Beyond a single patch: local and regional processes explain diversity patterns in a seagrass epifaunal metacommunity

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Abstract

Ecological communities are jointly structured by dispersal, density-independent responses to environmental conditions, and density-dependent biotic interactions. Metacommunity ecology provides a framework for understanding how these processes combine to determine community composition among local sites that are regionally connected through dispersal. In 17 temperate seagrass meadows in British Columbia, Canada, we tested the hypothesis that eelgrass (*Zostera marina* L.) faunal assemblages are dispersal limited, such that meadows separated by greater spatial distances host distinct epifaunal invertebrate fauna. We used hierarchical joint species distribution modelling to understand the relative contribution of environmental conditions, spatial distance between meadows, and unexplained variation on species distributions. We found that modelled species compositional similarity did not decay as a function of spatial distance, and sites in the same region were no more similar to each other than sites farther away. These results suggest that dispersal limitation of these invertebrates does not strongly influence diversity over 1000 km of coastline. Abiotic environmental conditions such as temperature, nitrate levels, and salinity partially explained regional patterns of abundance, but their relative importance varied across taxa. We found co-occurrence patterns between taxa that could not be explained by shared responses to the environment, suggesting the possibility of interspecific interactions influencing community structure. Our results support findings from previous studies that seagrass faunal communities tend to be somewhat homogenized across regional spatial scales even up to 1000 km. Minor variations in community structure across sites could be attributed to the abiotic environment, or intraspecific interactions at the site or meadow-level spatial scale. Our results give refined hypotheses about the specific ecological mechanisms driving community structure at various spatial scales, which in turn can inform targeted

experiments, monitoring, and management decisions for maintaining diversity in this important ecosystem.

Key words: Hierarchical Modelling of Species Communities, priority effects, dispersal, niche filtering, British Columbia, *Zostera marina*

Introduction

Understanding how local environmental conditions, regional connectivity by dispersal, biotic interactions, and ecological drift jointly structure the composition of communities is a central challenge in ecology (Ricklefs and Schluter 2003, Vellend 2010, Leibold and Chase 2017). Metacommunity theory (Leibold et al. 2004, Holyoak 2005, Leibold and Chase 2018) offers a promising framework for understanding drivers of community assembly across spatial scales. Applications of the framework to date have often focused on categorizing metacommunities into one of four discrete archetypes (e.g. Cottenie 2005, Logue 2011) that each reflect key hypothesized differences in the mechanisms that structure dynamics (Leibold et al. 2003). However, recent papers have called for metacommunity theory to move beyond the four archtypes and instead focus on the underlying processes that govern the dynamics of communities (Brown et al. 2017, Leibold and Chase 2018, Thompson et al. 2019). Thompson et al. (2019) reframed the metacommunity concept based on three fundamental processes that together govern the dynamics of populations and communities. These are: 1) Densitiy-independent responses to environmental heterogeneity, 2) Density-dependent biotic interactions (ie. inter and intra-specific competition influencing population growth and co-existence), and 3) Dispersal influencing connectivity across a landscape or seascape. We apply this framework to understand the relative contribution of core assembly processes to a seagrass-associated

93 invertebrate metacommunity.

94 Many coastal environments that host high biodiversity occupy spatially structured habitats
95 (e.g. coral reefs, kelp forests, seagrass meadows), and many marine species have dispersing life
96 histories that connect populations in distinct habitat patches. The importance of interspecific
97 interactions (Berlow 1999, Stachowicz 2001, Sala and Graham 2002), and dispersal-driven
98 population dynamics (Levin and Paine 1974, Gaines and Roughgarden 1985) in coastal and
99 marine communities has long been recognized. These combined roles of dispersal, the local
100 environment, and biotic interactions suggest patterns of marine biodiversity likely reflect more
101 than simple abiotic variation, and instead likely reflect metacommunity processes (Boström et al.
102 2006). To date, marine metacommunity dynamics have been investigated in sandy-bottom
103 benthic invertebrates (Valanko et al. 2015, Rodil et al. 2018), coral reef fishes (MacNeil et al.
104 2009), kelp-associated invertebrates and fishes (Lamy et al. 2018), rocky intertidal communities
105 (Salois et al. 2018), and temperate seagrass epifauna (Yamada et al. 2014, Whippo et al. 2018).

106 Seagrasses, like corals, salt marsh plants, and mangroves, are foundation species that support
107 high productivity and faunal diversity (Orth et al. 1984, Duffy et al. 2015). Seagrasses are often
108 prioritized in coastal protection plans because of the ecosystem services they provide, and many
109 of these services stem from their capacity to support high biodiversity and secondary
110 productivity. Seagrasses form meadows separated from each other by deeper water, un-vegetated
111 seafloor, or other vegetated habitats, and associated fauna disperse among meadows (Boström et
112 al. 2006, 2011). Highly diverse and productive assemblages of invertebrates live in and among
113 seagrass leaves, providing rich food sources for fish and birds. Invertebrates in this system such
114 as snails, gammarid amphipods, isopods, peracarid shrimp and polychaete worms are not only
115 important to seagrass-based food webs, but also process energy and organic matter in these

116 productive coastal ecosystems. The grazers within this group consume detritus, macroalgae, the
117 seagrass itself (Valentine and Heck 1999), and many of them exert top-down control on
118 epiphytic microalgae that compete with the seagrass for light and nutrients in the water column
119 (Duffy et al. 2015). The animals that live in seagrass meadows exhibit a range of dispersal modes
120 (fast swimming by adult isopods; slow crawling as in snails; and permanent attachment as in
121 some bivalves) and reproductive strategies (brooding versus broadcast spawning) that likely
122 influence dispersal rates and distances. Seagrass meadows can occur in a wide range of
123 temperature, salinity and hydrodynamic environments, such that meadows may differ in their
124 abiotic or biotic suitability for some invertebrate species. Finally, invertebrates on eelgrass
125 interact through facilitation, competition and predation.

126 Decades of research have identified the influence of local characteristics such as habitat
127 complexity (Orth et al. 1984, Hovel and Lipcius 2001), primary biomass (Cébrian and Duarte
128 1998, Gullström et al. 2012), and trophic interactions (Amunudrud et al. 2015, Huang et al.
129 2015) to faunal richness and abundance. However, more recent evidence suggests that when one
130 expands the spatial scale of observation to include many meadows within a region, these local
131 effects are overrided by regional effects such as habitat fragmentation and landscape
132 heterogeneity (Bostrom et al. 2010, Lefcheck et al. 2016, Yeager et al. 2019).

133 The conservation value of seagrass may reflect more than the simple presence of this
134 foundation species. The capacity of seagrasses to support biodiversity may also depend on how
135 meadows can support metacommunities of invertebrates in spatially structured landscapes
136 (Bostrom et al 2006). Metacommunity processes may play important roles maintaining the high
137 diversity of animals within and among seagrass meadows, and if this is true, then management of

138 seagrass for its ecosystem services may be more effective if biodiversity connectivity and
139 metacommunity processes are considered explicitly in the spatial scales of protection plans.
140 The main aim of this study is to better understand the ecological processes that form faunal
141 diversity across a seascape. To address this aim we ask three main questions: (1) What is the
142 contribution of spatial distance (a rough proxy for dispersal limitation) to community similarity?
143 (2) Does variation in local environmental factors drive cariation in the presence and abundance
144 of taxa across sites, and if so, which factors are most important? (3) Do species co-occurrence
145 patterns reveal any biotic interactions that might influence community structure?
146 We hypothesize that: (1) Spatial distance does not confer community dissimilarity because
147 sites are well-connected by dispersal, at even at larger spatial scales (Kinlan and Gaines 2003);
148 (2) Differences in local-scale environmental factors such seagrass shoot density and biomass,
149 temperature, salinity, and water column nutrient levels will drive differences in diversity, but not
150 necessarily taxonomic identity. (3) Species will not show any strong co-occurrence patterns due
151 to high dispersal and environmental responses overriding abiotic interactions.
152 We address these questions by fitting a joint species distribution model with Bayesian
153 estimation to an invertebrate biodiversity survey in 17 *Zostera marina* (L.) meadows spanning
154 the entire coast of British Columbia, Canada (approximately 1000 km). We found evidence of
155 connectivity between sites, even among the most distant sites within our dataset. We also found
156 that species responded differently to different environmental variables, with abiotic water quality
157 variables explaining the most variation in taxonomic abundance. Strong co-occurrence patterns
158 that could not be attributed to shared responses to the environment led us to hypothesize possible
159 biotic interactions influencing community structure.
160

Methods

Study sites and field sampling of eelgrass and associated epifauna

We sampled epifaunal biodiversity in 17 eelgrass *Zostera marina* (L.) meadows along 1000 km of coastline from late June through early August in 2017. The sites were located within five major regions: Haida Gwaii within Gwaii Haanas National Park Reserve, National Marine Conservation Area Reserve and Haida Heritage Site; the central coast of BC near Calvert Island and surrounding areas; southern Clayoquot Sound (one site was within Pacific Rim National Park Reserve); Barkley Sound on the West coast of Vancouver Island; the Southern Gulf Islands within Gulf Islands National Park Reserve (Fig. 1a). We used a spatially hierarchical sampling method to estimate biodiversity at three nested spatial scales: the quadrat (or plot) -level) scale, the meadow (or site) -level scale, and the regional scale (Appendix 1: Fig. A1). These sites varied in environmental conditions, such as seagrass shoot density and meadow size, site exposure and hydrological regimes, freshwater outflow influencing seawater salinity, and others.

We sampled three sites in Barkley Sound (SA, DC, RB) and the central coast (TB, TB, CI, CS) with SCUBA. All other sites were sampled by wading or snorkeling at low tide. We used 0.25 m x 0.25 m quadrats to collect all above ground eelgrass, epifaunal invertebrates, eelgrass detritus, and macroalgae in each sampled area. Six quadrats were set in a 15 m x 30 m array (Appendix 1: Fig. A1); the array was placed in the middle of the meadow to avoid edge effects where possible. We uprooted eelgrass shoots at the first node to avoid infaunal effects where possible, removed all other above-ground biomass (detritus, macroalgae, associated epifauna) within each quadrat by hand, and immediately placed all the contents into a 300 µm mesh or plastic Ziploc bag.

Abiotic environmental variables

We acquired water quality and biotic data. The water quality covariates were annual means pulled from Bio-ORACLE (Assis et al. 2018), including surface chlorophyll-*a*, dissolved oxygen, nitrates, salinity, maximum current velocity and temperature (mean and range). Bio-ORACLE is a database of marine environmental layers gathered from several satellite and in-situ sources at a spatial resolution of 0.08°, and has been been demonstrated in accurate species distribution modelling of shallow-water organisms (Tyberghein et al. 2012, Assis et al. 2018). Sea surface temperature and chlorophyll-a layers were taken from the Aqua-MODIS satellite, and values for nitrates, dissolved oxygen, pH, and salinity were interpolated from in-situ measurements reported in the World Ocean Database (Tyberghein et al. 2012). All sites (meadows) were situated in different spatial cells, and thus had distinct values for the aforementioned variables.

Seagrass, algae, and detritus biometrics

For each quadrat sampled, we measured five biotic attributes summarizing habitat structure and food availability: eelgrass leaf area index (LAI) and shoot density, and eelgrass dry mass, eelgrass detritus dry mass, and algal dry mass. To quantify LAI, we measured leaf length, width, and blade number in five haphazardly-chosen shoots from each quadrat, and multiplied the average blade area (m^2) per shoot by the shoot density (number of shoots per m^2). We separated and dried eelgrass, detritus, and macroalgae in a desiccator oven (60° C for 48 hours).

Invertebrate sample processing and identification

Immediately after collection from the field, we rinsed eelgrass blades with fresh water to remove epifaunal invertebrates; the collected water containing invertebrates was passed through

207 a 500 μm sieve. Invertebrates were preserved in 95% EtOH for identification with light
208 microscopy (10x magnification). We identified epifauna to the lowest taxonomic level possible
209 using keys in the Light and Smith manual (Carlton 2007) and Kozloff (1996). A complete
210 species list including rare species can be found in the Appendix 1.
211
212 *Analysis*
213 All statistical analyses were conducted in R (version 3.4.2; R Development Core Team 2014). We
214 followed the Hierarchical Modelling of Species Communities (HMSC) framework (Ovaskainen et
215 al. 2017) using the 'Hmsc-R' package (Tikhonov et al. 2019) to fit a hierarchical joint species
216 distribution model (JDSM) with Bayesian inference. The framework uses traditional single-
217 species distribution modelling by estimating the species responses to environmental covariates
218 across space, but does so for all species simultaneously. Residual variation from environmental
219 covariates can be used to explain species co-occurrences that are not resulting from shared
220 response to the environment (Ovaskainen et al. 2017). It is also capable of accounting for spatially
221 hierarchical sampling structures. In these ways, the HMSC framework overcomes statistical
222 limitations of previous methods used in metacommunity ecology (Gilbert and Bennett 2010,
223 Tuomisto et al. 2012, Brown et al. 2017).

224 Each species distribution model is given by a generalized linear model that describes the
225 abundance of species j (where $j = 1 \ldots n$), where y_{ij} *is* the count of species j at site i, D is the
226 statistical distribution of the data (Poisson distribution for count data in this study), is the linear
227 predictor, and σ^2_j is a variance term for count of species j.

228 $$y_{ij}^{D} \sim D(L_{ij}, \sigma_j^2).$$

229

The linear predictor L_{ij} is described by fixed (F) and random (R) effect terms:

$$L_{ij} = L^F_{ij} + L^R_{ij}$$

The fixed effect term L^F_{ij} is modelled as a regression:

$$L^F_{ij} = \beta_{jk} x_{ik}$$

where x_{ik} represents the measured value for environmental covariates k for a given sample i (ie., the measured eelgrass biomass in quadrat i), and parameter β represents the relationship between that environmental covariate k, and the abundance of a particular species j.

The random component L^R_{ij}, captures the variation in species occurrences and co-occurrences that cannot be explained by the measured covariates. It is further denoted as

$$L^R_{ij}, = \varepsilon_{ij}^{Q} + \varepsilon_{ij}^{S} + \varepsilon_{ij}^{R} + \varepsilon_{ij}^{D}$$

where the terms describe three hierarchical random effects associated with our sampling scheme (ε_{ij}^{Q}, ε_{ij}^{S}, ε_{ij}^{R} for Quadrat, Site, and Region), as well as a fourth spatially explicit random effect. The spatially explicit random effect ε_{ij}^{D} was calculated with latent factor analysis that takes into account spatial distance between all pairwise combinations of sampling sites (see Ovaskainen et al. 2016a for details).

The three sampling random effect terms are assumed to have multivariate normal distributions $\varepsilon_{ij}^{Q} \sim N(0, \Omega^{Q})$, $\varepsilon_{ij}^{S} \sim N(0, \Omega^{S})$, $\varepsilon_{ij}^{R} \sim N(0, \Omega^{R})$.Variance terms Ω^{Q}, Ω^{S}, Ω^{R}, are variance-covariance matrices (square matrices containing all taxa in the model), where the diagonal elements give species-specific residual variance in occurrences among sites, and the off-diagonal elements give residual co-variances between species pairs. The term “residual” refers to the fact that it is the

amount that is not explained by environmental covariates in the fixed effects predictor described above. These variance-covariance matrices (Ω^Q, Ω^S, Ω^R, and Ω^D) are parameters estimated using a latent variable approach described in Ovaskainen et al. (2016b). They were used to represent co-occurrence matrix R, where j_1 and j_2 refer to two species within the model, and $R_{j1j2} = \Omega_{j1j1}/\sqrt{\Omega_{j1j1}\Omega_{j2j2}}$. R describes the extent to which a given species pair co-occurs more positively or negatively than by chance, after controlling for possible shared responses to the same environmental covariates.

We estimated the parameters of the joint species distribution model with Markov chain Monte Carlo. The Markov chains were run to 200 000 iterations, a burn-in length of 1000 iterations, and was thinned to retain every 100th sample of the posterior distributions. We confirmed that Markov chains were well-mixed by visually inspecting trace plots. Parameter estimates of β_i (environmental responses across taxa) and Ω (variance-covariance matrices used to visualize species co-occurrence patterns independent of the environment) were extracted as 95% credible intervals. We evaluated the model fit using 2-fold cross-validation.

To test our three hypotheses about the contribution of metacommunity processes, we visualized different aspects of the parametrized JDSM (See Appendix 1: Table A1 for summary). We investigated three possible dispersal conditions: dispersal limitation, intermediate dispersal, and high dispersal. To investigate dispersal limitation at large spatial scales, we plotted distance-decay of similarity by randomly drawing 3000 pairwise distances between sampling units, and plotting predicted community similarity against spatial distance. Distance-decay of community similarity could reflect dispersal limitation due to prohibitively far travel distances, *or* due to differences in environmental conditions with increasing spatial scale. To distinguish between these possibilities, we compared the predicted community similarity using the full model

276 (including environmental covariates) with the predicted community similarity using an
277 alternative model where the effect of the environment was removed (all environmental covariates
278 were set to their mean values).

279 To test the hypothesis that differences in environmental conditions among meadows
280 allowed different species to colonize and persist in each meadow ('environmental niche
281 filtering'), we first partitioned variation among environmental covariates, spatial autocorrelation,
282 and random effects associated with the sampling design (quadrat, site, and region), and
283 visualized the contribution of these in a stacked bar plot.

284 To test the hypothesis that some species co-occurred more often than would be expected
285 by chance or by their shared environmental niches, we extracted correlations between species
286 from the residual variation in our model, with latent factor loading (Ovaskainen et al. 2017) and
287 represented modelled pairwise associations with correlation plots describing the extent to which
288 species pairs co-occurred more negatively or positively than predicted by their environmental
289 niches alone (Ovaskainen et al. 2017, Aivelo and Norberg 2018). We show species co-
290 occurrences at the quadrat, site, and region random effect levels. To visualize patterns in site-
291 level co-occurrences across sites, we conducted hierarchical cluster analysis on sites according to
292 observed species abundances using Ward's criterion (Ward 1963). We mapped the cluster
293 dendrogram onto an abundance heatmap of the 10 most abundant taxa in our analysis, and
294 colour-coded the cells according to the species co-occurrence groupings from the correlation
295 plots (groups of species that tended to positively co-occur amongst themselves). Full versions of
296 these figures with all species are provided in Appendix 1: Fig. A4 and Fig. A5.

297

298 **Results**

Species abundance and distribution patterns

We counted and identified 52 282 individuals representing at least 50 taxa across the region (Appendix 1: Table A2). We excluded rare species (those found in fewer than 5% of all samples, or fewer than 5 out of 102 quadrats) from our JDSM to avoid statistically over-inflating the importance of model covariates; this left 33 taxa in our analysis. The represented taxa span multiple phyla, diet types (herbivores, detritivores, suspension feeders, carnivores), and life history strategies (brooding, broadcast spawning). Mean quadrat-level species richness was 13 species, and mean site-level richness was 16 species. A full summary of diversity metrics can be found in Appendix 1: Table A3.

Several taxa were present at all 17 sites (Appendix 1: Fig. A2). These include harpacticoid copepod *Porcellidium* sp., bivalves *Saxidomus gigantea* and *Clinocardium nutallii*, snails *Alvania compacta*, *Lacuna* spp., and the tanaid *Leptochelia* sp. Genera *Mytilus* (a mussel) and *Nereis* sp. (a polychaete worm) were represented at all sites, however we were not confident the same species comprised these groups. Ten species were present in at least one site in every region: isopod *Penidotea resecata,* gammarid amphipods *Monocorophium insidiosum, Ampithoe valida, Pontogeneia rostrata, Ampithoe dalli, Aoroides* spp*.,* snails *Amphissa columbiana* and *Alia carinata,* and limpet *Lottia pelta*.

Dispersal: Distance-decay of community similarity due to spatial distance and environment

In the full joint species distribution model summarizing species' responses to environment and spatial distance, predicted community similarity decreased with increasing distance between sites (Fig. 1b, red points and line). However, community similarity showed a slight increase with distance when the effect of environmental variables was removed from the

322 model (all environmental variables set to their mean value). We infer that spatial distance alone
323 did not explain differences in invertebrate compositional similarity (Fig. 1b, blue points and
324 line), but that differences in habitat conditions among meadows better explained divergence in
325 community composition.
326
327 *Environmental niche filtering: variation partitioning*
328 Consistent with the previous analysis, we found that patterns in abundance and
329 distribution were consistent with weak environmental niche filtering along an abiotic axis. Water
330 quality variables (yellow bars in Fig. 2) explained the largest proportion of variation across
331 nearly all species distributions. Herbivore food availability (seagrass, algae and detritus biomass)
332 and habitat structure (eelgrass shoot density and LAI) had minimal influences on species
333 distributions (pink bars in Fig. 2). The importance of environmental covariates varied across
334 species; for example, Fig 2). While the mean R^2 across all species distribution models was 0.27,
335 individual R^2 values were highly variable (0 to 0.68, Appendix 1: Table A2).
336
337 *Species interactions: Patterns in pairwise species co-occurrences*
338 At the scale of interactions among individuals (site-level samples), positive co-
339 occurrences tended to be more common than negative co-occurences, suggesting facilitation as a
340 possible important species interaction. Co-occurrence patterns were not strong at the quadrat and
341 region–levels (Fig 3a and 3b).
342 At the site level (between-sites), we identified, *post hoc*, two main species co-occurrence
343 groupings. Members of the first group (hereafter we call this the "*Nereis"* group), *Leptochelia*
344 sp. (tanaid), *Nereis* polychaetes, spirorbid polychaetes, and *Caprella laeviuscula* (caprellid

amphipod) (Fig. 3b), tended to positively co-occur more than expected by chance or by environmental filtering, and negatively co-occur members of the second group. The second group included a Harpacticoid copepod species, the isopod *Porcellidium* sp., and an gammarid amphipod within the family Ischyroceridae (Fig. 3b). Other species did not show strong positive or negative co-occurrence values with others.

The two co-occurrence groups were present at all sites, indicating that members from these groups can be simultaneously present (Fig. 3d). However, their abundances tended to negatively co-vary; at sites JB, HL, CB, RA, EB, DC, and DU, members of the *Nereis* group were predicted to be most abundant, whereas other group members were predicted to be most abundant at SS, SA, LH, GB and RB. The site HL was strongly dominated by *Spirorbis* sp. The emergent species groupings identified in Fig. 3b do not clearly correspond with spatial distance because the cluster analysis did not group sites by spatial proximity (black symbols in Fig. 3d); this is another line of evidence suggesting that dispersal is not limited at this spatial scale.

Discussion

This work is the largest, spatially explicit seagrass metacommunity study in geographical extent to our knowledge. We tested the hypotheses that dispersal, environmental heterogeneity and species interactions influenced spatial patterns in this system, consistent with metacommunity dynamics. We found support for the importance of environmental niche filtering and biotic interactions as drivers of biodiversity patterns, but surprisingly, we found little support for dispersal limitation even across over 1000 km of coastline. Overall, these results suggest that seagrass-associated biodiversity patterns reflect ecological processes spanning local (meadow-scale) to regional scales.

368

369 *Is there evidence of dispersal limitation among eelgrass meadows?*

370 Our finding that the effect of spatial distance alone does not confer community
371 dissimilarity, along with the low spatial autocorrelation with environmental covariates, suggests
372 that spatial distance between sites likely does not result in dispersal limitation. This is true for the
373 six taxa that were present at all sites, and the additional ten taxa that were not present at every
374 site but present in all regions (Appendix 1: Fig. A2). These widely distributed groups had
375 representation from across phyla and life history traits, suggesting that no single taxonomic
376 group or dispersal life history strategy had a consistently greater spatial distribution than any
377 other. Many of the meadows were small (< 1 ha), and epifaunal abundances can vary
378 substantially within meadows from year to year (Adamczyk et al. in prep) such that local
379 extinctions followed by rescue from nearby populations are likely important (Thom et al. 1995).
380 However, the specific pathway the organisms travelled to arrive at these sites remains unknown.
381 We used Euclidean distances in our analysis, which preserved the rank order of distances
382 between sites, but actual distances are likely greater due to oceanographic circulation patterns
383 (Kinlan and Gaines 2003, Mitarai et al. 2008).

384 It is unclear whether distant sites share the same species because they are 1) linked by
385 direct dispersal via oceanographic processes such as currents; 2) indirectly linked by dispersal
386 via unsampled "stepping-stone" sites; or 3) were colonized by populations of the same species in
387 a historical dispersal event, but have not seen the exchange of individuals since. Seagrass-
388 associated epifauna generally disperse passively between meadows, either by larval transport in
389 currents or by "rafting" on floating pieces of seagrass or macroalgae. Rafts have been observed
390 hosting benthic and epifaunal invertebrates across phyla (echinoderms; peracarids; molluscs;

annelids), and contribute to connectivity between coastal ecosystems across 100s of kilometres (Wichmann et al. 2012).

Species that were only found at one site or region (e.g. *Jassa marmorata,* Appendix 1: Fig. A2) may be dispersal limited for reasons other than prohibitively long travel distances. Populations with low abundances may not disperse in appreciable numbers, and therefore cannot establish populations at all sites as readily as abundant species. This is supported by our observation of a generally positive relationship between range size (the number of sites a species was represented at) and abundance (Appendix 1: Fig. A6).

Theory predicts that intermediate dispersal (dispersal sufficiency) allows species to colonize sites where local environmental conditions are optimal for growth and reproduction, whereas high dispersal (dispersal surplus) overrides this (Mouquet and Loreau 2003). Therefore, it is likely that dispersal rates are high enough for several species to be present at most sites, but not so high as to completely overwhelm the effects of environmental conditions. A subset of species was present at all sites, but often at varying abundances (Fig 3d). This may indicate weak mass effects, where immigration allows populations to persist even if local conditions are not optimal (Schmida and Wilson 1985, Mouquet and Loreau 2003). Metacommunity theory predicts that such weak mass effects are likely to be found whenever dispersal rates are not limiting (Thompson et al. 2017), particularly in organisms that cannot control their own dispersal, (Leibold and Chase 2017) such as seagrass-associated invertebrates. This may be supported by our result on the contribution of the environment, particularly in ubiquitous species for which the model fit was poor (e.g. *Aoroides* spp., *Spirorbis* sp., $D^2_{adj} = 0$); the poor model fit may indicate that these persist at sites even if local environmental conditions are not optimal, due to sufficient immigration. An alternative explanation for the model's poor predictive power for

these species is that these taxa have broader environmental niches, and thus the regional environmental gradient is not sufficient to drive clear presence-absence patterns.

Seagrass epifauna show varying degrees of environmental niche filtering

The abiotic environmental axis had the largest influence on species distributions, with phosphates, salinity, and sea surface temperature explaining the largest fractions of variation on average in the joint species distribution model (Fig. 2). In some species distribution models that had a higher fit (e.g. *Ampithoe dalli* and *Caprella natalensis*, Appendix 1: Table A2), environmental niche filtering may be important, but overall there remains a large amount of variation unexplained by the environment.

Environmental heterogeneity may be influencing species distributions and abundances across the region in one of three ways. First, the most important abiotic environmental covariates (mean and range in ocean temperatures, nitrates, dissolved oxygen) may influence food availability through primary productivity. This is possible despite the fact that primary biomass explained less variation than abiotic parameters (Figure 2). While the primary biomass measurements were taken at a single time point, the abiotic parameters represent a four-year average (Assis et al. 2018) and may therefore better represent the conditions these organisms experience over their lifetimes or across generations. Second, sea surface temperature, dissolved oxygen, and salinity may affect species' distributions via environmental tolerance ranges. For example, the isopod *Idotea baltica* (a relative of *P. resecata* and *P. montereyensis* in our study) experiences significantly lower survival in prolonged exposure to higher temperatures and lower salinities than those experienced in their home habitat (Rugiu et al. 2018). Third, temperature may influence the metabolic demands of invertebrates (many of which are herbivores), thereby influencing grazing rates and altering the available primary biomass (O'Connor 2009). Decreased

437 food resources may increase competition, thus influencing the number and identity of species a
438 patch of seagrass can host. Determining whether population-level responses to competitive stress
439 influence whole-community structure would improve our understanding of how the environment
440 and species interactions combine to influence community structure.

441 Environmental conditions in temperate eelgrass meadows fluctuate seasonally, driving
442 changes in epifaunal community structure throughout the year (Wlodarska-Kowalczuk et al.
443 2014). Because these species may not show the same distributions year-round, sampling several
444 times in a year to capture these temporal changes would give a clearer picture of species'
445 responses to all metacommunity processes.

446 *Species co-occurrence patterns may suggest priority effects and trophic interactions*

447 We did not observe strong quadrat-level co-occurrence patterns; this is consistent with
448 previous findings that epifaunal diversity varies randomly within meadows (between quadrats)
449 (Whippo et al. 2018). We also did not observe strong region-level co-occurrence patterns,
450 suggesting that there do not appear to be clear regional assemblages organized according to the
451 bioregions we have defined (Fig. 1a). At the site-level, two main co-occurrence groupings
452 emerged showing generally antagonistic abundances across sites (Fig. 3d). Stochasticity alone is
453 unlikely to have produced such a strong pattern, especially given deterministic processes tend to
454 be more important in systems that are not dispersal limited (Lee and Bruno 2009, Ron et al.
455 2018). While there are multiple possible explanations for non-random species co-occurrence
456 patterns (Connor and Simberloff 1979), space and the measured environmental covariates were
457 ruled out since co-occurrence values were extracted from residual variation unexplained by
458 environment or spatial autocorrelation (Ovaskainen et al. 2017). This, along with the high
459 unexplained fraction in the variation partitioning leads us to hypothesize the importance of biotic

460 processes. Several types of interactions may be occurring in the metacommunity; the majority of
461 species are herbivores or detritivores, and thus may compete for primary biomass. Laboratory
462 experiments have shown that behaviours such as grazing rate and habitat selection in amphipods
463 are altered in the presence of morphologically and functionally similar interspecific competitors
464 (Beermann et al. 2018). Other species in our study are filter feeders, and thus may not be
465 competing for food resources but possibly predator-free space or substrate on the eelgrass blades.
466 The community structure of a given site with certain local environmental conditions and
467 access to a certain regional pool may have multiple possible compositional states depending on
468 the arrival order of species; this phenomenon is known as priority effects (Fukami et al. 2016, Ke
469 and Letten 2018) and has been documented in marine fouling communities (Vieira et al. 2018).
470 The antagonistic co-occurrence groupings in our analysis not arising from shared responses to
471 the environment may suggest priority effects at the site-level or meadow spatial scale (Fig. 3b). It
472 is possible that, following the establishment of a new meadow or a disturbance event, the first
473 few species to colonize a seagrass meadow determine the success of subsequent colonizers,
474 regardless of local environmental conditions. As an illustrative example, *Leptochelia* sp. might
475 have been among the first to colonize sites CS, DC, IN, and HL (Fig. 3b and 3d), thereby gaining
476 a numerical advantage over species in the alternative cohort. Distibution patterns in the sessile
477 calcifying polychaete *Spirorbis* sp. may also indicate priority effects. It dominated the HL site;
478 16 300 individuals were found, several orders of magnitude higher than its abundance elsewhere
479 (Data S1). Site HL also had the lowest species richness of all 13 sites (9 species). Eelgrass shoots
480 there were completely covered by these *Spirorbis* sp., possibly preventing grazers in the
481 community from accessing epiphytic algae or the seagrass itself. The age, colonization history,
482 and disturbance regime of the meadows likely matter if priority effects are occurring; further

483 work must be done to better understand these temporal dynamics in temperate seagrasses.

484 Negative co-occurrence patterns could also reflect the higher abundance of a predator at
485 some sites. Field experiments have shown that changes in predation pressure by fish, shorebirds,
486 and predatory invertebrates can shift seagrass-associated epifaunal assemblages in a matter of
487 weeks (Amundrud et al. 2015; Huang et al. 2015). Differential predation pressure could also lead
488 to the pattern of diverging community composition that we have witnessed (Guzman et al. 2018).
489 A more comprehensive sampling effort of fish and bird predators would be required to determine
490 the degree to which trophic interactions structure these communities.

491 Positive co-occurrence patterns between certain species may additionally be a result of
492 positive biotic interactions. An example is seen in *Orchomenella recondita* - a gammarid
493 amphipod that lives in the gastrovascular cavity of the anemone *Anthopleura elegans* (Carlton
494 2007). This species was only recorded at the SS site, and specifically only found in quadrats
495 where *A. elegans* was collected with the seagrass shoots.

496 **Conclusion**

497 Using a new statistical approach to characterizing dispersal, environmental niche
498 filtering, and biotic interactions, we have developed refined hypotheses about the
499 metacommunity processes driving temperate seagrass epifaunal diversity on a regional scale. Our
500 study also gives a baseline spatial scale (1000 km) for comparing the contribution of these
501 processes across spatial scales and other ecological systems (Viana and Chase 2018).
502 Manipulative experiments and monitoring are now needed to test our refined hypotheses. One
503 could test the hypothesis that species sorting is relatively weak by measuring fitness differences
504 along the most important environmental axes. Given our hypothesis on the importance of priority
505 effects, one might experimentally manipulate the colonization order of key species in our study

506 to determine if resulting compositional states differ (Fukami et al. 2016). Testing our hypothesis
507 that populations within the metacommunity are not dispersal limited is more challenging, but
508 could be done using particle tracking models similar to those used to estimate larval dispersal
509 between coral reefs across thousands of kilometres (Treml et al. 2008). A population genetic
510 analysis could also ground-truth the extent of dispersal between allopatric populations.

511 Our findings are particularly relevant to conservation initiatives that aim to maintain
512 diversity in seagrass meadows; identifying the importance of local and regional processes allows
513 the conservation practitioner to better predict how habitat fragmentation and climate change
514 might influence diversity. Seagrass epifaunal communities may be quite resilient, given our
515 findings that environmental conditions minimally contribute to species distributions, and several
516 species across functional groups are consistently present across a fairly large spatial scale.

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686 **Figure legends**

687 **Figure 1. a)** Map of coastal British Columbia showing eelgrass field sites in Haida Gwaii (HL,
688 RA), Clayoquot Sound (DK, EB, IN), Barkley Sound (SA, DC, RB), near Calvert Island in the
689 central coast (TB, TN, CS, CI), and the Southern Gulf Islands (GB, JB, CB, LH, SS). **b**) HMSC
690 model predictions of community similarity relative to the spatial distance (Euclidean) between
691 communities. The red circles show similarity predictions based on the full model. The blue
692 triangles show predictions wherein the effect of all environmental variables has been removed
693 (standardized to their mean values).

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Figure 1a)

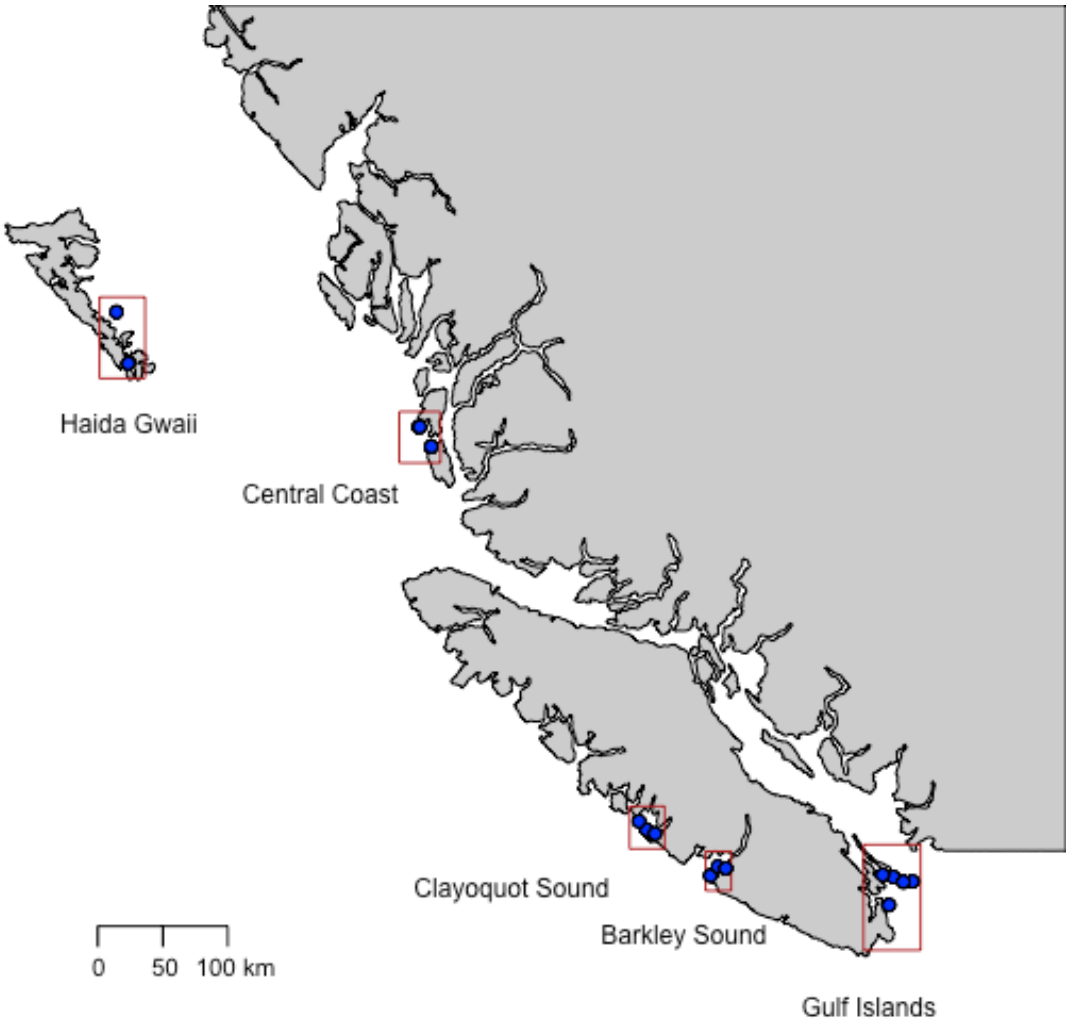
Haida Gwaii
Central Coast
Clayoquot Sound
Barkley Sound
Gulf Islands
0 50 100 km

Figure 1b)

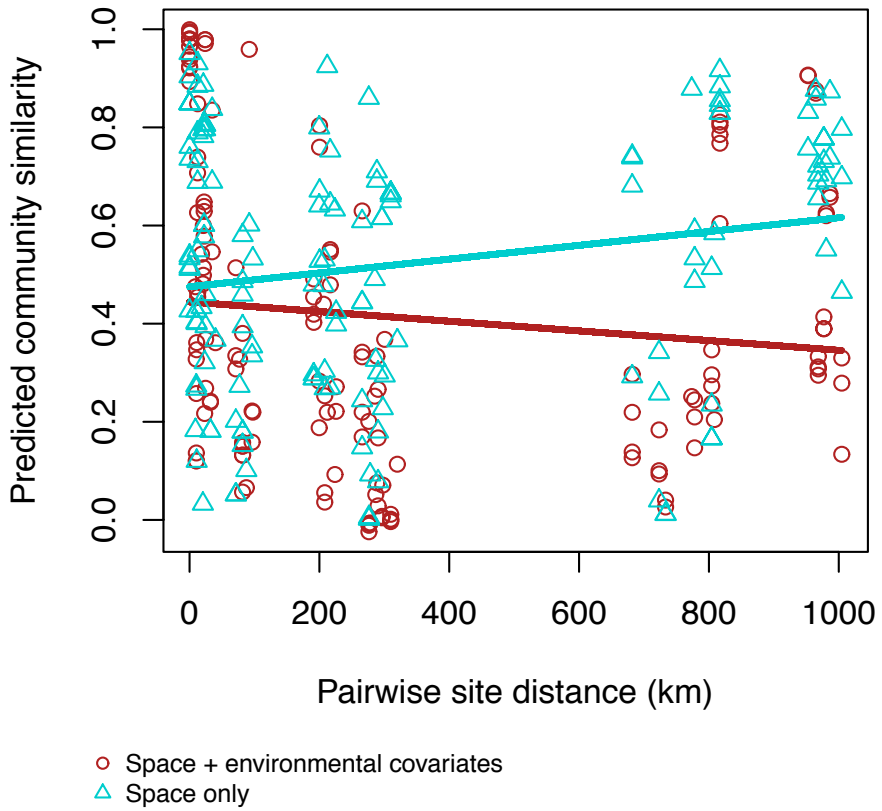
Predicted community similarity
0.0
0.2
0.4
0.6
0.8
1.0
0
200
400
600
800
1000
Pairwise site distance (km)
Space + environmental covariates
Space only

Figure 2.

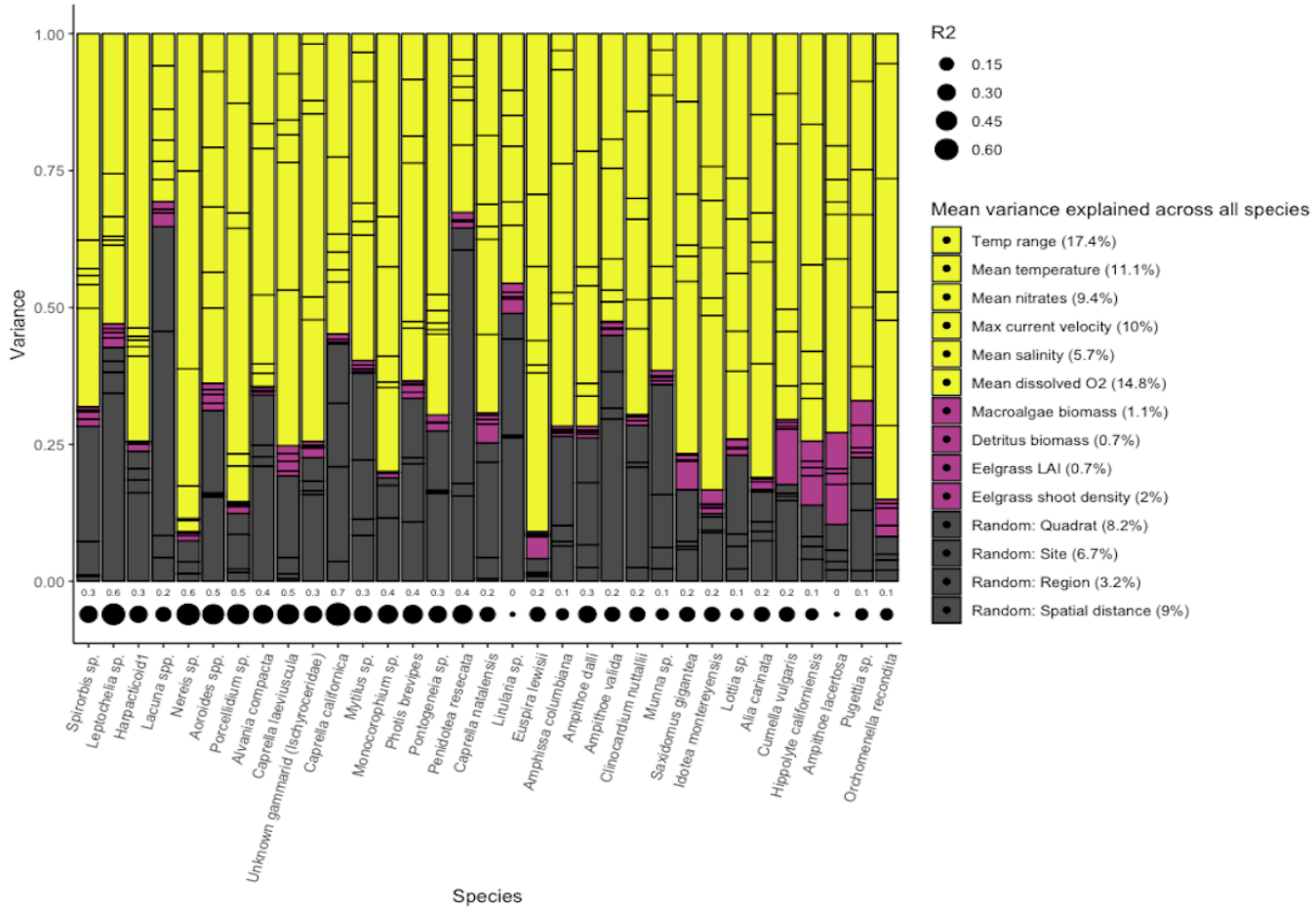

Figure 2. Variation partitioning of fixed and random effects within the joint species distribution model. Grey cells represent the contribution of random effects associated with the sampling design. Yellow cells represent the contribution of abiotic water quality covariates. Pink cells represent biotic covariates (food availability, habitat structure). Bars are organized according to species abundances in descending order from left to right (most abundant to least abundant). The percentages next to the legend labels indicate mean variation explained by that covariate/ random effect across all species distribution models. The black circles below each stacked bar describe the model fit to the data (R^2_{adj}). The mean R^2_{adj} of all species distribution models was 0.27.

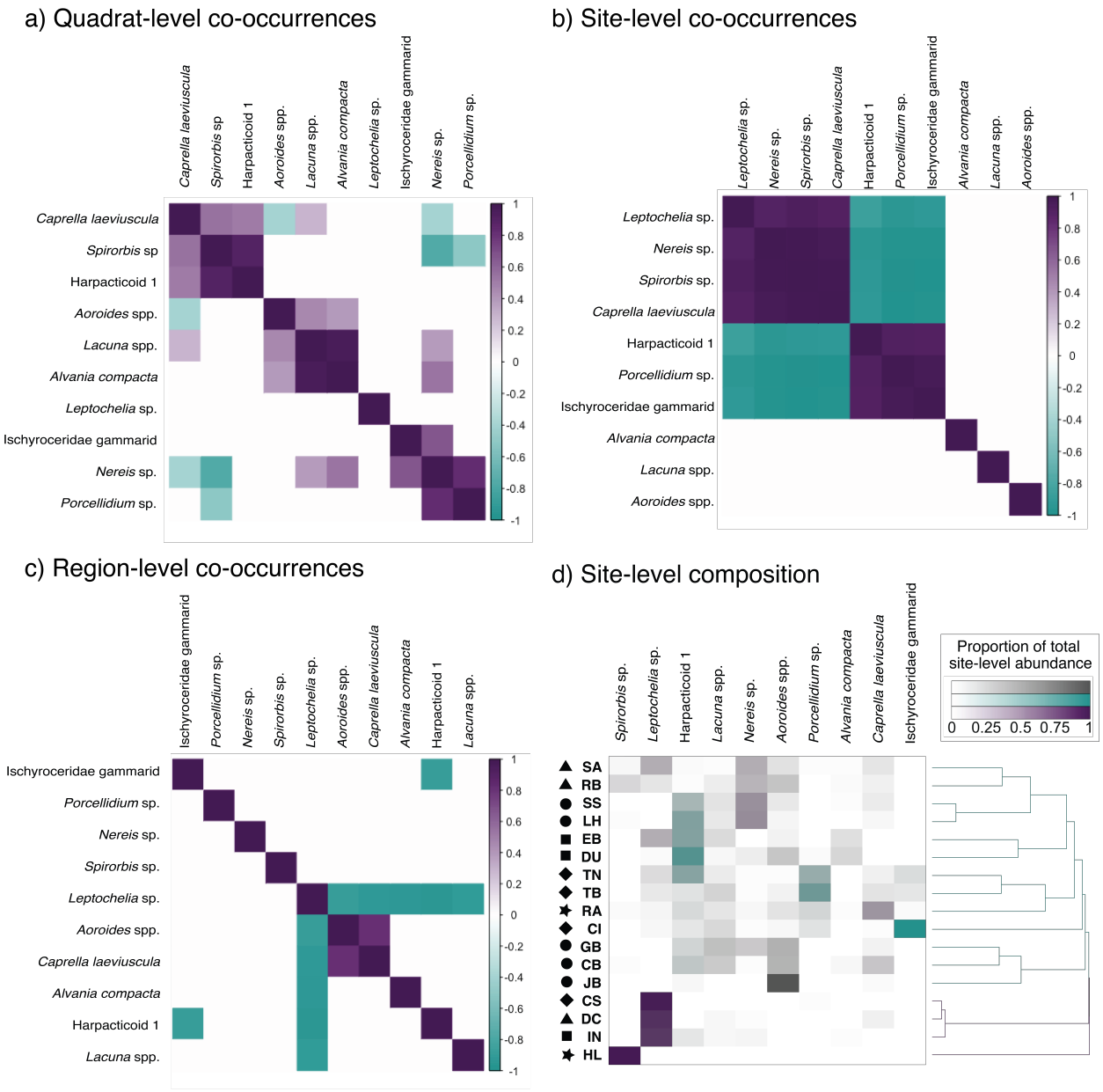

Figure 3. a-c) Correlation plots showing modelled a) quadrat-level, b) site-level, and c) region-level pairwise co-occurrences after removing the effect of shared responses to the environmental covariates in our model. Only the 10 most abundant species are represented. Purple cells represent positively co-occurring species pairs, and turquoise cells represent negatively co-occurring species pairs. Species names are ordered according to the output of hierarchical clustering with Ward's criterion on pairwise co-occurrence values. A version of this figure with all 33 species is shown in Appendix S1: Fig. S4. **d)** Heatmap and cluster dendrogram depicting species relative abundance and compositional similarity across sites. Species are ordered by

decreasing abundance from left to right. Cell colours correspond to the site-level co-occurrence groupings shown in Fig. 3b: turquoise or *Nereis* group, purple or *C. californica* group, and grey *Spirorbis* group. Cell shade strength indicates proportional abundance at a given site (darker means higher abundance). The black symbols to the left of the site abbreviations indicate region membership; stars indicate Haida Gwaii sites, diamonds indicate Central Coast sites, triangles indicate Barkley Sound sites, squares indicate Clayoquot Sound sites, and triangles indicate Southern Gulf Islands sites. A version of this figure with all 33 species is shown in Appendix S1: Fig. S5.