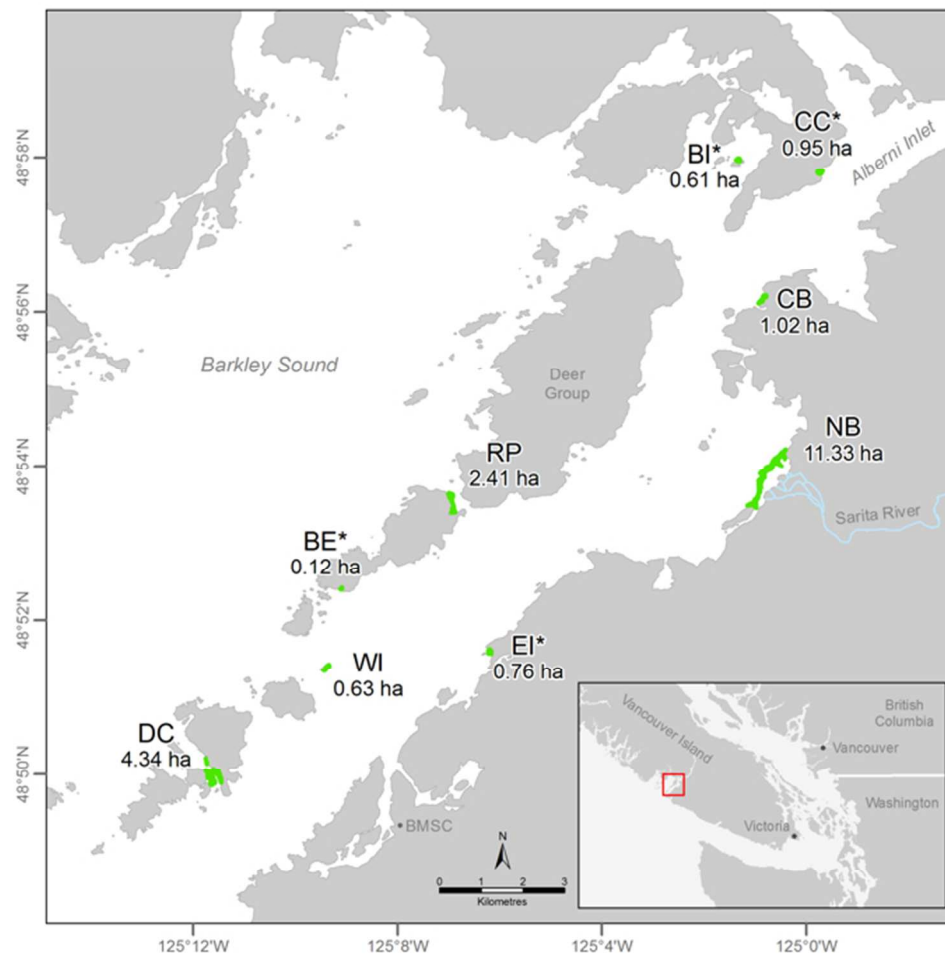


Figure 1: A) Seagrass is found at the coastal margins of Trevor Channel (approximately 200m deep), one of three channels in Barkley Sound that connect freshwater sources in Alberni Inlet and Numukamis Bay with the open Pacific Ocean. Eelgrass meadows sampled during summer 2012 between Alberni Inlet and the Pacific Ocean southwest of Dodger Channel (DC). Five meadows were sampled in May, July and August, while four additional meadows were sampled once in midsummer (asterisk). Site names as in Table 1. BMSC = Bamfield Marine Sciences Centre.

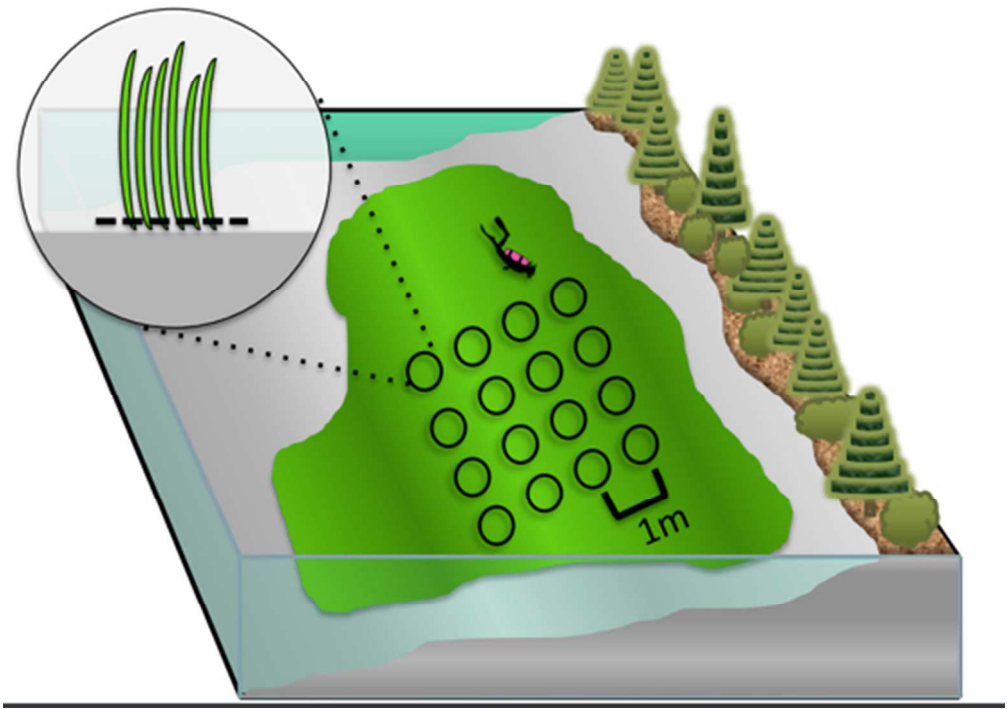


Figure 1: . B) In each meadow, 16 plots were sampled in a grid, at least two meters from the meadow edge, and >1 m depth. Samples were cut at the substrate (dashed line, inset).

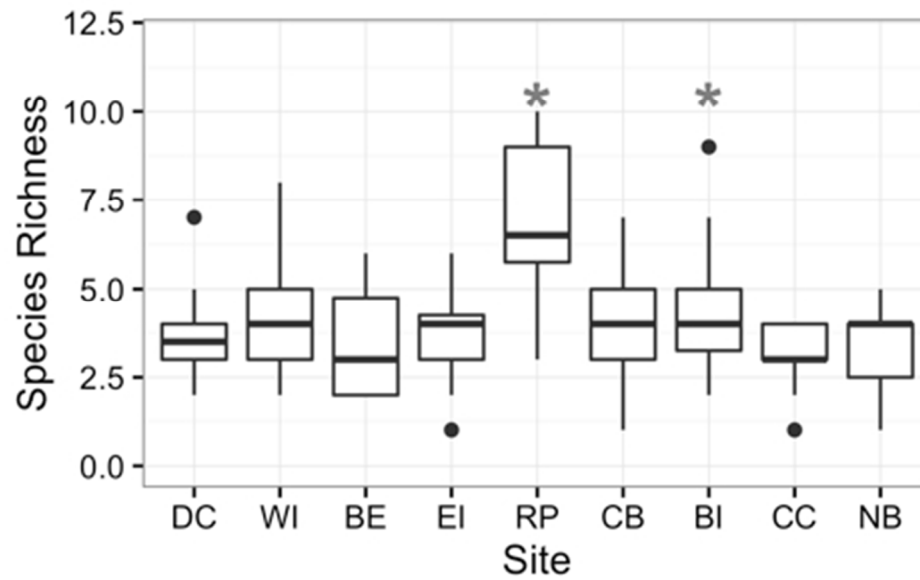


Figure 2: Fine-scale epifaunal diversity estimated from sampled plots (0.28 m², n = 16) in nine eelgrass meadows in Trevor Channel, British Columbia, in midsummer 2012. Asterisks indicate significant differences ($P < 0.01$) among sites, based on a one-way ANOVA. Sites are arranged left to right in terms distance from a freshwater source, with DC being the most marine and farthest from a freshwater source (Figure 1).

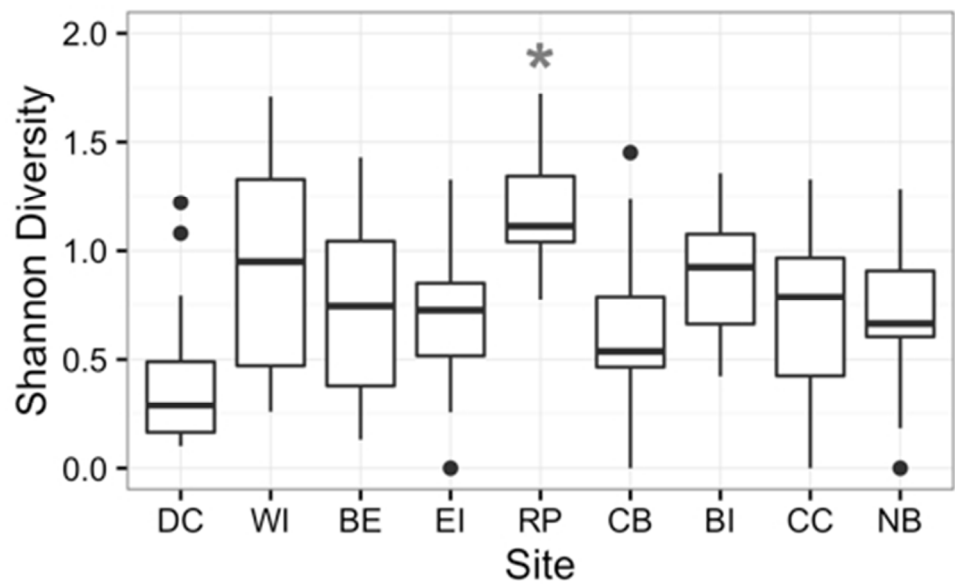


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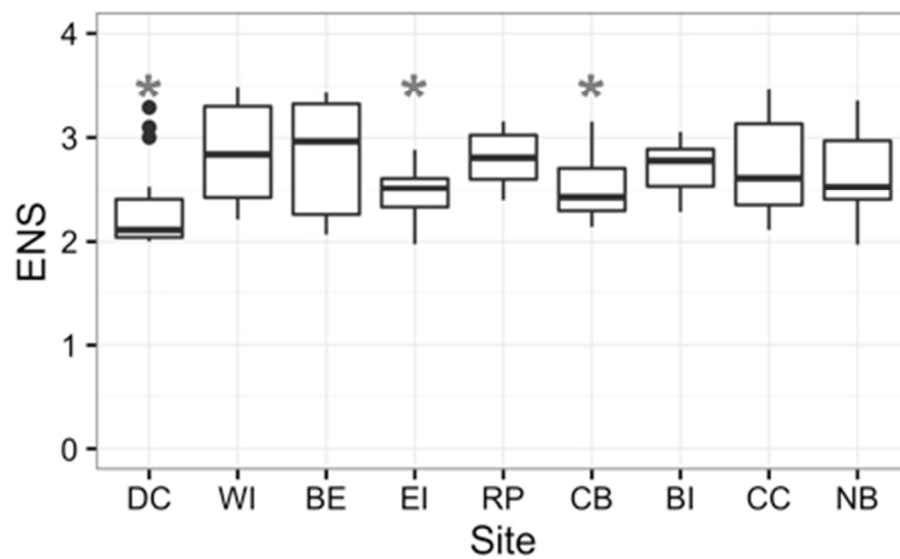


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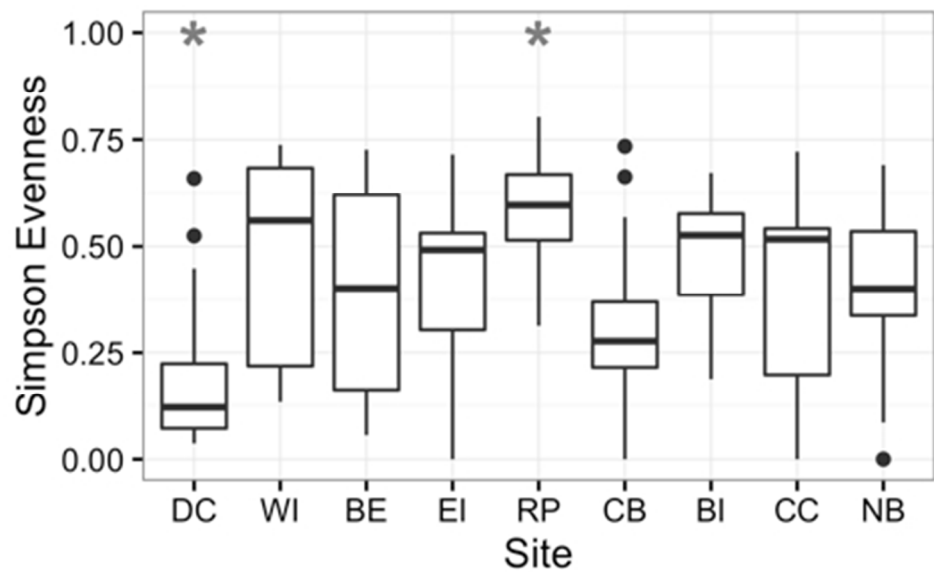


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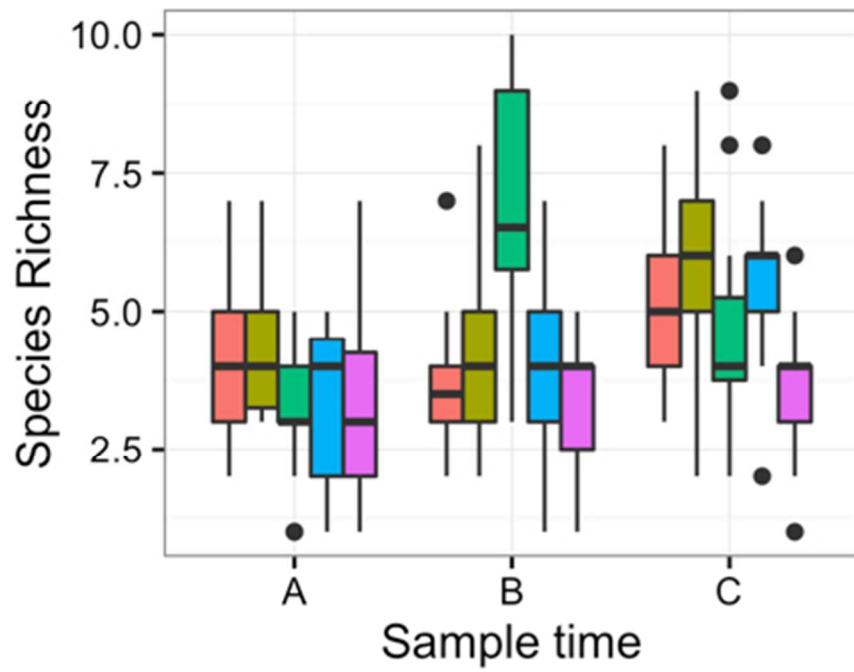


Figure 3: Temporal trends in rarified richness (A)

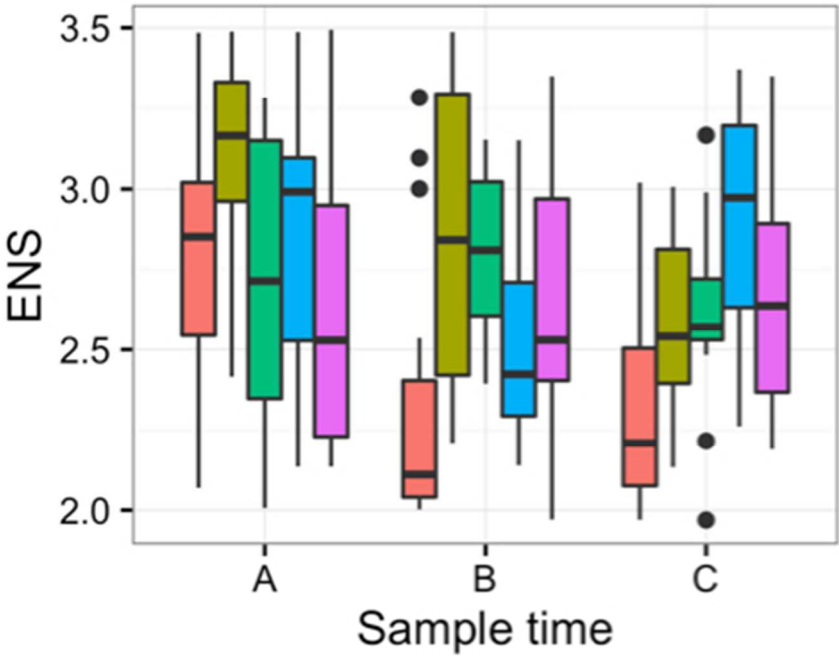
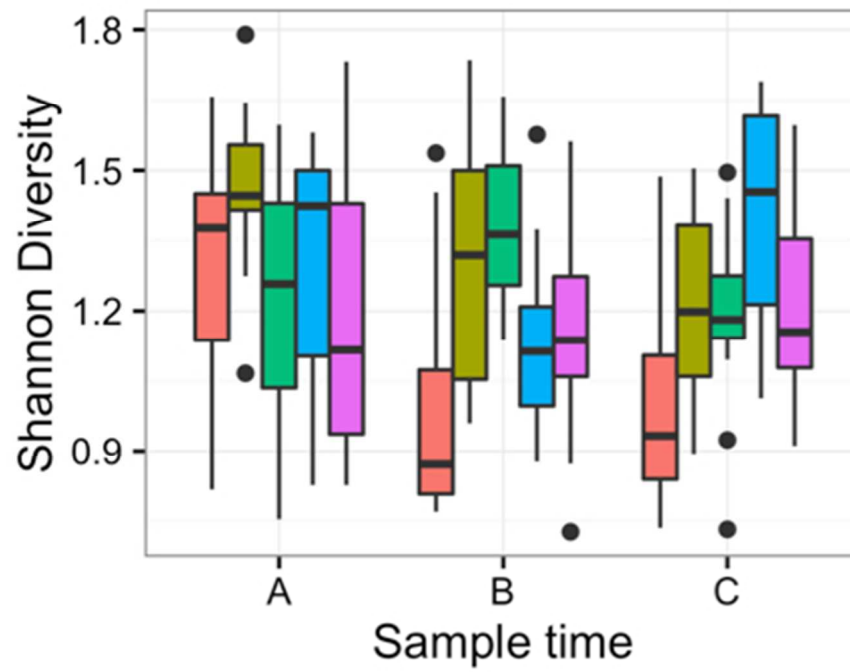
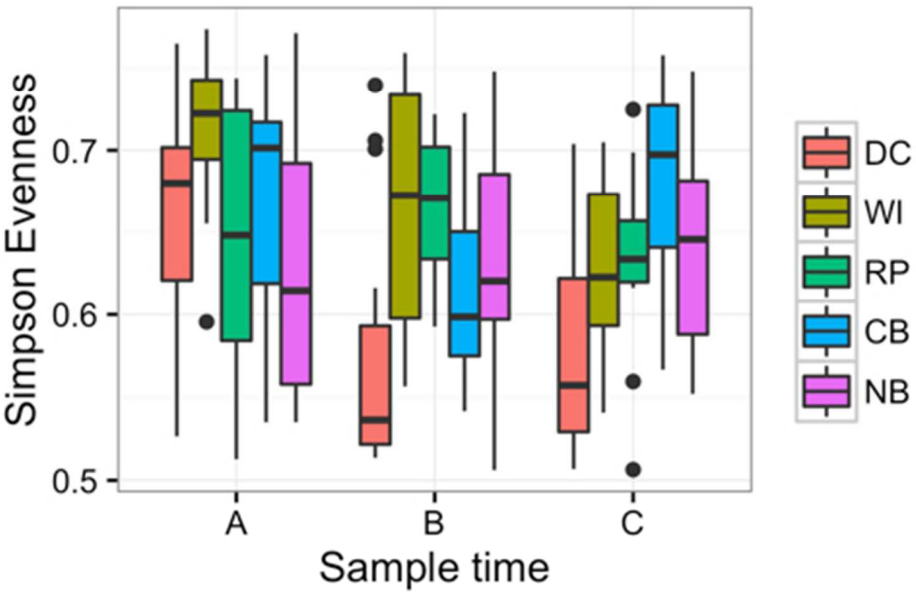


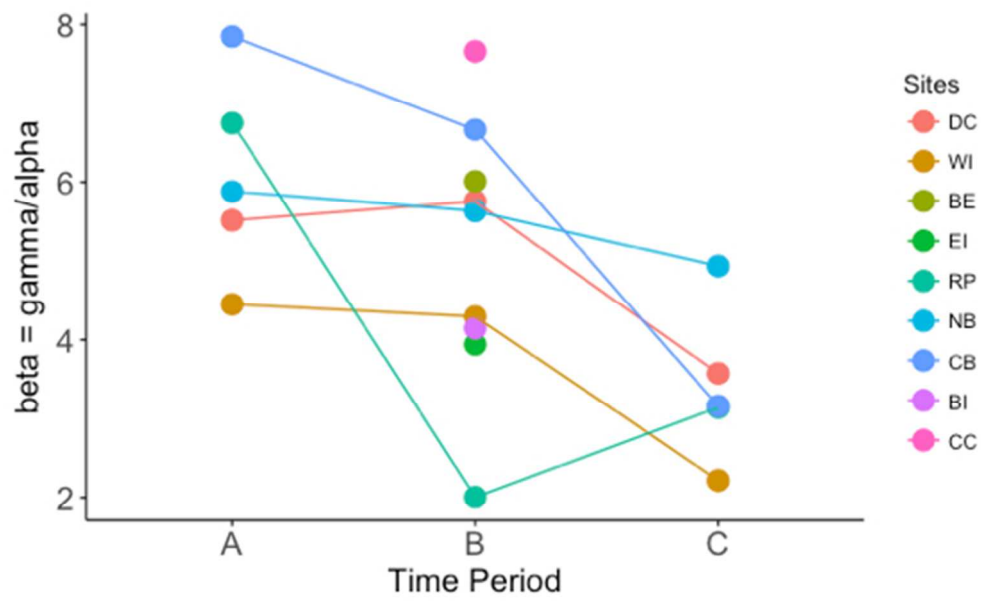
Figure 3: Temporal trends in effective number of species (B)



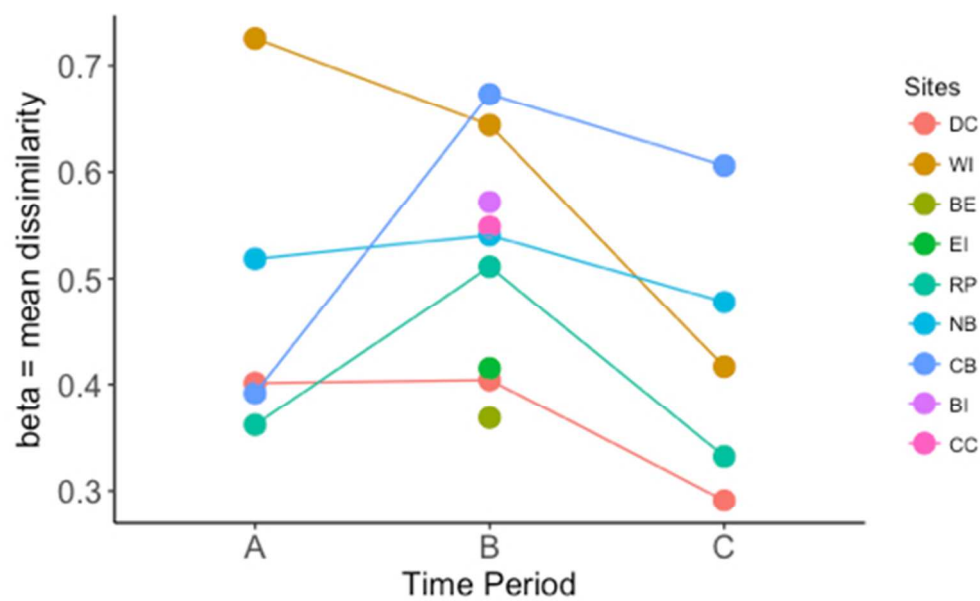
Temporal trends in Shannon diversity (C)



Temporal trends in Simpson evenness (D)



Temporal trends in beta diversity as gamma/alpha (E



Temporal trends in mean Bray-Curtis distance (F) within all sites and time periods in May ("A"), June/July ("B"), and August ("C"). Site abbreviations as in Table 1.

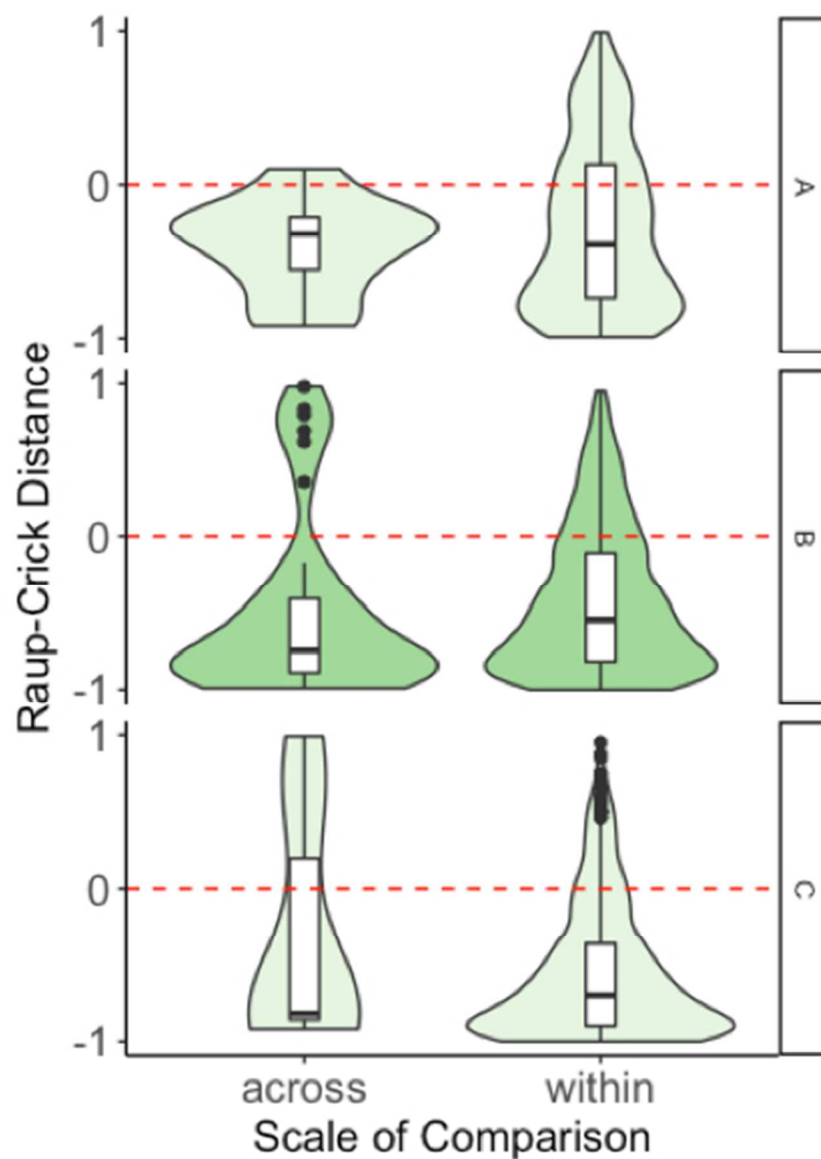


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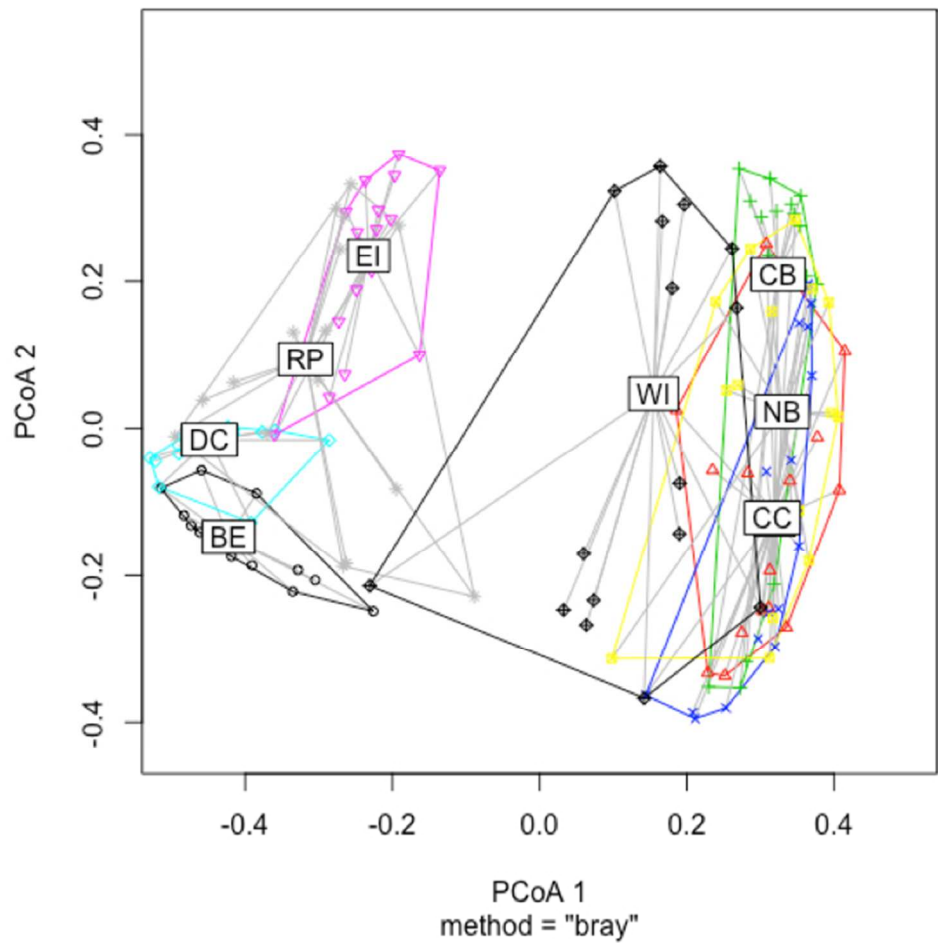


Figure 4: B) nMDS of community composition and abundance in mid-summer across all sites using Bray-Curtis metric. 2-D stress = 0.23.



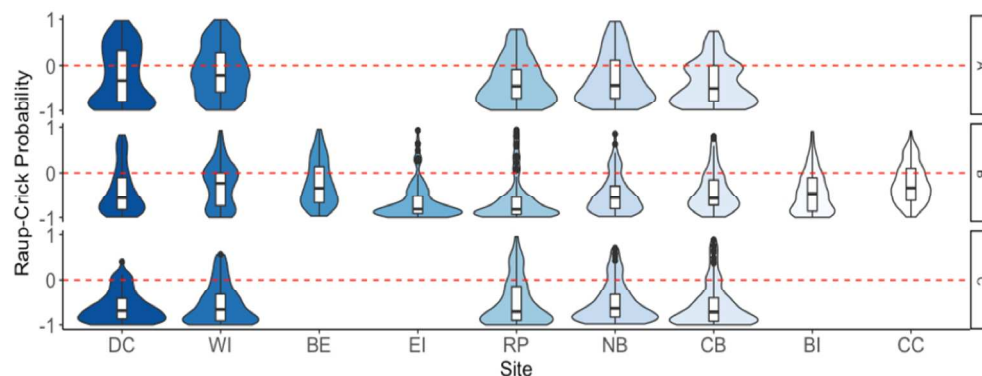


FIGURE S7: Beta diversity (species composition) within and among meadows varied less than expected. Expected beta diversity (rescaled Raup-Crick Probabilities, BRC) = 0, values approaching 1 show greater dissimilarity than null predictions, values approaching -1 show less dissimilarity than null predictions, with values at 0 being no different from the null predictions. Comparisons show among-site probabilities for 9 meadows over the course of summer 2012 (May = A, June/July = B, August = C). Box plots embedded with violin plots show median and quartiles, and width of violin plots show kernel probability density of those variables, with wider portions being more likely than narrower portions.