Regional connectivity, local environmental conditions, and biotic interactions jointly structure a temperate seagrass epifaunal metacommunity

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Abstract

Dispersal, environmental niche filtering, and biotic interactions all structure patterns of abundance and distribution in ecological communities. Metacommunity ecology provides a framework for understanding how these processes combine to determine community composition in sites across a region that are connected through the dispersal of multiple potentially interacting populations. Previous metacommunity approaches have had limited success due to statistical limitations and incompatibilities between theory and methods. Here, we use the Hierarchical Modelling of Species Communities statistical framework to individually assess the contribution of the aforementioned assembly processes to biodiversity patterns in an important coastal habitat, seagrass meadows, across approximately 1000 km along the coast of British Columbia, Canada. Following the HMSC framework, we parametrized a hierarchical joint species distribution model describing the relationship between multiple measured environmental covariates, spatial distance between sites, and unexplained random effects on epifaunal species distributions across thirteen eelgrass (*Zostera marina* (L.) meadows. Observed species distribution patterns suggest that seagrass epifauna form well-connected metacommunities at the present spatial scale, but that dispersal rates are not so high that they homogenize the region through mass effects. We found evidence of niche filtering in several species along an abiotic gradient, with surface phosphates, temperature and dissolved oxygen being the most important environmental variables. However, environmental conditions only explained a small fraction of the variation in observed species occurrences at the community level, and the predictive power (D^2_{adj}) of the model was poor for some species, suggesting that either some species have broader environmental niches, or niche filtering is not important at this spatial scale. Strong structuring in pairwise species co-occurrences led us to hypothesize that

local community composition may be influenced by priority effects resulting from biotic interactions. Our approach has yielded refined hypotheses about the specific local and regional dynamics influencing seagrass epifaunal community structure; these hypotheses in turn can inform targeted experiments, monitoring efforts, and management decisions for preserving biodiversity in this important coastal ecosystem.

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

Introduction

Understanding how local environmental conditions, biotic interactions, and regional connectivity combine to structure the composition of communities is a central challenge in ecology (Vellend 2016, Leibold and Chase 2017). Determining the relative importance of these assembly processes in particular ecosystems is a critical step in understanding the spatial and temporal scales of stability and resilience in spatially structured communities (Leibold and Chase 2017). Metacommunity theory offers an integrative framework for understanding drivers of diversity across spatial scales, however previous attempts to quantitatively apply metacommunity concepts to real-world ecological systems have had limited success (Logue et al. 2011, Brown et al. 2017). Over the past decade and a half, the primary focus of metacommunity studies has been seeking signatures of one of four idealized metacommunity paradigms in natural systems: the neutral model, patch-dynamics, species sorting and mass effects (Leibold et al. 2004, Cottenie 2005). An emerging perspective holds that natural metacommunities do not fit neatly under one of the four paradigms because they do not reflect all possible combinations of

91 the various assembly processes (Logue et al. 2011, Brown et al. 2017, Leibold and Chase 2017).
92 Thus, the revised goal is to determine how dispersal, environmental conditions, and biotic
93 interactions combine to structure species composition and relative abundance within a
94 metacommunity.

95 Many marine ecosystems that host high biodiversity occupy spatially structured habitats such
96 as rocky reefs, coral reefs, and seagrass meadows, and marine species have various dispersal
97 strategies that connect populations in distinct habitat patches. Marine systems are characterized
98 by strong local species interactions (Berlow 1999, Sala and Graham 2002) and the importance of
99 'supply-side' or dispersal-driven population dynamics has long been recognized (Levin and
100 Paine 1974, Gaines and Roughgarden 1985). These combined roles of dispersal, local
101 environment, and species interactions suggest that marine biodiversity patterns may in fact
102 reflect local and regional processes characteristic of metacommunities (Guichard et al. 2003).
103 Despite the historically strong focus on dispersal and species interactions in marine ecology,
104 metacommunity dynamics have only been explicitly investigated in a few marine systems
105 (Guichard et al. 2003, Yamada et al. 2014, Valanko et al. 2015, Whippo et al. 2018).
106 Consequently, the potential benefits to conservation prioritization that could be gleaned by
107 applying metacommunity theory to marine systems have not been fully realized (Economo
108 2011).

109 Seagrasses, like kelps, corals and salt marsh plants, are foundation species that support high
110 productivity and faunal diversity (Heck and Thoman 1984, Orth et al. 1984, Duffy et al. 2015).
111 Seagrasses form meadows separated from each other by deeper water, un-vegetated seafloor, or
112 other vegetated habitats such as kelp forests. Faunal species disperse among meadows and interact
113 through predation, competition, and facilitation (Boström et al. 2006). This scenario is consistent

114 with the type of landscape that supports communities governed by metacommunity dynamics
115 (Mouquet and Loreau 2003, Leibold et al. 2004). Yet, our understanding of seagrass-associated
116 faunal diversity and its consequences for conservation and ecosystem function does not yet reflect
117 the possibility that seagrass biodiversity is maintained by processes operating across numerous
118 seagrass meadows and adjacent habitats in a seascape. Numerous seagrass community ecology
119 studies have focused on the influence of local, site-level characteristics such as habitat structure
120 (Orth et al. 1984), primary biomass (Cébrian and Duarte 1998, Gullström et al. 2012), or trophic
121 interactions (Amunudrud et al. 2015, Huang et al. 2015) on faunal diversity. Few studies have
122 elucidated ecological processes occurring operating on a regional or inter-site scale. Failure to
123 identify the contribution of metacommunity processes could lead to underestimates of the amount
124 of habitat required to sustain biodiversity and ecosystem functions (Boström et al 2006).
125 Two studies that applied different metacommunity approaches to seagrass invertebrate
126 communities found evidence for the importance of regional-scale processes (Yamada et al. 2014,
127 Whippo et al. 2018), but their ability to characterize the individual contribution of all assembly
128 processes driving metacommunity structure was limited by the statistical methods available at
129 the time. Furthermore, neither approach was able to identify possible biotic interactions, thereby
130 entirely missing a critical aspect of community assembly. Using variation partitioning on
131 constrained ordinations (Borcard et al. 1992, Cottenie 2005), Yamada et al. (2014) found that the
132 relative contribution of space and environment varied among different invertebrate functional
133 groups, suggesting that the relative importance dispersal levels versus niche filtering could be
134 mediated by functional traits. However, the variation partitioning analysis was not able to
135 distinguish between multiple possible metacommunity dynamics at play owing to the ambiguous
136 statistical significance of the results (Yamada et al. 2014). Simulation studies have shown that

137 this variation partitioning method can over- or under-estimate spatial and environmental
138 components of variation, and produce inflated R^2 values depending on the researcher's statistical
139 choices (Gilbert and Bennett 2010, Tuomisto et al. 2012). Whippo et al. (2018) used another
140 method, elements of metacommunity structure (EMS) (Leibold and Mikkelson 2002, Presley et
141 al. 2010). While useful for visualizing regional diversity patterns, EMS does not elucidate the
142 potential processes contributing to these patterns (Brown et al. 2017).

143 These limitations, along with the revised goal of individually assessing the contribution of
144 dispersal, niche filtering, and biotic interactions to diversity in a metacommunity, invite novel
145 methodological approaches. A new statistical framework, Hierarchical Modelling of Species
146 Communities (HMSC) (Ovaskainen et al. 2017), shows promise for achieving this goal. HMSC
147 uses Bayesian inference to parametrize a hierarchical joint species distribution model
148 summarizing the influence of space, environment, patterns of co-occurrence, phylogeny and
149 traits on species distributions. The framework allows the partitioning of explained variation due
150 to environmental covariates, spatial distance, and random effects for all species distributions,
151 allowing the observer to discern patterns at the whole community level as well as in individuals.
152 Additionally, the framework models the residual variance in species distributions unexplained by
153 environment and space as a variance-covariance matrix, which can be used to visualize patterns
154 of positive or negative pairwise species co-occurences. For these reasons, HMSC achieves what
155 researchers aimed to achieve with the previous methods, and much more.

156 Here we test the hypothesis that seagrass-associated epifaunal invertebrate communities are
157 jointly structured by the spatial distances (a proxy for inferring dispersal dynamics) between
158 meadows, local environmental conditions, and biotic interactions. Our approach moves away
159 from the four original metacommunity paradigms, instead focusing on individually

160 characterizing the effects of dispersal, environmental niche filtering, and biotic interactions on
161 the community structure. We follow the HMSC framework (Ovaskainen et al. 2017) to answer
162 the following questions: (1) Is the metacommunity characterized by dispersal limitation,
163 intermediate dispersal, or high dispersal? (2) Do species distribution patterns suggest
164 environmental niche filtering, and if so along which environmental axes? (3) Do species co-
165 variance patterns suggest possible biotic interactions influencing community assembly? The
166 order in which these questions are posed matters. For example, if dispersal limitation is found to
167 be significant, this knowledge affects how we may interpret observed species co-occurrence
168 patterns. In answering these questions with a biodiversity survey of invertebrates in 13 meadows
169 in British Columbia, we also provide a comprehensive assessment of species abundance and
170 diversity from local to regional scales. We find evidence of intermediate dispersal rates among
171 meadows across 1000 km, but no sign of complete biodiversity homogenization resulting from
172 high dispersal. We also find that local environmental conditions have some influence on species
173 distributions across the 13 sites, but that individual species' responses to environmental gradients
174 vary dramatically. Strong species covariance patterns led us to hypothesize possible biotic
175 interactions influencing local community composition.
176

177 **Methods**

178 *Study sites*

179 We sampled epifaunal biodiversity in 13 eelgrass *Zostera marina* (L.) meadows across a
180 spatial scale of 1000 km from late June through early August in 2017. The sites were located
181 within four coastal areas: Haida Gwaii within Gwaii Haanas National Park Reserve, National
182 Marine Marine Conservation Area Reserve, and Haida Heritage Site; southern Clayoquot Sound

183 (one site was within Pacific Rim National Park Reserve), Barkley Sound on the West coast of
184 Vancouver Island, and the Southern Gulf Islands on the south-eastern tip of Vancouver Island
185 within Gulf Islands National Park Reserve (Fig. 1).
186 *Zostera marina* (L.) is the most common subtidal seagrass species in the Northeast Pacific
187 (Alaska to southern California). In British Columbia, Canada, *Z. marina* meadows are found in
188 discrete patches along the coast. They vary in several biotic and abiotic conditions, such as
189 seagrass shoot surface area and density, macroalgal species composition, fish community
190 structure, temperature, salinity, and water column nutrient levels.
191
192 *Field sampling of eelgrass and associated epifauna*
193 We sampled three sites in Barkley Sound (SA, DC, RB) with SCUBA because they
194 required boat access, and the deepest parts of the meadow reached a depth of 5m during
195 sampling. All other sites were sampled by wading or snorkeling at a low tide of 0.6 m or less.
196 We used a standardized, nested sampling regime with 0.25 m x 0.25 m quadrats to collect
197 aboveground eelgrass, epifaunal invertebrates, detritus, and macroalgae (Whippo et al. 2018).
198 Six quadrats were set in a 15 m x 30 m array, such that every quadrat was situated 15 metres
199 from its nearest neighbour (Appendix S1: Fig. 1). The array was placed in the middle of the
200 eelgrass meadow to avoid edge effects where possible. We removed all above-ground biomass
201 (eelgrass, detritus, macroalgae) within each quadrat by hand and immediately placed the contents
202 into a 250 µm mesh bag at the Barkley Sound and Southern Gulf Islands (GB, LH, SS, CB, JB)
203 sites, and into a Ziploc bag at the Clayoquot Sound (IN, EB, DK) and Haida Gwaii (HL, RA)
204 sites.
205

206 *Acquiring biotic and abiotic environmental variables*

207 To test our hypothesis on environmental niche filtering, we quantified 14 environmental
208 attributes of each meadow and quadrat sampled. We used in-situ field measurements and
209 satellite-derived averages from the Bio-ORACLE dataset (Assis et al. 2018) as estimates of
210 water quality conditions associated with hypothesized niche differences among epifauna. We
211 gathered in-situ measurements of water quality parameters (pH, salinity, dissolved oxygen,
212 nitrates and chlorophyll-*a*) at each meadow. We also acquired data on mean surface chlorophyll-
213 *a* ($\mu g\ L^{-1}$), dissolved oxygen, surface nitrates, surface silicates, surface phosphates, pH, salinity,
214 and mean sea surface temperature (°C) from Bio-ORACLE: a global database of marine
215 ecological variables gathered from several satellite and in-situ sources at a spatial resolution of
216 0.08° (Assis et al. 2018). All sites (meadows) were situated in different spatial cells, therefore all
217 sites had distinct values for the aforementions parameters. However, all quadrats within a given
218 meadow (spaced 5-15m from its adjacent neighbor) were situated in the same spatial cell and
219 thus were given the same site-level value for all the Bio-ORACLE variables; we accounted for
220 this spatially nested random effect while constructing our model. We also quantified fetch, which
221 is a proxy for site exposure. We chose these abiotic variables because we expected them to be the
222 most important variables influencing species distributions, either through variation in
223 physiological tolerances, or through influencing primary productivity and food quality.

224 For each sample, we measured five biotic attributes: eelgrass leaf area index (LAI), shoot
225 density, eelgrass dry mass, total algal dry mass, and detritus dry mass. We measured leaf length,
226 width, and number of blades in five representative shoots within each quadrat. Leaf Area Index
227 (m^2 eelgrass blade area per m^2 of ground) was calculated by multiplying the average blade area
228 (m^2) per shoot by the shoot density (number of shoots per m^2). We standardized blade length

229 measurements from the end of the blade to just above the first rhizome node because some
230 shoots had intact rhizomes while others were missing after uprooting in the field. We separated
231 and dried eelgrass, detritus, and macroalgae in a desiccator oven (60° C for 48 hours) to measure
232 dry mass.
233
234 *Response variable: Quantifying epifaunal diversity*
235 We rinsed the eelgrass blades from each quadrat to remove epifaunal invertebrates, and
236 passed samples through a 500 μm sieve. Invertebrates were transferred into a centrifuge tube and
237 preserved in 95% EtOH for identification with light microscopy (10 times magnification). We
238 identified invertebrates to the lowest taxonomic level possible using keys in the Light and Smith
239 Manual (Carlton 2007) and Kozloff (1996).
240
241 *Analysis*
242 We followed Ovaskainen et al. (2017) to construct a hierarchical joint species distribution
243 modelling the relationship between measured environmental variables, spatial distance, species
244 co-occurrences and species distributions using the HMSC package (Guillaume Blanchet et al.
245 2018) in R (version 3.4.2; R Development Core Team 2014). The model comprises two linear
246 predictor terms: one describing fixed effects of environment (9 water quality and 5 biotic
247 variables) and space, and one describing random effects that cannot be attributed to environment
248 or space (Equations 2 & 3 in Ovaskainen et al. 2017). The random-effects linear predictor term
249 describes random variation in individual species distributions as well as covariation for every
250 species pair in the analysis.
251 We used Markov chain Monte Carlo to estimate the model parameters. Species'

252 responses to environmental variables were assumed to follow a multivariate Gaussian
253 distribution. We assumed a Poisson likelihood distribution for species count data and used the
254 same priors as in the examples presented in Ovaskainen et al. (2017). The Markov Chain
255 included 100 000 iterations, a burn-in length of 1000 iterations, and thinning of 100. We
256 confirmed that parameters were well mixed by visually inspecting trace plots. We tested the
257 model's performance by calculating explained deviance (D^2_{adj}) as described in Appendix S1: Eq.
258 S1. D^2_{adj} is comparable to R^2_{adj} in least square regression analysis (Guisan and Zimmermann
259 2000); in this context, it describes the model fit where a D^2_{adj} value of 1 means the model
260 perfectly predicts the observed data. This yielded a D^2_{adj} value for each individual species
261 distribution model, and the mean explained deviance across all species gave a single
262 metacommunity-level value of the model's predictive power.

263 To answer our three main questions about the relative roles of dispersal, environment,
264 and species interactions, we visualized the parametrized model in several ways. We investigated
265 three possible dispersal conditions: dispersal limitation, intermediate dispersal, and dispersal
266 surplus. To investigate dispersal limitation at large spatial scales, we plotted distance-decay of
267 community similarity. To do so we randomly drew 200 pairwise distances between sampling
268 plots, and plotted predicted community similarity against distance. Distance-decay of community
269 similarity could reflect dispersal limitation, or it could reflect differences in environmental
270 conditions with increasing spatial scale. To distinguish these two possibilities, we compared
271 predicted species compositional similarity as a function of both distance and environmental
272 covariates (the full HSMC model), and predicted compositional similarity using an alternative
273 model in which the effect of the environment was removed (all environmental covariates were
274 set to their mean value across all sites; Equation 5 in Ovaskainen et al. 2017). To distinguish

275 between dispersal sufficiency (intermediate) and dispersal surplus (high), we looked for evidence
276 of biodiversity homogenization across sites- a signature of swamping by high dispersal- through
277 visual inspection of our site-by-species matrix. We used estimates of environmental niche
278 filtering strength (as measured by the proportion of deviance explained) as another line of
279 evidence to distinguish intermediate and high dispersal: theory predicts that intermediate
280 dispersal allows species to settle at sites where local environmental conditions are optimal for
281 growth and reproduction, whereas high dispersal overrides this (Mouquet and Loreau 2003).
282 To estimate the strength of environmental niche filtering, we conducted variation
283 partitioning analysis of the fixed and random effects as defined in Ovaskainen et al. (2017) in the
284 HMSC R package (Guillaume Blanchet et al. 2018). This summarized the relative contribution
285 of every abiotic and biotic environmental variable, spatial distance, and random effects to the
286 distribution of each species in the HMSC model; we visualized this in a stacked bar plot. We
287 then estimated the fractions of variation explained by environment only, space only, the shared
288 variation between space and environment, and the residual or unexplained variation in a way
289 similar to Borcard et al. (1992), but using the HMSC model as opposed to constrained
290 ordination. To do so, we estimated three versions of the HMSC model: 1) the original global
291 model which included environmental and spatial variables, site- and region-level random effects,
292 2) environmental variables only with the random effects, and 3) spatial distances only with
293 random effects. From each model, we extracted the total variation explained by environment and
294 space, the variation explained by environment, and the variation explained by space. To
295 determine the shared fraction of variation between environment and space, we multiplied each
296 whole fraction by the calculated community-level D^2_{adj} to reflect the model deviance in our
297 variance partitioning estimates, and followed the equations in Appendix S1: Eq. 2. A Venn

298 diagram illustrating all fractions is shown in the Appendix S1: Fig. 3.

299 To identify species co-occurrence patterns possibly resulting from biotic interactions, we
300 represented modelled pairwise associations in a correlation matrix describing the extent to which
301 species pairs co-occurred more negatively or positively than by random chance, controlling for
302 the effect of environmental covariates. We included only the twenty most abundant species in the
303 main figure, but provide a full species co-occurrence matrix in Appendix S1: Fig. S4. We then
304 conducted hierarchical cluster analysis on sites according to predicted species proportional
305 abundances from the HMSC model using Ward's criterion (Ward 1963). We mapped this
306 dendrogram onto an abundance heatmap of the 20 most abundant species, and colour coded the
307 cells according to the species co-occurrence groupings (groups of species that tended to
308 positively co-occur amongst themselves). A version of this figure with all species is provided in
309 Appendix S1: Fig. S5.

310

311 **Results**

312 *Species abundance and distribution patterns*

313 The aim of this section is to describe basic biodiversity patterns across the seagrass
314 meadows. Specific results aimed at answering our three questions about metacommunity
315 processes follow in the subsequent sections. Seagrass-associated biodiversity varied spatially,
316 both within meadows and among meadows. We counted and identified 39 644 individuals
317 representing at least 58 species across all sites (Table 2). The metacommunity represented
318 multiple phyla, diet types (herbivores, detritivores, suspension feeders, and carnivores), and life
319 history strategies (brooding, broadcast spawning). A full summary of traditional diversity metrics
320 can be found in Appendix S1: Table S1.

321 Several taxa were present at all sites (Appendix S1: Fig. S2). These include the
322 harpacticoid copepod *Porcellidium* sp., bivalves *Saxidomus gigantea* and *Clinocardium nutallii*,
323 snails *Alvania compacta*, *Lacuna variegata* and *Lacuna vincta*, and the tanaid *Leptochelia* sp.
324 Genera *Mytilus* (a mussel) and *Nereis* (a polychaete worm) were also present at all sites, however
325 the number of species represented remains unknown because we were unable to confidently
326 identify these organisms to species. Ten species were present in at least one site in every region:
327 the pycnogonid *Anoplodactylus viridintestinalis,* isopod *Idotea resecata,* gammarid amphipods
328 *Monocorophium insidiosum, Ampithoe valida, Pontogeneia rostrata, Ampithoe dalli, Aoroides*
329 spp*.,* snails *Amphissa columbiana* and *Alia carinata,* and limpet *Lottia pelta*.
330
331 *Dispersal: Distance-decay of community similarity due to spatial distance and environment*
332 In the full HMSC model with latent variables summarizing species' responses to
333 environment and distance between sites, predicted community similarity decreased with
334 increasing distance between meadows (Fig. 2, red points and line). However, this decrease in
335 community similarity with spatial distance disappeared, and community similarity showed a
336 slight increase with distance when the effect of environmental variables was removed from the
337 model (all environmental variables set to their mean value), suggesting that spatial distance alone
338 did not correspond with differences in invertebrate compositional similarity (Fig. 2, blue points
339 and line). The range of predicted similarities was greater at small distances than larger distances,
340 indicating that spatial proximity between sites does not necessarily confer compositional
341 similarity resulting from the exchange of individuals.
342
343 *Environmental niche filtering: variation partitioning*

344 Patterns in abundance and distribution are consistent with weak environmental niche
345 filtering along an abiotic axis, however the importance of environmental conditions varies across
346 species. The relative contribution of all 14 environmental variables, spatial distance and random
347 effects in the HMSC model can be seen in Fig. 3. Out of all the measured environmental
348 variables, the water quality variables (all blue bars in Fig. 3) explained the largest proportion of
349 variation across nearly all species distributions Across all taxa, herbivore food availability
350 (seagrass, algae and detritus biomass) and habitat structure (eelgrass shoot density and Leaf Area
351 Index) had smaller influences on species distributions than abiotic predictors (Fig. 3). The
352 relative contribution of abiotic parameters to species abundance and distribution patterns also
353 varied among species and major taxonomic groups. For instance, site and region membership,
354 food availability and habitat structure generally explained less variation in gastropod
355 distributions than gammarid amphipod distributions. While the mean deviance explained (D^2_{adj})
356 across all species distribution models was 0.29, individual values varied dramatically (0 to 0.82,
357 Table 2), implying high variation in the match between our model and the observed data.
358 Accounting for this, the true fraction of variation explained by environment was 22.4%, space
359 explained -3%, the shared fraction between environment and space was 4%, and the residual
360 fraction of variation was 0.76 (Appendix S1: Fig. S3).
361
362 *Species interactions: Patterns in pairwise species co-occurrences*
363 We identified, post hoc, three main site-level species co-occurrence groupings across all
364 78 samples from 13 meadows and 4 regions after controlling for effects of environmental
365 covariates. The six species in the first group (*Nereis* sp. through *Caprella laeviuscula* in Fig. 4a)
366 henceforth known as the purple group, tended to positively co-occur with each other, and

negatively co-occur with non-members of this group. The second group- henceforth known as the turquoise group- included *Caprella californica* through *Ampithoe valida,* and Harpacticoid 2 through *Lacuna* sp. *Spirorbis* sp. – which had an unusually high abundance of approximately 16 000 individuals at the HL site- did not fall into either category. *Alvania compacta* and *Lacuna* sp. negatively co-occurred with members of the purple group and positively co-occurred with members of the turquoise group, however their co-occurrence values tended to be weaker.

Species interactions: Mapping co-occurrence groupings onto a site by species matrix

Species associated with all three major co-occurrence groupings were present at all sites (Figure 4b), indicating that presences of these species are not mutually exclusive. It is their abundances that tended to negatively co-vary; when species of one assemblage were abundant, species of the other assemblages were less abundant (Figure 4b). Fig. 4b shows clustering of sites according to the identity of the most abundant species by co-occurrence colour grouping. At JB, HL, CB, RA, EB, DC, and DK, members of the blue group tended to be most abundant, whereas purple group members were most abundant at SS, SA, LH, GB and RB. IN was an outlier site, as *Spirorbis* sp. was predicted to vastly outnumber other species. The emergent species assemblages identified in Fig. 4a from the HMSC modeled distributions do not clearly correspond with the spatial distance because the cluster analysis did not group sites by spatial proximity or regional membership (black symbols in Fig. 4b).

Discussion

By applying a new statistical framework, we have gained new insight into the metacommunity processes structuring seagrass-associated biodiversity in coastal British

390 Columbia. We report evidence suggesting that both biotic interactions and environmental
391 conditions have an influence on seagrass meadow invertebrate composition. Spatial patterns of
392 species abundance and distribution suggest regional-scale dispersal patterns such that even
393 distant meadows may host the same species. However, these dispersal rates are clearly not so
394 high as to overwhelm the local meadow scale effects of biotic interactions and environmental
395 conditions. Below, we review these conclusions and the evidence to support them.
396
397 *Seagrass animal communities are well-connected and may experience intermediate dispersal*
398 *rates*
399 Seagrass epifaunal communities appear to be well-connected by dispersal at the present
400 spatial scale and distribution of seagrass habitat along the British Columbia coast. This is true for
401 the seven species that were present at all sites, and the additional ten species that were not
402 present at every site but present in all regions (Appendix S1: Fig. S2). It is noteworthy that these
403 groups had representation from across phyla and life history traits (polychaete worms, gammarid
404 amphipods, snails, bivalves, tanaids), suggesting that no single taxonomic group or dispersal life
405 history strategy had a consistently greater spatial distribution among the sites sampled. However,
406 the specific pathway the organisms travelled to arrive at these sites remains unknown. We used
407 Euclidan distances in our analysis, which preserved the rank order of distances across sites, but
408 actual distances are likely greater due to oceanographic circulation patterns (Kinlan and Gaines
409 2003, Mitarai et al. 2008, Treml et al. 2015). It is unclear whether distant sites share the same
410 species because they are (1) linked by direct dispersal; (2) indirectly linked by dispersal via
411 unsampled "stepping-stone" sites; or (3) were colonized by populations of the same species in a
412 historical dispersal event, but have not seen the exchange of individuals since. Incidences of

413 direct dispersal between the farthest sites (ie. between Haida Gwaii and the Southern Gulf
414 Islands) may be rare, but are not impossible. Seagrass-associated epifauna are generally passive
415 dispersers, with individuals colonizing neighbouring sites either by larval transport in currents or
416 by "rafting" on floating pieces of seagrass, detritus, or macroalgae. Kelp rafts have been
417 observed hosting benthic and epifaunal invertebrates across phyla (echinoderms; peracarids;
418 molluscs; annelids), and are important in maintaining connectivity between coastal ecosystems
419 across 100's of kilometres (Wichmann et al. 2012). Thus, our results suggest that this passive
420 dispersal is sufficient to facilitate connectivity of these sites across the region so that species
421 distributions are not limited by dispersal through isolation by distance.

422 Species in our analysis that were only found at one site or region may be dispersal limited
423 for reasons other than isolation by distance. Those with low site-level abundances (fewer than
424 five individuals detected across all plots from a site) may not disperse in appreciable numbers,
425 and thus are not able to establish populations at all sites as easily as more abundant species. This
426 group included gammarid amphipods *Jassa marmorata*, *Orchomenella recondita,* polychaete
427 worms *Glycinde armigera, Neoamphitrite robusta, Lepidonotus squamatus,* and others
428 (Appendix S1: Fig. S2).

429 We can also conclude that dispersal rates are high enough for several species to be
430 present at most sites, but not so high as to completely overwhelm the effects of environmental
431 differences at the local scale. Thus, dispersal rates are likely intermediate. Co-occurrence
432 patterns indicate that a subset of species was present at all sites, but often at varying abundances.
433 This may be indicative of weak mass effects, which allow these populations to persist even if
434 local conditions are not sufficient for them to persist without immigration (Mouquet and Loreau
435 2003). Metacommunity theory predicts that such weak mass effects are likely to be found

436 whenever dispersal rates are not limiting (Thompson et al. 2017), particularly in organisms that
437 cannot control their own dispersal (Leibold and Chase 2017), such as seagrass-associated
438 epifauna. This may be supported by our result on the contribution of environmental conditions,
439 particularly in ubiquitous species for whom the model fit was poor (e.g.'s *Aoroides* spp.,
440 *Spirorbis* sp., $D^2_{adj} = 0$); the poor model fit may indicate that they may persist sites even if
441 environmental conditions are not optimal, due to sufficient immigration. An alternative
442 explanation is that species distribution models with low D^2_{adj} values indicate species with broader
443 environmental niches, or their abundances along environmental gradients do not follow a
444 Gaussian distribution as assumed in the model. As a result, the HMSC model could not
445 accurately predict their occurrences given local environmental conditions. It is difficult to
446 discern between these possibilities without empirical tests of species niches.
447
448 *Seagrass epifauna show varying degrees of environmental niche filtering*
449 The fact that environmental covariates across space- and not space alone- are associated
450 with differences in community composition may suggest some influence of environmental niche
451 filtering (Fig. 2). The most important environmental axis informing species distributions is the
452 abiotic one, with phosphates, salinity, and dissolved oxygen being the top three parameters by
453 percent variation explained (Fig. 4a). However, the actual amount of variation explained by the
454 environment was small (Appendix S1: Fig. 3), leaving a great deal of unexplained variation in
455 the observed data at the whole-community level. However, in some species for whom our model
456 had high predictive power (including *Ampithoe dalli, Pontogeneia rostrata, Caprella natalensis)*,
457 environmental niche filtering may be important.
458 Species may respond to environmental heterogeneity across the metacommunity in one of

459 four ways. First, the most important abiotic environmental parameters (nitrates, phosphates, sea
460 surface temperature, and dissolved oxygen) may indirectly influence epifaunal presence and
461 abundance via primary productivity levels. This is possible despite the fact that primary biomass
462 explained less variance than the abiotic parameters in our HMSC model (Figure 3). Our measure
463 of primary biomass was based on a measurement at a single time point. But, our abiotic
464 parameters represent a four-year average (Assis et al. 2018) and so may provide a better
465 representation of what the organisms experience over their lifetimes. Second, sea surface
466 temperature, dissolved oxygen, and salinity may also directly influence optimal tolerance ranges.
467 For example, estuarine isopod *Idotea baltica* (a relative of *I. resecata* and *I. montereyensis* in our
468 study) experiences significantly lower survival in prolonged exposure to higher water
469 temperatures and lower salinities than those experienced in their home habitat (Rugiu et al.
470 2018). Third, temperature may influence the metabolic demands of the epifauna (most of which
471 are grazers such as some gammarid amiphopids, *Idotea* spp., *Lacuna* spp.), thereby influencing
472 grazing rates and altering the available primary biomass (O'Connor 2009). Decreased food
473 resources may result in competition, thereby influencing the number of individuals, number of
474 species, or identity of species a seagrass patch can host. It is not easy to determine whether
475 individual species' responses to competitive stress can influence whole-community structure,
476 however doing so may provide key information on how environmental conditions and
477 interspecific interactions interact to influence biodiversity.
478 Environmental characteristics of temperate eelgrass meadows fluctuate with the seasons,
479 likely driving changes in the relative abundance of epifaunal taxa throughout the year
480 (Wlodarska-Kowalczuk et al. 2014, Markel et al. 2017). As a result, the epifaunal
481 metacommunity may not evince these abundances or distributions year-round; sampling several

482 times in one year to capture temporal changes in community structure would give a clearer
483 picture of species' responses to environmental conditions, as well as biotic interactions and
484 dispersal events.
485
486 *Do species co-variance patterns reveal possible biotic processes influencing community*
487 *assembly?*
488 After controlling for effects of space and environment, two main co-occurrence
489 groupings emerged showing antagonistic abundances across sites rather than mutually exclusive
490 presences (Fig. 4b). Stochasticity alone is unlikely to have produced such a strong pattern. While
491 there may be multiple possible explanations for non-random observations in species occurrences,
492 we were able to rule out environmental heterogeneity (Connor and Simberloff 1979) as the co-
493 occurrence values represented pairwise species covariation unexplained by the spatial and
494 environmental covariates. This along with the high residual variation in our variation partitioning
495 result (Appendix S1: Fig. 3) leads us to suggest the potential importance of biotic processes in
496 structuring the epifaunal metacommunity. Several types of interactions may be occurring in the
497 metacommunity; the majority of species in the present study are known to be herbivores or
498 detritivores, and thus may compete for primary biomass. Laboratory experiments have
499 demonstrated that behaviours such as grazing rate and habitat selection in the marine amphipods
500 are altered in the presence of morphologically and functionally similar intrerspecific competitors
501 (Beermann et al. 2018), however it is difficult to empirically test limited food resources result in
502 competition in natural systems. Other species in our study are filter feeders, and thus may not be
503 competing for food resources but possibly space.
504 The community structure of a given site with a certain regional pool and local

environmental conditions may have multiple stable states depending on the arrival order of species and the structure of competitive interactions; this phenomenon is known as priority effects (Waters et al. 2013, Fukami et al. 2016, Ke and Letten 2018) and has been documented in marine fouling communities (Vieira et al. 2018). The fact that we found antagonistic co-occurrence groupings that did not result from space or environment may suggest priority effects (Fig. 4a and 4b). We hypothesize that following the establishment of a new meadow or a disturbance event, the first few species to colonize a seagrass meadow greatly determine the success of subsequent colonizers, regardless of the environmental conditions in the meadow. The high abundance and negative co-occurrence between *Nereis* sp. and *Lacuna* sp. suggests that these species may be key determinants of community structure (Fig. 4b). As an illustrative example, *Nereis* sp. might have been among the first to colonize sites SS, SA, LH, and RB (Fig. 4b), thereby gaining a numerical advantage over *Lacuna* sp. and others. Distibution patterns in the sessile calcifying polychaete *Spirorbis* sp. may also be indicative of priority effects. While it did not appear to strongly negatively or positively co-occur with other species approximately, it dominated other species in abundance at the HL sites. 16 300 individuals were found across the six quadrats, several orders of magnitude higher than its abundance at other sites (Data S1). HL also had the lowest species richness of all 13 sites. Eelgrass shoots there were completely covered by these *Spirorbis* sp., possibly preventing grazers in the community from accessing epiphytic algae or the seagrass itself. The age, colonization history, and disturbance regime of the meadows themselves likely matter if priority effects are an important influence on community assembly. A key piece of information that would confirm the nature of biotic processes is whether species from different co-occurrence groupings compete more strongly with each other than with themselves (Ke and Letten 2018), but this would require an experimental

test.

The positive co-occurrence patterns between certain species may be a result of positive interspecific interactions. An example is *Orchomenella recondita*: a gammarid amphipod found living in the gastrovascular cavity of the anemone *Anthopleura elegans* (Carlton 2007). This species was only recorded at the SS site, and specifically only found in quadrats where *A. elegans* was collected with the seagrass shoots.

A potentially important biotic interaction missed in our analysis is the trophic effect of predators. Field experiments have demonstrated that changes in predation pressure by fish, shorebirds, and predaceous invertebrates can shift seagrass-associated epifaunal assemblages in a matter of weeks (Amundrud et al. 2015; Huang et al. 2015; Lewis & Anderson 2016). Differential predation pressure or composition of predators could also lead to the pattern of diverging community composition that we have witnessed (Guzman et al. 2018). Further study is required to determine the degree to which these seagrasses associated communities are structured by trophic interactions.

Conclusion

Using a new statistical approach to characterizing dispersal, environmental niche filtering, and biotic interactions, we have gained greater insight into the local and regional metacommunity processes driving temperate seagrass epifaunal diversity. Our study also gives a baseline spatial scale (1000 km) for comparing the contribution of these assembly processes across spatial scales and marine systems (Viana and Chase, 2018). We have generated new hypotheses about the relative importance of dispersal, environmental heterogeneity, and biotic interactions in shaping these communities- manipulative experiments and ongoing monitoring

are now needed test and refine these hypotheses. We could test our hypothesis that species sorting is relatively weak by measuring fitness differences along the most important environmental axes in key species identified in this study, or constructing an experiment that allows individuals to disperse to sites where we expect them to be optimally adapted to local abiotic conditions. Given our hypothesis that priority effects play a potential role in structuring these communities, experiments are now required to test whether the composition of seagrass meadows depends on the order of species colonization (Fukami et al. 2016). Testing our hypothesis that these communities are not dispersal limited is more challenging, but could be studied using particle tracking models similar to those used to estimate connectivity between coral reefs via larval dispersal across thousands of kilometres (Treml et al. 2008). A population genetic analysis could also ground-truth the extent and time scale of dispersal by determining whether populations share alleles, or have been isolated for some time. All together, we suggest that a modern metacommunity perspective combined with new advances in our statistical toolbox provide a powerful and relevant framework for studying natural ecosystems.

Our findings are particularly relevant to conservation initiatives that aim to maintain diversity or prevent species loss in seagrass meadows. Specifically, identifying the contribution of dispersal, environmental conditions, and interspecific interactions allows the conservation practitioner to better predict how habitat fragmentation and climate change might influence diversity. Epifaunal invertebrate communities in British Columbia seagrass meadows may be quite resilient, given our findings that environmental conditions make a minimal contribution to species distributions, and several species across phyla and functional traits are consistently present and abundant across a fairly large spatial scale.

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735 **Table 1.** Summary of evidence used to answer questions about metacommunity processes

Question	Analyses	Figure number
(1) Is the metacommunity characterized by dispersal limitation, intermediate dispersal, or high dispersal?	*Dispersal limitation:* Distance-decay of community similarity from HMSC joint species distribution models with and without accounting for environmental similarity	Fig. 2
	Intermediate versus high dispersal: Biodiversity patterns across sites for signatures of high dispersal (compositional homogenization); HMSC model results indicating structured co-occurrence patterns and variation in composition explained by environmental	Fig. 4a, 4b
(2) Do species distribution patterns suggest environmental niche filtering, and if so along which environmental axis?	HMSC model: Variation partitioning of modelled site and region-level fixed and random effects of environmental covariates and calculating predictive power (proportion of deviance) of the fixed effects model	Fig. 3
(3) Do species co-variance patterns suggest possible biotic interactions influencing community assembly?	HMSC model: Correlation matrix of pairwise species co-occurences, after controlling for the effect of space and environment	Fig. 4a & 4b

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739 **Table 2.** Species names, taxonomic groupings, and proportion of deviance (predictive power).

740 Numbers correspond to the axes in Figure 3. The top twenty species with highest predicted

741 abundances according to the HMSC model are bolded.

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Number	Species name	Broad taxonomic group	Adjusted deviance explained for the HMSC model (D^2_{adj})
1	*Alia carinata*	Gastropod (snail)	0.15
2	***Alvania compacta***	**Gastropod (snail)**	**0.4**
3	*Amphissa columbiana*	Gastropod (snail)	0
4	*Crepidula* sp.	Gastropod (snail)	0.64
5	*Euspira lewisii*	Gastropod (snail)	0.46
6	*Harmothoe imbricata*	Gastropod (snail)	0
7	***Lacuna* spp. *(L. variegata and L. vincta)***	**Gastropod (snail)**	**0.45**
8	*Lirularia parcipincta*	Gastropod (snail)	0.46
9	*Lirularia* sp.	Gastropod (snail)	0
10	*Littorina* sp.	Gastropod (snail)	0.5
11	*Margarites pupillus*	Gastropod (snail)	0.45
12	*Lottia pelta*	Gastropod (limpet)	0.53
13	***Clinocardium nuttallii***	**Bivalve**	**0**
14	***Mytilus* sp.**	**Bivalve**	**0.28**
15	*Saxidomus gigantea*	Bivalve	0
16	*Unknown clam 1*	Bivalve	0.68
17	*Unknown clam 2*	Bivalve	0.35
18	*Dorvillea longicornis*	Polychaete	0.52
19	*Exogone sp.*	Polychaete	0.25
20	*Glycinde armigera*	Polychaete	0.05
21	*Lepidonotus squamatus*	Polychaete	0.55
22	*Neoamphitrite robusta*	Polychaete	0.22
23	*Unknown polychaete (Family Oenoidae)*	Polychaete	0.15
24	*Unknown polychaete (Family Opheliidae)*	Polychaete	0.36
25	***Spirorbis* sp.**	**Polychaete**	**0**
26	***Nereis* sp.**	**Polychaete**	**0.55**
27	***Ampithoe dalli***	**Gammarid amphipod**	**0.47**

28	*Ampithoe lacertosa*	Gammarid amphipod	0.34
29	***Ampithoe valida***	**Gammarid amphipod**	**0**
30	***Aoroides* spp.**	**Gammarid amphipod**	**0**
31	*Ceradocus spinicauda*	Gammarid amphipod	0
32	*Grandidierella japonica*	Gammarid amphipod	0
33	*Ischyocerus anguipes*	Gammarid amphipod	0.33
34	*Jassa marmorata*	Gammarid amphipod	0
35	***Monocorophium insidiosum***	**Gammarid amphipod**	**0.23**
36	*Orchomenella recondita*	Gammarid amphipod	0.73
37	***Photis brevipes***	**Gammarid amphipod**	**0**
38	***Pontogeneia rostrata***	**Gammarid amphipod**	**0.65**
39	*Unknown gammarid (Family Hyalidae)*	Gammarid amphipod	0.12
40	*Unknown gammarid (Family Isaeidae)*	Gammarid amphipod	0.10
41	*Unknown gammarid (Family Ischyoceridae)*	Gammarid amphipod	0.24
42	***Caprella californica***	**Caprellid amphipod**	**0.36**
43	***Caprella laeviuscula***	**Caprellid amphipod**	**0.06**
44	***Caprella natalensis***	**Caprellid amphipod**	**0.82**
45	*Cumella vulgaris*	Cumacean	0.36
46	***Leptochelia sp.***	**Tanaid**	**0.49**
47	*Nebalia gerkinae*	Leptostracan	0.39
48	***Porcellidium sp.***	**Copepod**	**0.33**
49	***Harpacticoid 1***	**Copepod**	**0**
50	***Harpacticoid 2***	**Copepod**	**0**
51	*Harpacticoid 3*	Copepod	0.50
52	*Anoplodactylus viridintestinalis*	Pycnogonid	0.01
53	*Idotea montereyensis*	Isopod	0.73
54	***Idotea resecata***	**Isopod**	**0.36**
55	*Munna sp.*	Isopod	0.20
56	*Pugettia producta*	Brachyuran crab	0.36
57	*Pugettia richii*	Brachyuran crab	0.34
58	*Hippolyte californiensis*	Caridean shrimp	0.45

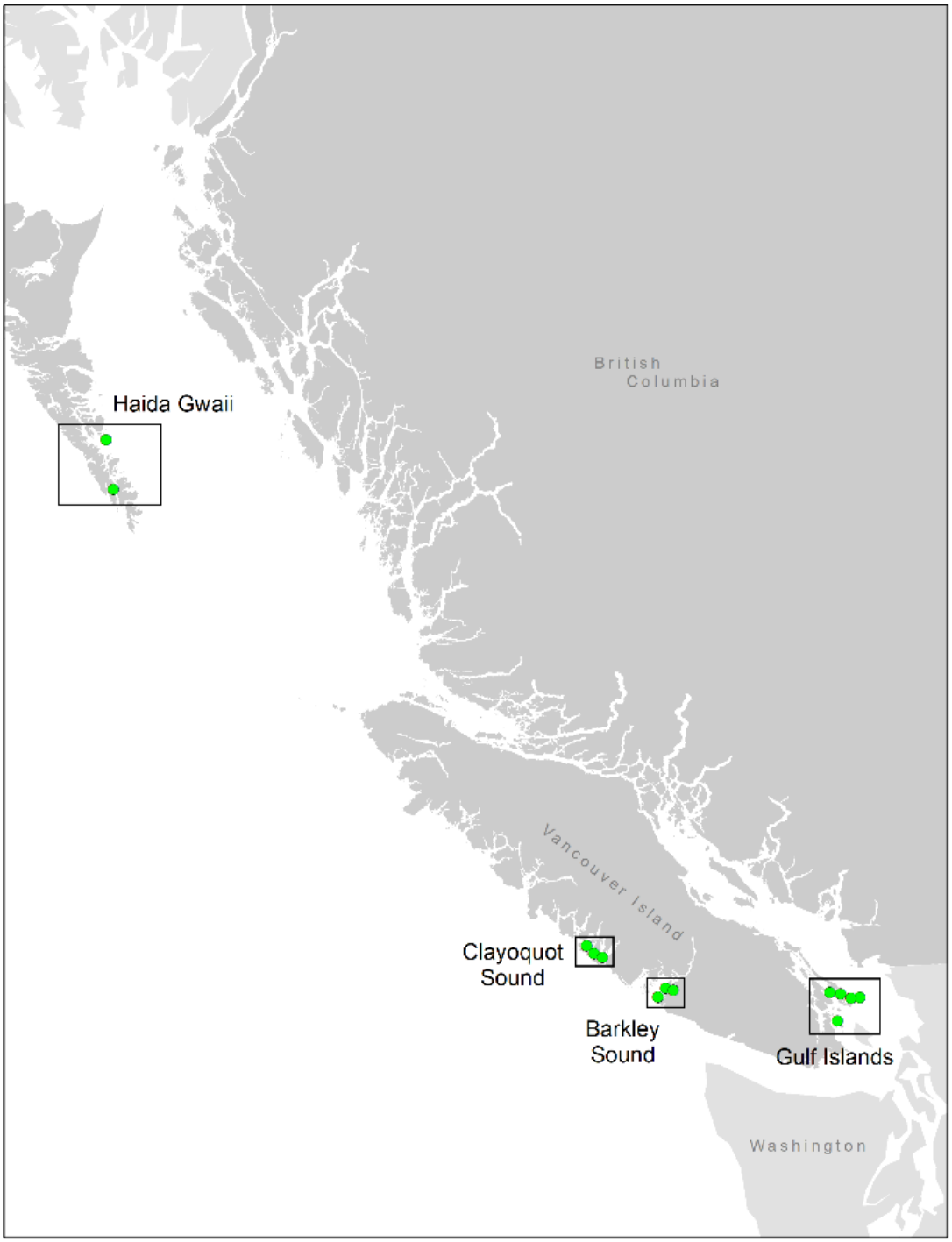

Figure 1. Map of coastal British Columbia showing eelgrass field sites in Haida Gwaii (HL, RA), Clayoquot Sound (DK, EB, IN), Barkley Sound (SA, DC, RB), and the Southern Gulf Islands (GB, JB, CB, LH, SS).

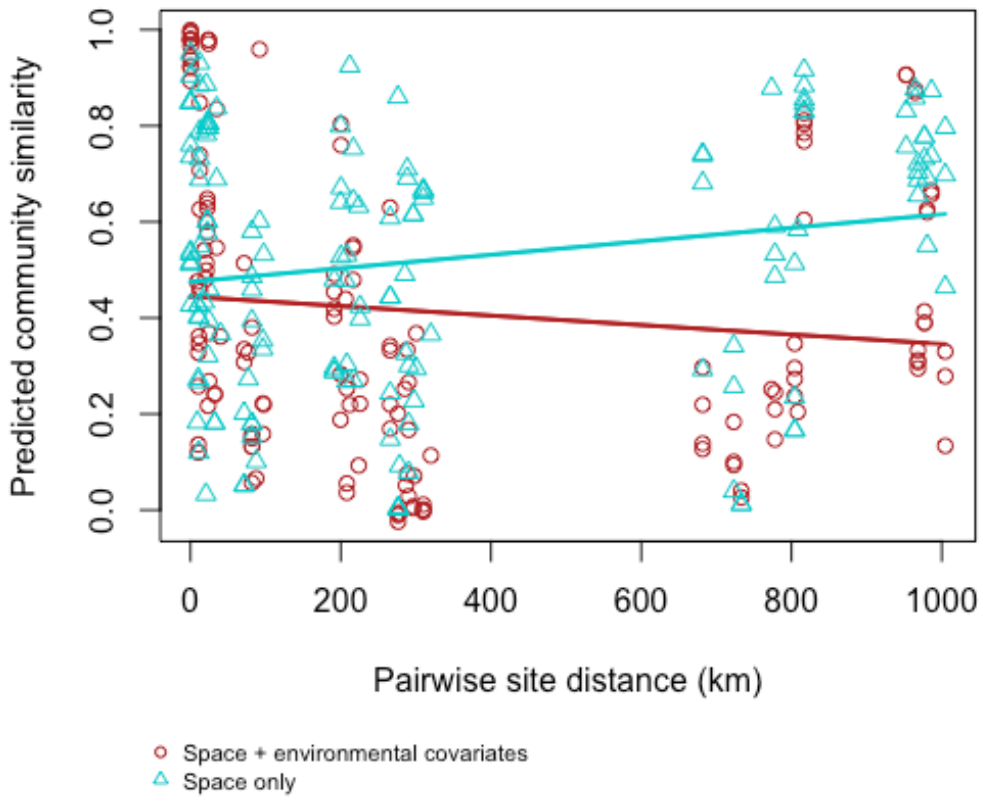

Figure 2. HMSC model predictions of community similarity relative to the spatial distance (Euclidean) between communities. The red circles show similarity predictions based on the full model. The blue triangles show predictions wherein the effect of all environmental parameters (9 water quality and 5 biotic) has been removed (standardized to their mean values), thus showing predicted community similarity as a result of spatial distance only.

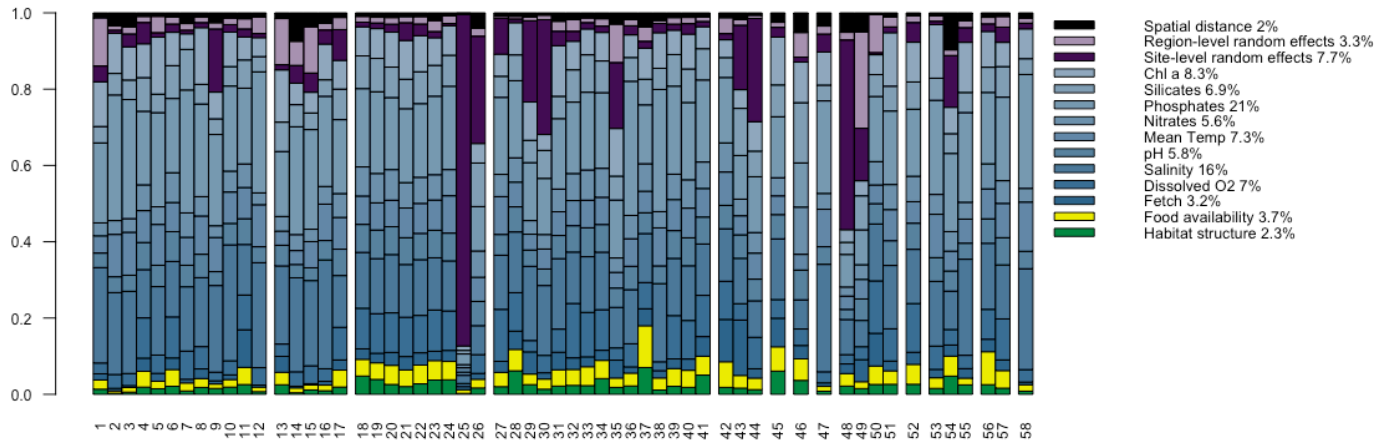

Figure 3. Variance partitioning of fixed (environmental variables, spatial distance) and random effects across all species (numbers correspond to Table 2) in the HMSC model. Purple cells represent site and region-level random effects. Blue cells represent abiotic water quality parameters. Yellow cells represent food availability (sum of variances explained by eelgrass, algae and detritus biomass). Green cells represent habitat structure, which is the sum of variances explained by eelgrass leaf area index and shoot density. Bars are organized according to broad taxonomic groupings as indicated in Table 2. The percentages shown next to the legend labels indicate mean variance explained by that environmental variable across all species. Adjusted deviance explained (D^2_{adj}) for the individual species distribution model fits varied (see Table 2). The mean D^2_{adj} across all species was 0.29.

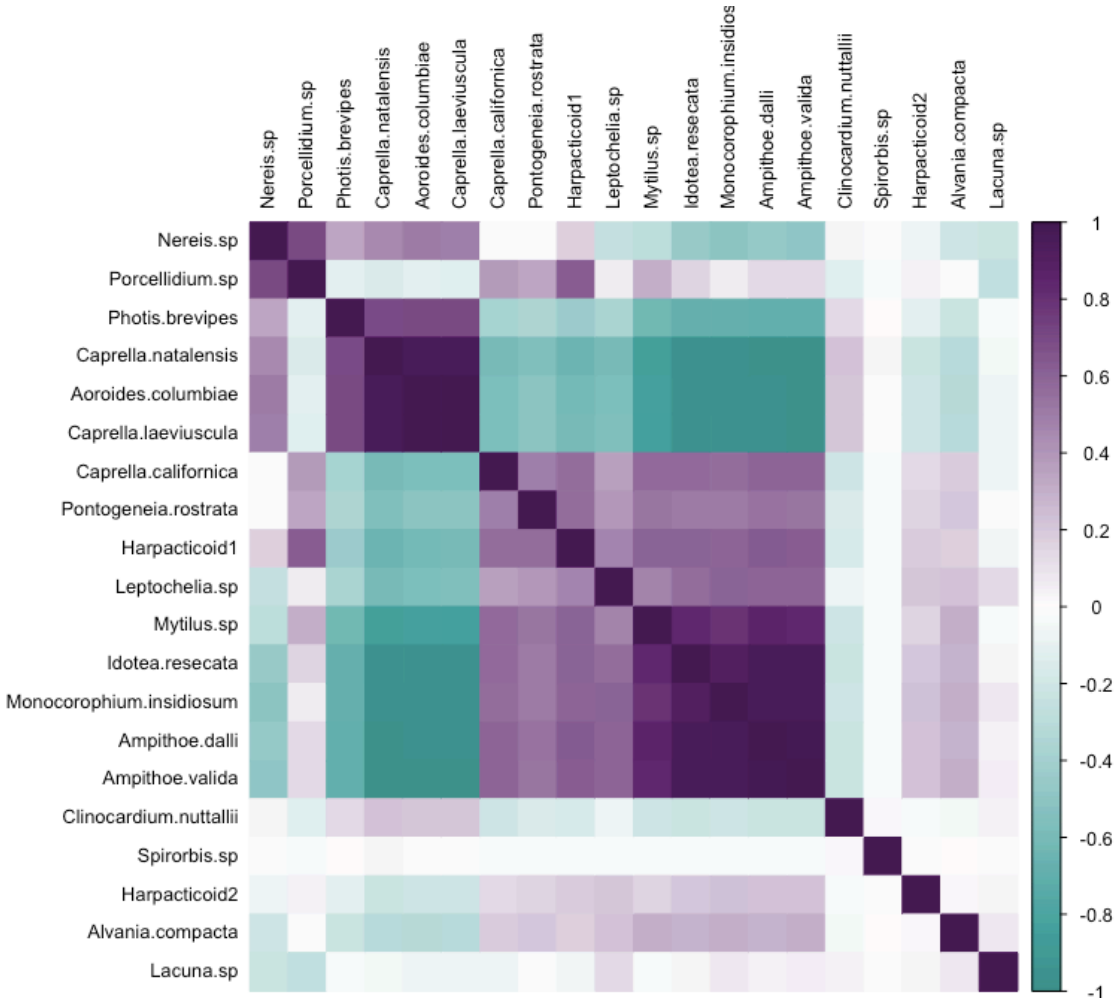

Figure 4a. A correlation plot showing modelled site-level co-occurrence of species pairs in the 20 most abundant species. Purple cells represent positively co-occurring species pairs, and turquoise cells represent negatively co-occurring species pairs. Species names along both axes are ordered according to the output of hierarchical clustering with Ward's criterion on pairwise co-occurrence values. A version of this figure with all 58 species is shown in Appendix S1: Fig. S4.

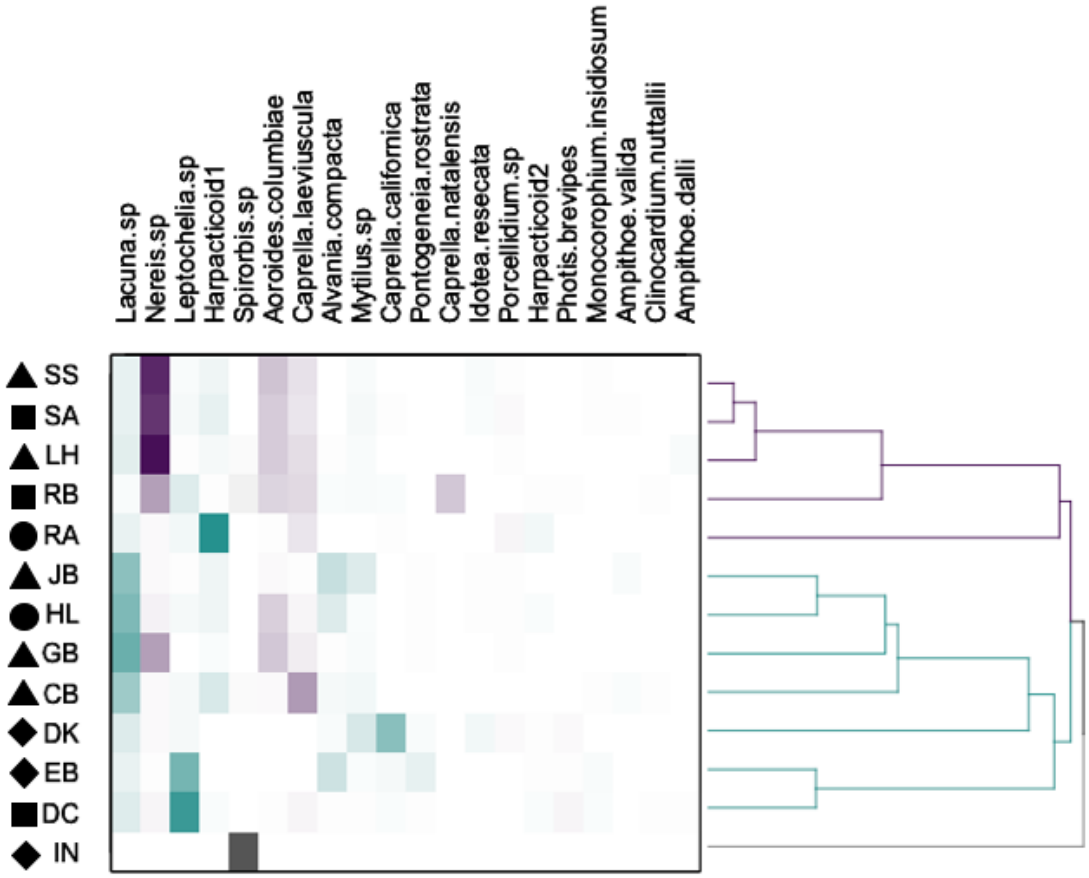

Figure 4b. Heatmap and cluster dendrogram depicting modelled (HMSC) species abundance and compositional similarity across sites. The dendrogram was produced using hierarchical cluster analysis with Ward's criterion on predicted species proportional abundances. The heat map shows the twenty species with the highest predicted mean proportional abundance at the site level, and is ordered from highest to lowest predicted mean proportional abundance. Cell colours correspond to the HMSC co-occurrence groups shown in Fig. 4a: turquoise group, purple group, and grey group. Cell shade strength represents proportional abundance at a given site (darker means higher abundance). The symbols to the left of the site abbreviations indicate region membership; circles show Haida Gwaii sites, squares show Barkley Sound sites, diamonds show Clayoquot Sound sites, and triangles show Southern Gulf Islands sites. A version

of this figure with all 58 species is shown in Appendix S1: Fig. S5.

827 **Appendix S1:** Supporting Information

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830 **Equation S1.** Equations for D^2_{adj} calculations

831 Explained deviance or D^2 (Guisan and Zimmerman 2000) was calculated by the equation:

832

833 $$D^2 = 1 - \text{Residual deviance} / \text{Null deviance}$$

834

835 Where the residual deviance refers to the deviance in predicted species occurrences, and the null
836 deviance refers to deviance in observed species occurrences.

837

838 Adjusted D^2 (Guisan and Zimmerman 2000) was calculated by the equation:

839

840 $$D^2_{adj} = 1-(((n-1)/(n-p-1)*(D^2-1))$$

841

842 Where n is the number of sites (13) in our study, and p is the number of parameters the model
843 estimated (4, Ovaskainen et al. 2017, Supporting Information). Negative D^2_{adj} values (those which
844 had greater residual deviance than null deviance) were set to 0.

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Equation S2. Calculation for type III variation partitioning result

m1 = the fraction of variation explained by all environmental variables in the HMSC model estimated with only environmental variables;

m2 = the fraction of variation by spatial distances in the version of the HMSC model estimated with only spatial distances;

m3 = the global model including both;

Fraction *ab* (pure environment + shared fraction) = D^2_{adj} *m1*

Fraction *bc* (pure space + shared fraction) = D^2_{adj} *m2*

Fraction *abc* (pure environment + shared fraction + pure space) = D^2_{adj} *m3*

Fraction *a* (pure environment) = *abc* - *bc*

Fraction *c* (pure space) = *abc* - *ab*

Fraction *b* (shared fraction) = *ab* + *bc* - *abc*

Fraction *d* (residuals) = 1 - *abc*

Fractions *a* ("Environmental conditions"), *c* ("Spatial distance"), *b* (shared fraction), and *d* ("Residuals") are shown in the Venn diagram in Fig. S3.

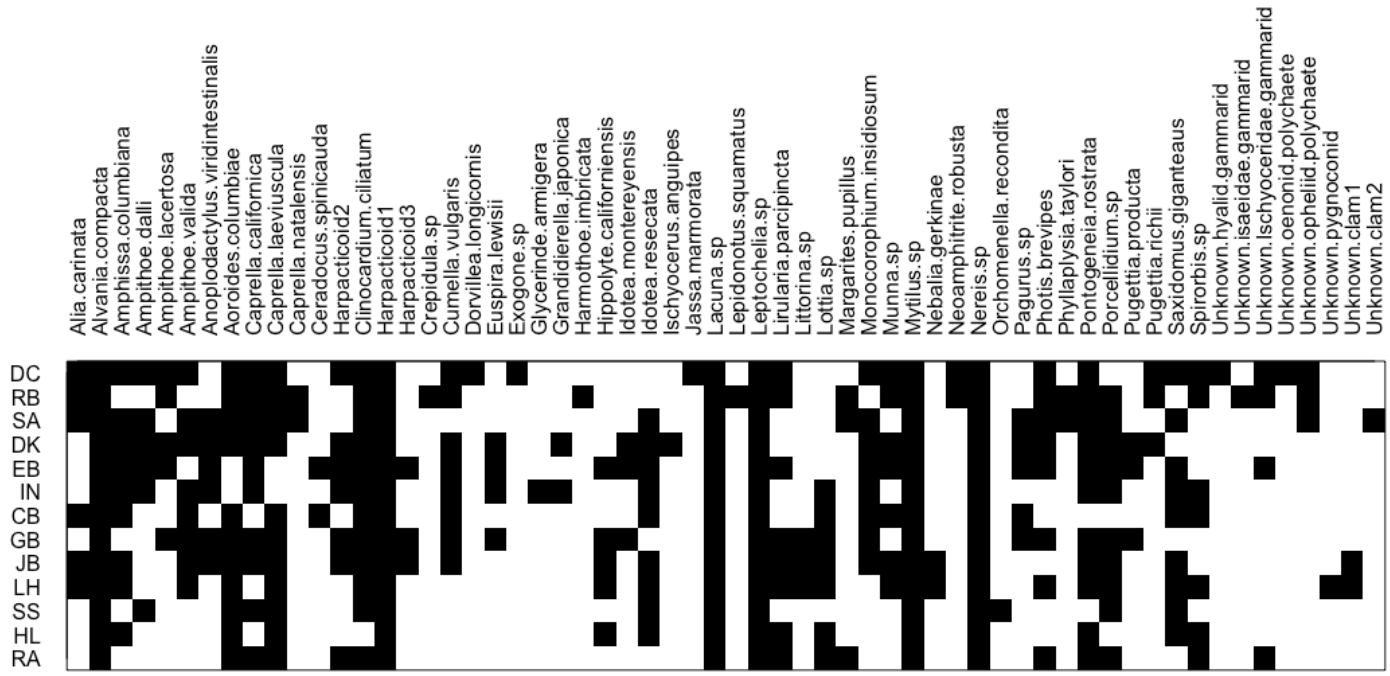

Figure S2. Site-by-species presence-absence matrix of all 58 invertebrate species in the study listed in alphabetical order. Black cells indicate species presences.

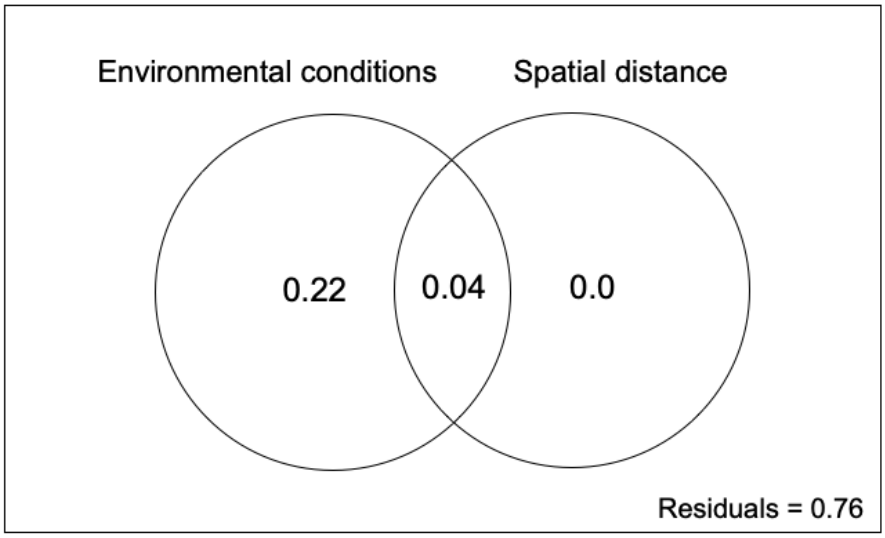

Figure S3. Venn diagram summarizing the fractions of variation explained by environmental covariates only (9 water quality and 5 biotic variables), spatial distance only, and the shared fraction explained by environment and space.

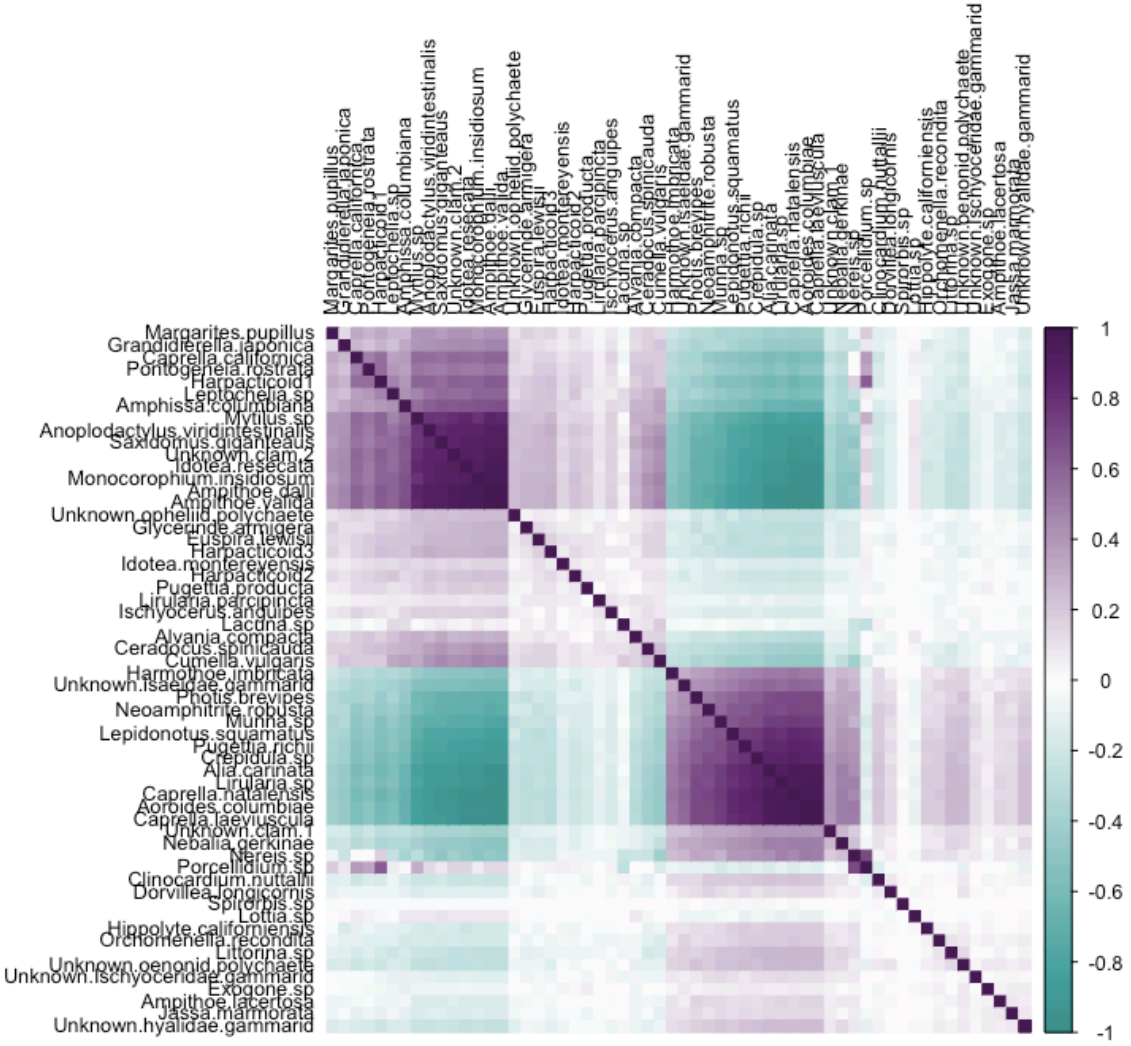

Figure S4. A correlation plot showing modelled site-level co-occurrence of species pairs across all species. Purple cells represent positively co-occurring species pairs, and turquoise cells represent negatively co-occurring species pairs. Species names along both axes are ordered according to the output of hierarchical clustering with Ward's criterion (Ward 1963) on pairwise co-occurrence values. This figure is a supplement to Fig. 4a in the main text.

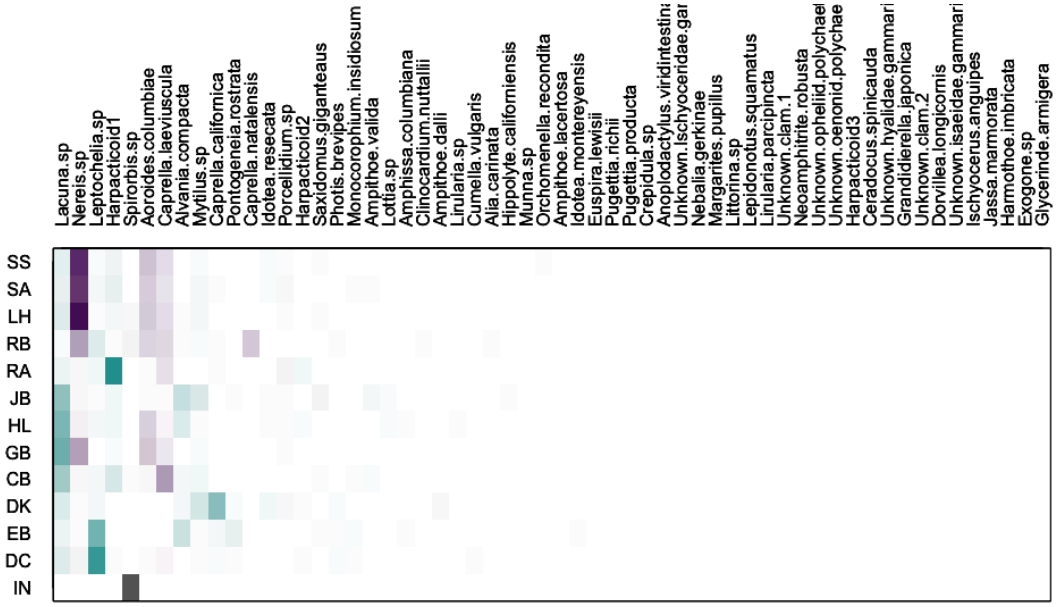

Figure S5. Heat map depicting abundance patterns in all 58 species in the study. Species names are ordered from highest to lowest predicted mean proportional abundance. Cell colours correspond to the co-occurrence groups in Fig. 4b, with turquoise cells representing members of the turquoise assemblage, purple cells indicating members of the purple assemblage, and grey cells indicating species that did not significantly co-occur negatively or positively with other species. Cell shade strength represents proportional abundance at a given site (darker means higher abundance). Most species outside the top twenty most abundant had extremely low predicted proportional abundances owing to their low raw abundances. This figure is a supplement to Fig. 4b in the main text.