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Journal

Proceedings of the Royal Society B, 289(1969)

ISSN

0962-8452

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Publication Date

2022-02-23

DOI

10.1098/rspb.2021.1762

Peer reviewed

1 **The biogeography of community assembly: latitude and predation drive variation in**
2 **community trait distribution in a guild of epifaunal crustaceans**

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139 **Abstract**

140 While considerable evidence exists of biogeographic patterns in the intensity of species
141 interactions, the influence of these patterns on variation in community structure is less clear.
142 Studying how the distributions of traits in communities vary along global gradients can inform
143 how variation in interactions and other factors contribute to the process of community assembly.
144 Using a model selection approach on measures of trait dispersion in crustaceans associated with
145 eelgrass (*Zostera marina*) spanning 30° of latitude in two oceans, we found that dispersion
146 strongly increased with increasing predation and decreasing latitude. Ocean and epiphyte load
147 appeared as secondary predictors; Pacific communities were more overdispersed while Atlantic
148 communities were more clustered, and increasing epiphytes were associated with increased
149 clustering. By examining how species interactions and environmental filters influence
150 community structure across biogeographic regions, we demonstrate how both latitudinal
151 variation in species interactions and historical contingency shape these responses. Community
152 trait distributions have implications for ecosystem stability and functioning, and integrating
153 large-scale observations of environmental filters, species interactions, and traits can help us
154 predict how communities may respond to environmental change.

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170 **Introduction**

171 Community ecology is fundamentally concerned with the assembly and maintenance of
172 diversity across space and time. Key to this endeavour is the idea that the composition of a local
173 community is the result of multiple ecological filters selecting species from a regional pool (Poff
174 1997; Thompson *et al.* 2020). Different kinds of filters apply different kinds of selective
175 pressures on the species pool, and because species' traits are what allow them to pass through
176 filters, studying the distribution of traits within the community can help us understand how these
177 filters act on the species pool as a whole. Strong environmental filters (i.e., abiotic filters *sensu*
178 Kraft *et al.* 2015) such as climate are thought to act on large spatial scales to constrain trait
179 diversity such that species are more alike (clustered) in traits that respond to these factors than
180 we would expect under a purely random assembly process (Webb *et al.* 2002; Cavender-Bares *et*
181 *al.* 2009; Starko *et al.* 2020; Thompson *et al.* 2020). Biotic filters, such as competition, then act
182 at smaller spatial scales to enhance or reduce trait diversity among species with broadly similar
183 abiotic tolerances, depending on which traits are affected (Mayfield & Levine 2010). When traits
184 related to the acquisition of distinct resources are considered, competition for these resources
185 drives the distribution of traits to be wider than expected by chance (overdispersed) as there are
186 multiple resource niche optima that can be occupied (Webb *et al.* 2002; Cavender-Bares *et al.*
187 2009; Pavoine & Bonsall 2011). In contrast, competition for a single, dominant limiting resource
188 can also act as a filter, selecting for traits related to acquiring this resource to converge around an
189 optimal value, because species deviating from the optimum are otherwise competitively
190 excluded. All else being equal, as richness increases, an increase in trait dispersion may point to
191 stronger stabilising mechanisms and limiting similarity, while a decrease in trait dispersion can
192 suggest stronger equalising mechanisms promoting unstable coexistence. (Chesson 2000;
193 Mayfield & Levine 2010).

194 Despite well-known geographic patterns in the strength of both biotic interactions and
195 environmental filters (Schemske *et al.* 2009; Reynolds *et al.* 2018; Longo *et al.* 2019; Zvereva &
196 Kozlov 2021), few studies have examined the global-scale consequences of geographic variation
197 in these filters for community trait distributions (Ford & Roberts 2018, Skeels *et al.* 2020). In
198 particular, intense predation, competition, and mutualistic interactions at lower latitudes
199 (Freestone & Osman 2011; Longo *et al.* 2019; Zvereva & Kozlov 2021), may lead to the
200 predominance of biotic interactions over environmental filters in structuring low-latitude

201 communities. This may cause stronger trait clustering near the poles that shifts towards more
202 overdispersed communities at lower latitudes. On the other hand, selection for tolerance of
203 extreme heat conditions could also cause trait clustering at low latitudes. Finally, patterns in
204 community structure along latitudinal gradients could be dominated by idiosyncratic and
205 historically-contingent effects of predators, prey, competitors, and mutualists that vary among
206 biogeographic provinces (Sanford & Bertness 2009; Mittelbach & Schemske 2015; Ford &
207 Roberts 2019; Whalen *et al.* 2020). Local abiotic factors, habitat complexity, assemblage
208 composition, and adaptation to these local factors could further obscure broader geographic
209 patterns of community assembly (Sanford & Bertness 2009; Lavender *et al.* 2017), stressing the
210 importance of assessing patterns across multiple independent species pools. For example, the
211 effects of regional gradients in predation may be overshadowed by local increases in habitat
212 complexity, which can decrease predation pressure (Reynolds *et al.* 2018) and increase trait
213 dispersion as species assort into disparate microhabitat niches (Best & Stachowicz 2014).
214 Understanding trait distributions and their drivers should provide insight into the likely responses
215 of communities to environmental fluctuations or perturbations in the same way that
216 understanding the diversity of traits within a population can inform us on its evolutionary
217 potential (Cadotte *et al.* 2011; Rumm *et al.* 2018).

218 Here we examine geographic patterns in the trait distribution of epifaunal invertebrates
219 living on eelgrass throughout the northern hemisphere to assess the extent and causes of
220 geographic variation in the drivers of the assembly of these communities. Eelgrass (*Zostera*
221 *marina*) is the world's most widespread species of temperate seagrass, a marine angiosperm
222 found throughout the Northern Hemisphere from 30° to 67° N latitude in both the Atlantic and
223 Pacific Oceans (den Hartog 1970; Green & Short 2003). Much of the animal community in
224 eelgrass beds is made up of invertebrate mesograzers that primarily feed on the epiphytic
225 microalgae fouling the seagrass blades (Valentine & Duffy 2006). Competition for food and
226 microhabitat space occurs among mesograzers, and can significantly affect community
227 composition (Edgar 1990; Best *et al.* 2013; Best & Stachowicz 2014; Amundrud *et al.* 2015).
228 Peracarid crustaceans (amphipods, isopods, and tanaids) are the most widespread, abundant, and
229 species-rich mesograzer taxon in these eelgrass beds, and they experience elevated predation in
230 low-latitude eelgrass beds (Reynolds *et al.* 2018) which could either cause clustering of
231 communities around traits that increase resistance or tolerance to predation, or cause dispersion

232 of communities due to competition for enemy-free space. *Z. marina*'s wide range across latitudes
233 provides an opportunity to assess the role of gradients of ecological filters on global scales
234 without the confounding influence of changing habitat type. We predicted: (1) that trait
235 dispersion would increase with decreasing latitude as species interactions become more intense
236 and (2) that abiotic filters would be strongest and result in clustering at higher latitudes and
237 where biotic interactions are weak. While marine systems often show non-linear variation in
238 species diversity and interaction strength with latitude (peaking at mid-latitudes; Chaudhary *et*
239 *al.* 2017; Whalen *et al.* 2020), our predictions are reasonable within the range of latitudes
240 occupied by eelgrass (~30-70°N). We test these predictions in separate ocean basins with largely
241 unique fauna, allowing us to assess whether the unique histories of these zoogeographic
242 provinces result in different patterns and drivers of trait distribution in each ocean basin (Roy *et*
243 *al.* 2009; Dyer & Forister 2019).

244 **Methods**

245 *Study design and sample collection.* Between May and September 2014, we sampled 42
246 sites across the range of *Z. marina*, spanning 30 degrees of latitude along both coasts of Eurasia
247 and North America (30.4°N to 60.1°N; Fig. 1) to characterize the biological and physical
248 structure of eelgrass beds using standardized measurements. We implemented a hierarchical
249 sampling design consisting of two oceans (Atlantic and Pacific), each with two coasts (east and
250 west), each with 6-14 sites, each with 20 plots, for a total of 840 plots in 42 sites sampled as part
251 of the *Zostera* Experimental Network (ZEN; Fig. S1). Plots were 1 m² and spaced 2 m apart at
252 each site. Along each coastline, sites were separated by 4.9 km (Virginia, USA) to 485.4 km
253 (Washington State, USA) of water.

254 *Assessing eelgrass habitat characteristics.* We sampled eelgrass biomass by haphazardly
255 placing and pushing a 20-cm diameter core tube 20 cm into the sediment within each plot. We
256 gathered all shoots rooted within the core bottom area into the core tube to ensure that no shoots
257 were cut off during sampling. We then removed the shoots from the sediment, transferred the
258 core contents into a mesh bag. In the lab, we rinsed the core contents, removed fouling algae and
259 sediment from the eelgrass tissue, and separated above- and belowground biomass by cutting the
260 plant above the rhizome. In addition to eelgrass, we also removed all of the macroalgae from the
261 plot. All eelgrass and macroalgal tissue was dried to a constant weight at 60°C and weighed.

262 From five haphazardly collected eelgrass shoots per plot, we also collected 3-cm lengths of
263 tissue from a healthy, unfouled inner leaf and processed these samples for tissue nitrogen using a
264 CHN analyser (Thermo Fisher Scientific Inc., Waltham, MA, USA).

265 We quantified eelgrass habitat structure at the plot level by measuring shoot density and
266 canopy height. We estimated shoot density by counting the number of shoots emerging within a
267 20-cm diameter ring placed haphazardly in the plot. In plots where density was particularly low
268 (less than 50 shoots m⁻², about 5% of plots), we counted all of the shoots in the plot. We
269 measured canopy height by haphazardly collecting five shoots from each plot and measuring
270 their length from the tip of the longest leaf to the leaf sheath.

271 We sampled epiphyte load on the eelgrass blades by selecting four shoots from each plot
272 and removing them from the substrate either by gently uprooting or clipping at the meristem and
273 placing them in a plastic bag on ice for transport. In the lab, we scraped both sides of all the
274 leaves with a glass slide to remove fouling material, which was then filtered, transferred to an
275 aluminium pan, dried to a constant weight at 60°C, and weighed.

276 *Measuring predation intensity.* Predation intensity was quantified by tethering locally-
277 collected prey (“gammarid” amphipods) in each plot for 24 hours. These data and methods are
278 reported in detail in Reynolds et al. (2018). Briefly, each individual amphipod was glued to a 10-
279 cm piece of monofilament line 0.133 mm in diameter (Berkley Fireline™, Spirit Lake, IA, USA)
280 tied to a transparent acrylic stake anchored in the sediment, so that it could swim freely in the
281 water column and cling to adjacent eelgrass blades. After 24 hours, we removed the stakes and
282 scored prey as present (uneaten) or absent (eaten); partially-consumed prey were considered
283 eaten, and moulted prey were excluded from analyses. Site-level predation was calculated by
284 averaging scores across plots.

285 *Abiotic environmental variables.* To characterize the abiotic environment experienced by
286 epifauna across the range of eelgrass, we measured in-situ temperature and salinity at each site at
287 the time of sampling. To characterize the overall abiotic environment of each site, we also
288 retrieved estimates of annual mean sea surface temperature (SST), photosynthetically active
289 radiation (PAR), and surface chlorophyll A (Chl a) from the surrounding region, available in the
290 Bio-ORACLE data set (Tyberghein *et al.* 2012). These data were taken from monthly readings of
291 the Aqua-MODIS and SeaWiFS satellites at a 9.6 km² spatial resolution from 2002 to 2009. We
292 used the raster package in R v. 3.6.3 (Hijmans & Etten 2020; R Development Core Team 2021)

293 to extract the annual mean SST, SST range, PAR, and Chl a from all cells within 10 km of each
294 site, and averaged these cell-level estimates to generate site-level predictors. Other water quality
295 parameters, including dissolved nitrate and other nutrients, were spatially interpolated based on
296 surface measurements in the World Ocean Database 2009 (Garcia *et al.* 2010).

297 *Epifaunal community composition.* To sample the macrofauna associated with the
298 eelgrass blades, we carefully placed an open-mouthed fine-mesh drawstring bag (500 μm mesh,
299 18 cm diameter) over a clump of shoots in the centre of the plot so that the mouth of the bag was
300 flush with the sediment surface. We then cut the shoots where they emerged from the sediment
301 and quickly closed the drawstring to capture the shoots and associated animals. The shoots were
302 transferred to the lab on ice, rinsed and hand-inspected to dislodge the epifauna, which were then
303 passed through a 1-mm sieve and ultimately transferred into 70% ethanol. Epifauna were then
304 identified to the lowest possible taxonomic level (typically species). Epifaunal abundance was
305 standardized by the aboveground biomass of the eelgrass sample from which they were
306 collected.

307 We scored all peracarids (amphipods, isopods, and tanaids) for a series of traits based on
308 information available in the literature, including body size, fecundity, body shape, living habit,
309 motility, bioturbation, and diet components (Table 1, Appendix 1 for literature). Due to a paucity
310 of data on intraspecific trait variation for most species, literature values were assumed to be
311 representative for all individuals in our study. For subsequent analyses, we categorized each of
312 these traits as related to microhabitat or dietary niche; we also performed analyses with all traits
313 ungrouped. While we acknowledge that these broad categories may overlap, we elected to sort
314 traits into these categories because they represent two potential components of trait dispersion
315 exhibited by peracarids in field studies and laboratory experiments (Best *et al.* 2013; Best &
316 Stachowicz 2014). Correlations among traits were generally weak, save for strong positive
317 relationships between eating live seagrass tissue and macroalgae, detritivory and consuming
318 seagrass detritus, and suspension feeding and bioturbation (Fig. S2).

319 *Characterizing community dispersion.* For all the peracarid species observed in our
320 dataset, we used the trait dataset to generate three matrices of Gower distances between species:
321 one of all traits, one for diet traits, and one for microhabitat traits using the FD package in R
322 (Laliberté *et al.* 2014). Using subsets of these matrices for communities at the site level (summed
323 across 20 plots at each site, $n = 42$), we measured the trait distance between species as the Mean

324 Pairwise Distance (MPD) and Mean Nearest Taxon Distance (MNTD) for each set of traits
325 (Webb *et al.* 2002; Sessa *et al.* 2018). MPD is the average of the trait distances between all pairs
326 of species found within a given sample unit (site), while MNTD is the average minimum
327 distance between species pairs in a site. Both are independent of species richness, but the two
328 metrics can behave differently depending on the clustering of species in trait space within a
329 sample (Sessa *et al.* 2018).

330 To determine whether the observed species traits in each community differed from those
331 expected by chance, we standardized MPD and MNTD against null distributions generated
332 according to two permutation algorithms. The first, independent swap, is a semi-constrained
333 model that randomly re-assembles the sample-by-species community matrix while maintaining
334 the species richness of each sample and the presence/absence of each species across samples.
335 The second, tip shuffle, is a more constrained model that directly shuffles the traits of the species
336 in the community while maintaining richness, occurrence, and trait distances between
337 community members, effectively moving the tip labels on a trait dendrogram. Imposing more
338 constraints on permutation controls for patterns in the data that are not directly relevant to the
339 question at hand, such as species richness, occurrence, or identity, ultimately reducing type I
340 error rates (Swenson 2014). Because of the relatively low overlap in species pools across the
341 range of our study, comparing the results relative to both types of models can be informative of
342 the importance of species identity in these types of permutations, and also facilitate comparison
343 with other studies in which the independent swap algorithm has been used together with less
344 constrained permutations (e.g., Best and Stachowicz 2014). These permutations were each
345 completed 999 times for each community, and null distributions of MPD and MNTD were
346 generated based on values calculated from randomized communities.

347 We examined the effect of the species pool on community dispersion, using varying
348 degrees of constraint on the matrix and trait dendrogram used to generate null distributions. To
349 make comparisons among sites, we permuted within the global species pool (all sites) and ocean-
350 level Atlantic and Pacific species pools. Using a global pool in our permutations is appropriate
351 because while all species were not present in all regions, there were no traits that were exclusive
352 to any region (Fig. S2).

353 Each observed value of community trait distance was then compared to the corresponding
354 null distribution by calculating the standard effect size (SES_{MPD} or SES_{MNTD}). A positive value of

355 SES indicates that the observed community trait distance (as measured by MPD or MNTD) is
356 greater than the null mean, meaning that community members are more dissimilar than expected
357 under a random draw (overdispersion), while a negative SES indicates that trait distance is less
358 than the null mean, meaning that community members are more similar to each other than
359 expected under a random draw (clustering). MPD, MNTD, null distributions and SES values
360 were calculated using the picante package in R (Kembel *et al.* 2010).

361 *Data analysis.* Two distance metrics (MPD and MNTD), two permutation algorithms
362 (independent swap and tip shuffle), three species pools (global, Pacific, and Atlantic), and three
363 trait sets (all, diet, and microhabitat) totalled 36 sets of SES values. However due to missing diet
364 data for some species, we were unable to calculate diet SES_{MNTD} with the tip shuffle algorithm,
365 leaving us with a total of 33 sets. For each distance metric, algorithm, species pool, and trait set,
366 SES values were used as response variables in a set of 16 linear models incorporating latitude,
367 ocean, continental margin (east vs. west), in-situ temperature and salinity, annual mean and
368 range of SST, total crustacean abundance and median crustacean size, epifaunal and peracarid
369 richness, macroalgal biomass, average predation intensity, epiphyte load, Chl a, PAR, water
370 column nitrate, mean leaf nitrogen content, and two axes of eelgrass habitat structure as derived
371 from a principal component analysis incorporating shoot density, leaf sheath width and length,
372 longest leaf length, and aboveground biomass (PC1 and 2, Fig. S4) as predictor variables, as well
373 as select interactions between them (Table 2). Predictors were log-, square-root-, or arcsin-
374 transformed where appropriate to conform to a normal distribution based on Shapiro-Wilk
375 normality tests and visual examinations of histograms. Collinearity of predictors was accounted
376 for using variance inflation factors (VIF) for variables in composite models using the car
377 package in R (Fox & Weisberg 2019). Predictors with a VIF greater than five were removed
378 from composite models. We also examined the effects of predictors on the SES of individual
379 traits to understand what traits may drive the patterns we see across environmental gradients
380 (Appendix 2).

381 We ranked these initial hypothesis-driven models of SES using AICc scores (MuMIn
382 package; Bartoń 2020), and then incorporated predictors from the three lowest-scoring models of
383 each set into a set of composite models to examine the combined effects of multiple predictor
384 types. We then used backwards elimination to select the lowest-scoring model from these

385 composite models. Where two models had a ΔAICc less than 3 units, we selected the model with
386 the fewest parameters for interpretation.

387 **Results**

388 Peracarid assemblages at Pacific sites had greater trait dispersion than Atlantic sites, and
389 dispersion increased with increasing predation and decreasing latitude, though there were some
390 differences among the two oceans that we outline below. Across our sites, we found a total of
391 105 species, 55 of which were found in the Atlantic, and 60 of which were found in the Pacific,
392 with 10 species found in both oceans. There were 15 species in the Northwest Pacific, 48 species
393 in the Northeast Pacific, 36 species in the Northwest Atlantic, and 24 species in the Northeast
394 Atlantic (Fig. S3). The patterns and predictors of trait dispersion were robust across SES metrics
395 and permutation algorithms (Table S1; Fig. S5); here we present and interpret the results of
396 model selection on SES_{MNTD} calculated using the tip shuffle algorithm, with exceptions
397 presented where relevant.

398 *Dispersion of traits by ocean basin.* Of the set of all traits examined, communities at
399 Atlantic sites were on average clustered ($\text{SES} < 0$) relative to the global null, particularly for
400 body size and living habit (Fig. A2-2) – species clustered around a mean body size of 14.09 mm
401 (47.5% smaller than the mean Pacific body size), and most were free-living. Communities at
402 Pacific sites were overdispersed ($\text{SES} > 0$) on average relative to the global null (Fig. 2, Table
403 S1, Table S2). This pattern held for both metrics and null models but was significant only for
404 SES_{MPD} (SES_{MPD} independent swap $t_{38.097} = 2.43$, $p = 0.020$; SES_{MPD} tip shuffle $t_{38.242} = 2.31$, $p =$
405 0.027 ; two-sample t tests). Within the global pool, the separate calculations of SES using
406 microhabitat and feeding traits showed a similar pattern; for microhabitat traits, Pacific
407 communities were more overdispersed and Atlantic communities more clustered (SES_{MNTD} tip
408 shuffle $t_{35.654} = 3.64$, $p = 0.00086$; Fig. 2).

409 *Correlates of among-site variation in trait dispersion.* Predation intensity, latitude,
410 epiphyte load, and ocean basin (within the global species pool) were the strongest and most
411 consistent predictors of SES across all species pools and all trait sets (Table S1, Fig. S5). In-situ
412 temperature, bed characteristics, epifaunal richness, continental margin, nitrate, and salinity also
413 appeared occasionally (less than 30% of models) across the best models of SES. Mean annual
414 sea surface temperature, epifaunal richness, salinity, nitrate, in-situ temperature, and crustacean
415 abundance also varied significantly with latitude (Fig. S8).

416 In all of the best models, peracarid communities at sites with higher predation intensity
417 had more overdispersed traits, whereas those with less intense predation had more clustered traits
418 relative to a random draw from the species pool (Fig. 3a, Table S1, Fig. S5a-c). Predation
419 (removal of amphipod baits) varied from 20% in Quebec to 100% in Sweden, San Francisco
420 Bay, Ireland, Korea, and British Columbia; the average predation rate was significantly greater in
421 the Pacific than in the Atlantic Ocean (Table S3, Fig. S7, S8), but this did not translate to a
422 difference in the effect of predation on dispersion across the two basins when permuting within
423 the global pool ($p = 0.48$; Fig. 3a). Across the three species pools, the predation effect was
424 stronger on average when permuting within the Pacific than the Atlantic or global pools, (Fig.
425 S5a), and strongest in models of the dispersion of all traits together (Fig. S5b).

426 As predicted, trait dispersion decreased with increasing latitude in the best models (global
427 species pool, microhabitat traits); communities became more clustered at higher latitude, while
428 communities toward the equatorward edge of *Z. marina*'s range were more overdispersed (Fig.
429 3b, Fig. S5d-f). These latitude effects were stronger in the Pacific Ocean than in the Atlantic
430 ($F_{1,38} = 7.95$, $p = 0.0076$; Fig. 3b) although they did not appear in the top models when
431 permuting within the Pacific species pool (Fig. S5d); the best model including latitude was 1.3
432 AICc units better than the top model, but it was not selected as the top model because of the
433 small difference in AICc score and greater number of parameters. Like predation, the latitude
434 effect was strongest in models including all traits together (Fig. S5e).

435 Communities were more clustered (more negative SES) at sites with high epiphyte loads,
436 but this effect was most obvious in the Atlantic species pool when only microhabitat traits were
437 considered (Fig. 3c; Fig. S5g-h). There was rarely an effect of epiphyte load on SES when using
438 other species pools (Fig. S5g, Table S1) and never for diet traits (Fig. S5h).

439 Discussion

440 Using a global dataset of eelgrass-associated peracarid crustaceans, we found a strong
441 increase in community trait dispersion with decreasing latitude and increasing predation (Fig. 3a,
442 b). Latitudinal clines in different ecological filters have been well-characterized in a wide variety
443 of systems (Schemske *et al.* 2009; Reynolds *et al.* 2018; Zvereva & Kozlov 2021), particularly
444 temperature and the strength of species interactions (Schemske *et al.* 2009; Longo *et al.* 2019;
445 Zvereva & Kozlov 2021), both of which decrease at high latitudes. Stronger biotic interactions,
446 in particular stabilizing interactions (*sensu* Chesson 2000), at lower latitudes may select for an

447 overdispersed community (Webb *et al.* 2002; Mayfield & Levine 2010; Pavoine & Bonsall
448 2011), while stronger abiotic filters (or relatively weaker biotic filters) at either end of range (e.g.
449 cold at the poleward edge or hot at the equatorward edge) could select for a clustered community
450 (Webb *et al.* 2002; Cavender-Bares *et al.* 2009; Kraft *et al.* 2015). We found similar total
451 numbers of species in the two oceans (Fig. S3) given similar sampling effort, and all traits were
452 found in both oceans, so the differences we observe among oceans are not simply the result of
453 different diversities in the underlying species pool.

454 Several lines of evidence point to the relatively greater effect of biotic interactions over
455 temperature in structuring our communities. First, temperature rarely appeared as a significant
456 factor in our best models (Fig. 3d, Table S1). Second, latitudinal clines in dispersion were more
457 dependent on ocean basin than continental margins, which differ significantly in their
458 temperature gradients (western side of oceans are warmer at an equivalent latitude; Fig. 3b;
459 Reynolds *et al.* 2018). Third, predation in this system decreases with latitude, as it does in many
460 others (Reynolds *et al.* 2018; Longo *et al.* 2019; Zvereva & Kozlov 2021). Fourth, we observed
461 greater dispersion in living habit, motility, and macroalgae consumption at lower latitudes (Fig.
462 A2-1b-d), all of which can be reasonably linked to stabilizing competition for food or enemy-
463 free space. Finally, for some traits (body size, fecundity), we would expect clustering at both
464 ends of a thermal gradient, but around different optima: large-bodied and highly fecund
465 peracarids at cool sites, and small-bodied peracarids that produce fewer eggs at warm sites
466 (Sainte-Marie 1991; Jaramillo *et al.* 2017). However, in ectotherms like peracarids, decreases in
467 temperature at higher latitudes are less likely to be strong drivers of community structure than
468 increases in temperature at lower latitudes as a result of asymmetrical performance curves
469 (Martin & Huey 2008; Vasseur *et al.* 2014). While we saw that high-latitude sites tended to have
470 species with high fecundity (65 to <135 eggs per brood; part of a general trend for clustered sites
471 to have high or very high fecundity; Fig. A2-1a), we saw no similar trend towards clustering at
472 low latitudes around low fecundity values or any other traits.

473 The decline in trait dispersion with latitude was significantly greater in the Pacific than
474 the Atlantic. This difference in latitudinal clines and trait dispersion more generally between the
475 two ocean basins (Fig. 2, Fig. 3b) may be in part due to differences in these assemblages'
476 biogeographic and evolutionary histories (Mittelbach & Schemske 2015). First, glaciation in the
477 north Atlantic during the last Ice Age means that many of the areas in which eelgrass now occurs

478 would have been colonized after glaciers retreated (Vermeij 1991; Olsen *et al.* 2004), leaving
479 less time for in-situ adaptation and specialization that might lead to increased trait dispersion
480 (Cavender-Bares *et al.* 2009). Similarly, given *Z. marina*'s origin in the Pacific and more recent
481 Pleistocene expansion into the Atlantic (Olsen *et al.* 2004), we might also generally expect
482 Atlantic species to have colonized eelgrass from other Atlantic-native habitats, perhaps
483 predisposing them to be less overdispersed in their traits as they cluster around a single mean.
484 Consistent with this, we found that species in Atlantic sites were clustered around a smaller mean
485 body size, which may be selected for by the denser eelgrass habitat in the Atlantic (Fig. S4, Fig.
486 A2-2a; (Bartholomew *et al.* 2000). Finally, gastropod relative abundance increases with latitude,
487 and gastropods are a more abundant and speciose component of the epifaunal community in the
488 north Atlantic than in the Pacific (Gross *et al.* unpublished). Competition with gastropods for
489 epiphytes or other shared resources may push the peracarids there into a more constrained area of
490 trait space, leading to the clustering we observed.

491 The precise impacts of these and other historical factors are difficult to quantify but may
492 be further investigated with analyses of phylogenetic dispersion or more detailed studies of trait
493 distributions in the regional species pool (Denelle *et al.* 2019; Skeels *et al.* 2020). However, we
494 currently lack a phylogeny of peracarids with sufficient resolution and taxon sampling with
495 which to evaluate underlying differences in phylogenetic diversity between the two ocean basins.
496 We do note that richness of species, genera and families did not vary substantially between the
497 ocean basins (Fig. S3).

498 One of the most striking results of our study was the positive effect of predation intensity
499 on community dispersion among sites that was consistent in both oceans (Fig. 3a); peracarid
500 species were more dissimilar in their traits than expected by chance in sites with high predation
501 intensity. This effect appeared across trait sets, species pools, dispersion metrics and methods
502 (Table S1), although we rarely saw this signal at the level of individual traits (Table A2-1, Fig.
503 A2-3). Changes in predator community structure, predation intensity, or both could lead to an
504 increase in competition for predator-free space, an ecological selective filter that may result in
505 overdispersion, particularly with respect to microhabitat and predator avoidance traits (Best &
506 Stachowicz 2014). Herbivorous arthropods in both marine and terrestrial systems are known to
507 select their microhabitat niches based largely on their effectiveness as shelter from predators
508 rather than the availability or quality of food (Bernays & Graham 1988; Duffy & Hay 1991;

509 Lasley-Rasher *et al.* 2011). Consequently, competition for enemy-free space can be an important
510 factor structuring communities. Alternatively, predation could affect trait dispersion by reducing
511 competition (Pianka 1966; Amundrud *et al.* 2015), but we would expect this to lead to an
512 increase in dispersion from strongly clustered ($SES < 0$) to random communities ($SES = 0$) as
513 stabilizing competition lessened, rather than the observed shift from clustered to overdispersed
514 ($SES > 0$, Fig. 3a, Fig. S5b).

515 Latitudinal patterns of species interactions are now broadly appreciated (Schemske *et al.*
516 2009; Freestone & Osman 2011; Reynolds *et al.* 2018; Longo *et al.* 2019; Whalen *et al.* 2020;
517 Zvereva & Kozlov 2021), but rarely are these results explicitly connected to variation in the
518 structure of communities. By examining both how species interactions and environmental drivers
519 vary within a single habitat type across a broad geographic gradient, we demonstrate an
520 important role for latitudinal variation in species interactions in driving patterns of community
521 assembly. Diversity in important traits can increase the completeness with which epiphytes are
522 removed, leading to increased seagrass growth (Duffy *et al.* 2003), an effect that is strongest in
523 the presence of predators (Duffy *et al.* 2005). More generally, trait clustering and dispersion have
524 implications for redundancy, stability, and ecosystem functioning (Cavender-Bares *et al.* 2009;
525 Cadotte *et al.* 2011; Leibold *et al.* 2017). For instance, communities may be less resilient to
526 environmental change if they are clustered by environmental filters (Cadotte *et al.* 2011, Rumm
527 *et al.* 2018). Clustering that occurs as a result of equalizing mechanisms (*sensu* Chesson 2000)
528 can weaken the relationship between diversity and ecosystem functioning, or certain ecosystem
529 functions may be enhanced in communities with overdispersed effect traits, especially if
530 diversity-function relationships arise through complementarity (Leibold *et al.* 2017; Thompson
531 *et al.* 2020). Thus, historical contingency and broad-scale ecological drivers may play an
532 important role in constraining not only the assembly of local communities, but the resulting trait
533 diversity can affect the functioning of the entire ecosystem. This approach, if applied broadly,
534 offers the potential for developing a predictive understanding of how entire communities respond
535 to environmental change.

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678
 679 **Acknowledgements**

680 We thank the many lab and field assistants that participated in this research and whose
 681 contributions of time and effort were invaluable for making this project happen. The manuscript
 682 was improved with comments from SP Lawler, ED Sanford, SY Strauss, and two anonymous
 683 referees. This research was funded by National Science Foundation grants to JED, JJS, and KAH
 684 (NSF-OCE 1336206, OCE 1336905, and OCE 1336741). CB was funded by the Åbo Akademi
 685 University Foundation. This manuscript was prepared as a chapter for CPG’s doctoral
 686 dissertation.

687
 688 **Tables**

689 Table 1. Traits used in analyses of ZEN peracarid communities. Full citations, as well as sources
 690 for individual species traits, are listed in Appendix 1.

Trait	Type	Values	Category	Interpretation	Citations
Maximum fecundity (number of eggs)	Ordered categorical	Very low (0 to <18), Low (18 to <31), Medium (31 to <65), High (65 to <135), Very high (>135)	Neither	Competitive ability, population resilience, population density	Sainte-Marie 1991, Best and Stachowicz 2013, Lefcheck and Duffy 2015, Ashford <i>et al.</i> 2018
Maximum adult length	Continuous	2-50 mm	Microhabitat	Susceptibility to predators, ability to occupy physical space	Sainte-Marie 1991, Best and Stachowicz 2013, Lefcheck and Duffy 2015, Ashford <i>et al.</i> 2018
Body shape	Categorical	Laterally compressed, Dorsoventrally compressed, Vermiform	Microhabitat	Ability to occupy physical space, palatability	Lefcheck and Duffy 2015
Living habit	Categorical	Free, Parasite/direct commensal, Tube/burrow dweller	Microhabitat	Degree of substrate association, substrate type, population density	Best and Stachowicz 2013, Ashford <i>et al.</i> 2018
Motility	Categorical	Swimmer, Crawler	Microhabitat	Susceptibility to predators, dispersal ability, degree of substrate association	Lefcheck and Duffy 2015, Ashford <i>et al.</i> 2018
Bioturbator?	Binary		Microhabitat	Degree of substrate association, substrate type	Ashford <i>et al.</i> 2018

Microalgae feeding	Binary	Diet		
Macroalgae feeding	Binary	Diet		
Seagrass feeding	Binary	Diet		
Seagrass detritus feeding	Binary	Diet	Dietary niche partitioning	Duffy and Harvilicz 2001, Best and Stachowicz 2012, 2013
Suspension feeding	Binary	Diet		
Detritivory, deposit feeding	Binary	Diet		
Carnivory, parasitism, scavenging	Binary	Diet		

691

692 Table 2. A priori models used to analyse site-level SES values. These 16 models were separately

693 applied to 33 sets of SES values for different trait distance metrics, permutation algorithms,

694 species pools, and trait sets, for a total of 528 models.

Model name	Predictors				
Biogeography 1	Latitude				
Biogeography 2	Latitude	Continental Margin	Ocean		
Biogeography 3	Latitude	Continental Margin	Latitude × Continental Margin		
Biogeography 4	Latitude	Continental Margin	Ocean	Latitude × Continental Margin	
Biogeography 5	Latitude	Continental Margin	Ocean	Latitude × Continental Margin	Latitude × Ocean
Abiotic Environment	in-situ Temperature	in-situ Salinity	Mean Leaf % N		
Temperature Regime 1	Mean SST				
Temperature Regime 2	SST Range				
Temperature Regime 3	Mean SST	SST Range	Mean SST × SST Range		
Community	log(Mean Standard Total Crustacean Abundance)	Median Crustacean Size			
Total Biodiversity	log(Site Epifaunal Richness)				
Peracarid Biodiversity	log(Site Peracarid Richness)				
Habitat	PC1	PC2	log(Macroalgal Biomass + 1)		
Predation	arcsin(Mean Amphipod Predation)				
Resource 1	log(Mean Epiphyte load)	log(Mean Chl a)			
Resource 2	$\sqrt{\text{NO}_2}$	Mean PAR			

695

696 Figure legends

697 Figure 1. *Zostera* Experimental Network (ZEN) sites used in our analyses. Sites spanned 30° of

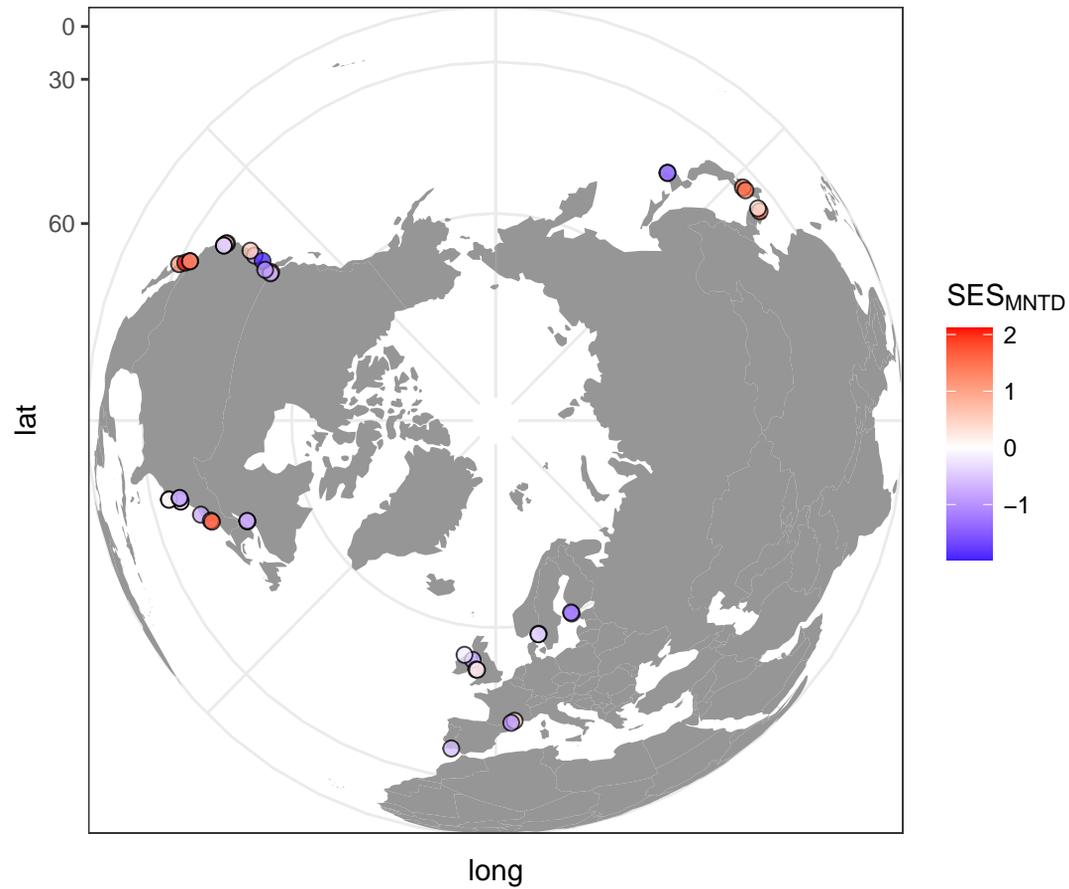
698 latitude on the Pacific and Atlantic coasts of North America and Eurasia, including the

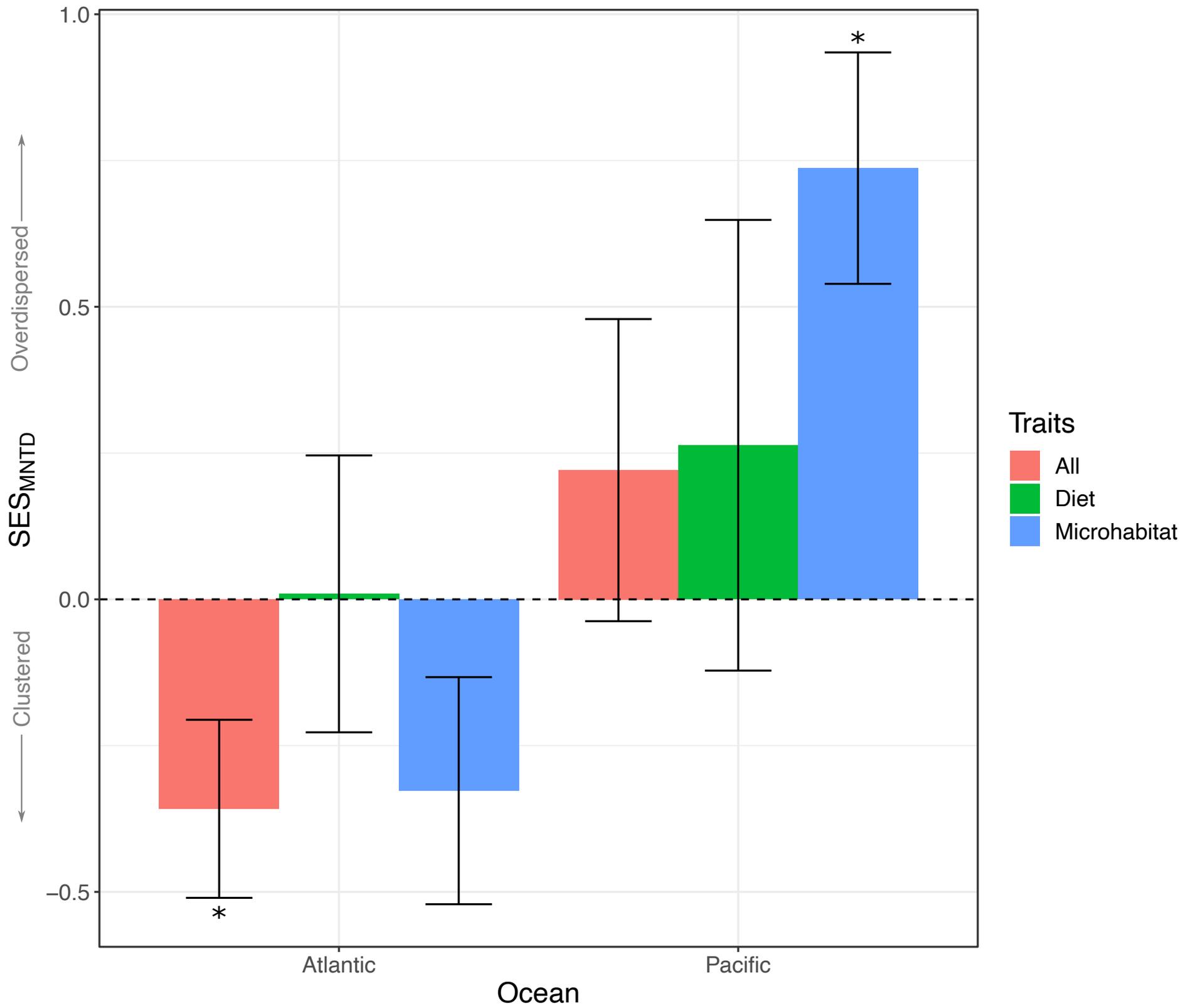
699 Baltic and Mediterranean seas, covering most of the range of *Zostera marina* (eelgrass).
700 Colours indicate trait dispersion (SES_{MNTD} calculated using the tip shuffle algorithm);
701 positive values of SES_{MNTD} indicate greater dispersion in traits than expected from a
702 random draw from the global species pool, whereas negative values of SES_{MNTD} indicate
703 clustering in traits relative to a random draw. See Fig. S1 for more detailed information
704 about site locations.

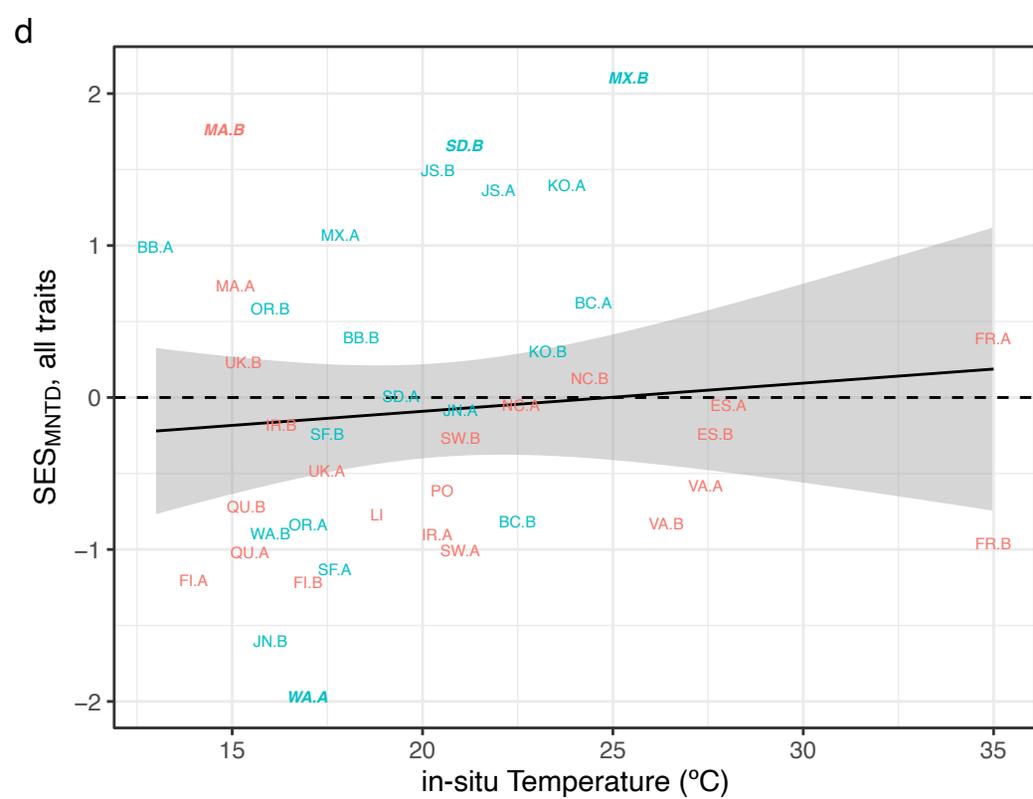
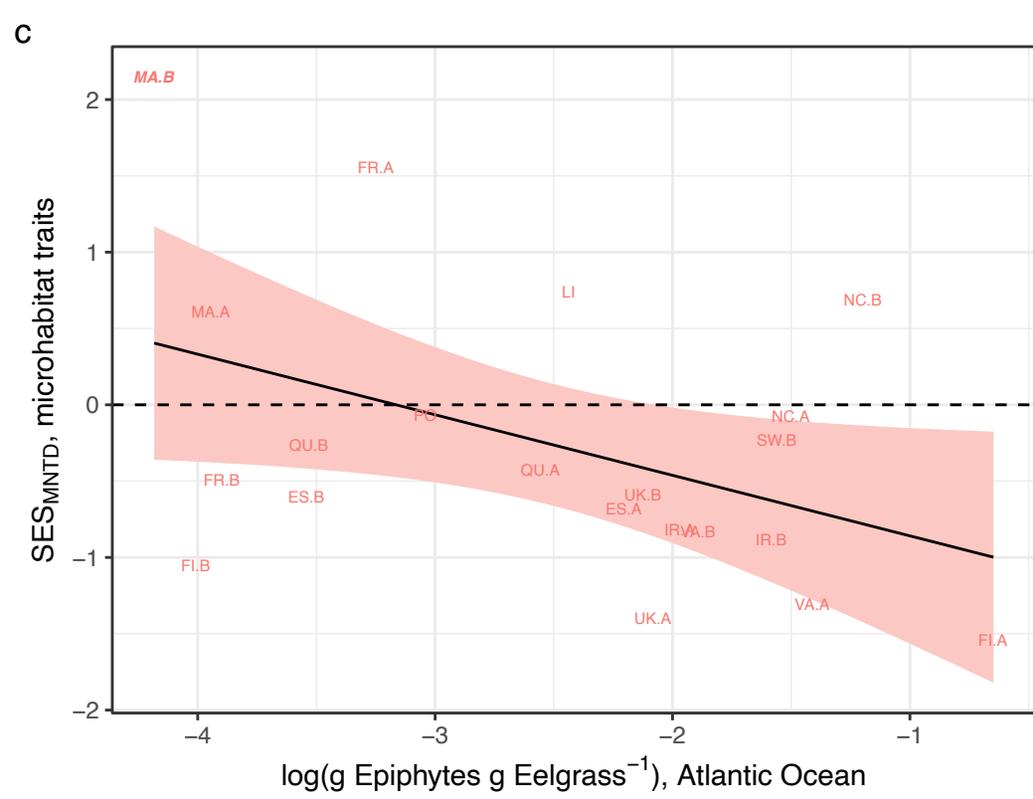
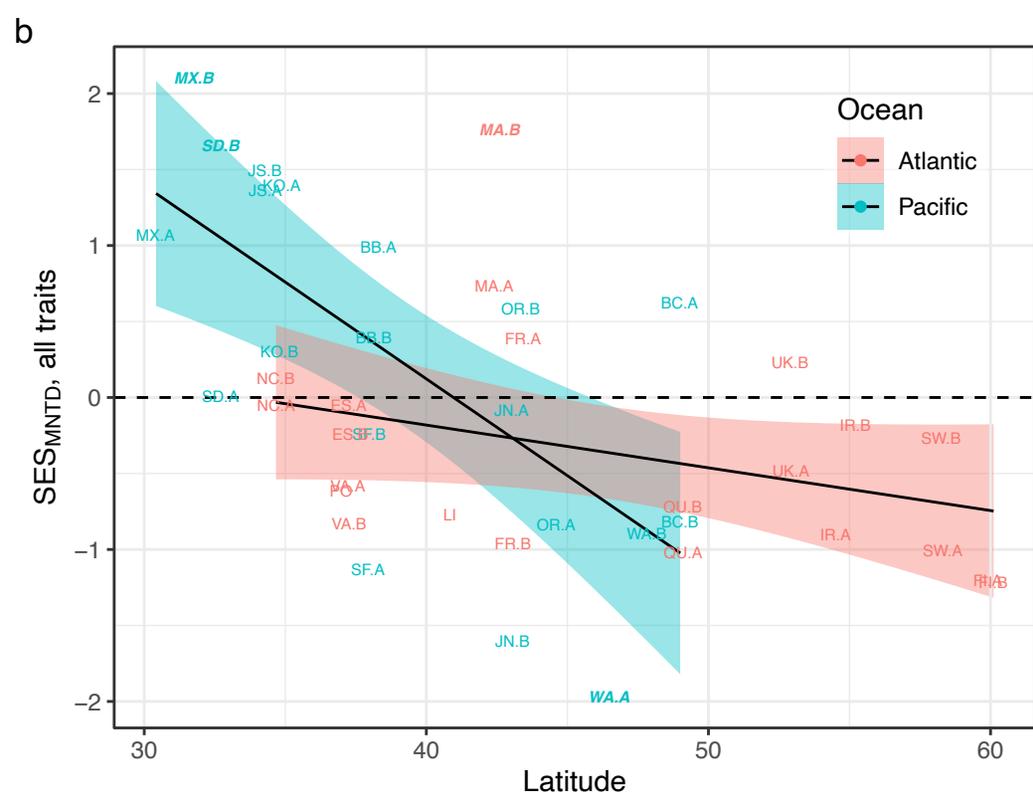
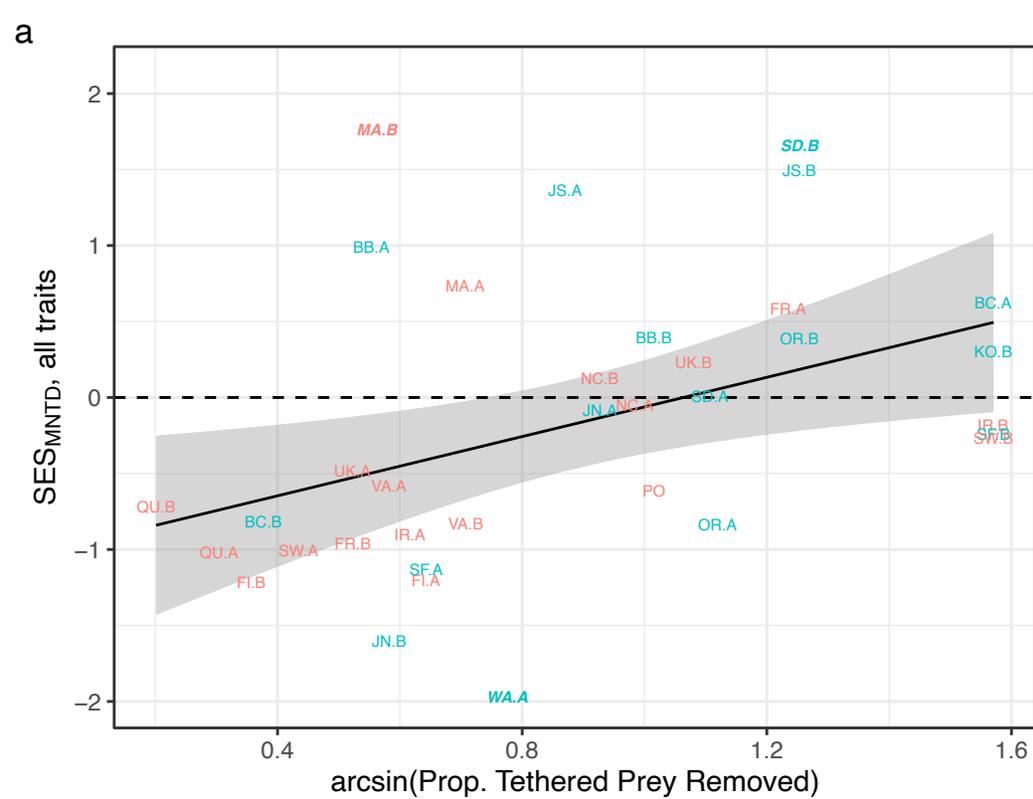
705 Figure 2. Trait dispersion (SES_{MNTD}) in eelgrass-associated peracarid crustacean communities
706 across trait sets. In general, communities at sites in the Pacific Ocean were more
707 overdispersed, while communities at Atlantic sites were less dispersed than expected. The
708 dashed horizontal line represents an SES_{MNTD} value of 0, indicating random assembly.
709 Asterisks indicate means significantly different from zero (two-tailed one-sample t tests;
710 see table S2); error bars represent standard errors. Figure shows SES_{MNTD} calculated
711 according to the Tip Shuffle permutation algorithm; results were comparable across
712 permutation algorithms and SES values.

713 Figure 3. The effects of predation (a), latitude (b), epiphyte load (c), and in-situ temperature (d)
714 on trait dispersion (SES_{MNTD} using the tip shuffle algorithm) in univariate analyses. In all
715 of the best models of dispersion, sites with higher predation intensity had more
716 overdispersed communities, while those with lower predation intensity had more
717 clustered communities (a; $R^2 = 0.15$, $p = 0.012$). In the best models that had a non-zero
718 latitude effect, sites at lower latitudes had more overdispersed communities, while those
719 at higher latitudes had more clustered communities. This effect was stronger in the
720 Pacific than the Atlantic species pool (b; $R^2 = 0.36$, interaction $p = 0.0076$). In the best
721 models with a non-zero epiphyte effect, sites where eelgrass had lower epiphyte density
722 had more overdispersed communities, while sites with more heavily fouled blades had
723 clustered communities (c; plot shows SES_{MNTD} for microhabitat traits in the Atlantic
724 species pool; $R^2 = 0.15$, $p = 0.046$). In-situ temperature appeared only sporadically across
725 permutations and dispersion metrics, and was not significant for total trait dispersion (R^2
726 $= 0.0094$, $p = 0.54$). The dashed horizontal line represents an SES value of 0, indicating
727 random assembly; sites in bold italics are those for which SES is significantly different
728 from 0 at $\alpha = 0.05$. See Fig. S1 for an explanation of site codes.

729







Supplemental tables and figures

Table S1. Top models of trait dispersion (SES) selected by backwards elimination by AICc scores. Models highlighted in grey are discussed in the main text. (table uploaded in separate Excel document).

Table S2. Results of t-tests comparing average SES values within ocean basins to zero. SES values are calculated relative to the global species pool; p values in bold represent significance at an α level of 0.05.

Ocean	Metric	Permutation Algorithm	Trait Set	Mean SES	t	df	p
Pacific	MPD	Independent Swap	All	0.393	2.27	19	0.0352
			Microhabitat	0.404	2.41	19	0.0261
			Diet	0.415	1.66	19	0.114
		Tip Shuffle	All	0.363	2.12	19	0.0479
			Microhabitat	0.412	2.86	19	0.0101
			Diet	0.381	1.56	19	0.135
	MNTD	Independent Swap	All	0.155	0.589	19	0.563
			Microhabitat	0.686	3.48	19	0.00254
			Diet	-0.0449	-0.155	17	0.879
		Tip Shuffle	All	0.221	0.855	19	0.403
			Microhabitat	0.737	3.73	19	0.00143
			Diet	0.263	0.684	14	0.505
Atlantic	MPD	Independent Swap	All	-0.156	-1.07	21	0.295
			Microhabitat	-0.0959	-0.518	21	0.61
			Diet	-0.0998	-0.532	20	0.601
		Tip Shuffle	All	-0.699	-4.23	21	0.000375
			Microhabitat	-0.505	-2.55	21	0.0185
			Diet	-0.382	-2.06	20	0.0531
	MNTD	Independent Swap	All	-0.364	-2.4	21	0.026
			Microhabitat	-0.314	-1.74	21	0.0974
			Diet	-0.272	-1.77	19	0.0935
		Tip Shuffle	All	-0.358	-2.35	21	0.0285
			Microhabitat	-0.3327	-1.69	21	0.011
			Diet	0.00933	0.0394	14	0.9691

Table S3. Average predation rate and epiphyte load across ocean basins. Values in the first two rows are mean \pm standard deviation. Values in the third row represent the results of two-sample t-tests on untransformed (predation) and log-transformed (epiphytes) data across oceans.

Ocean	Prop. Tethered Prey Removed	g Epiphytes g Eelgrass ⁻¹
Pacific	0.80 \pm 0.20	0.30 \pm 0.31
Atlantic	0.64 \pm 0.24	0.13 \pm 0.12
Difference	t = 2.18 p = 0.037	t = 1.13 p = 0.27

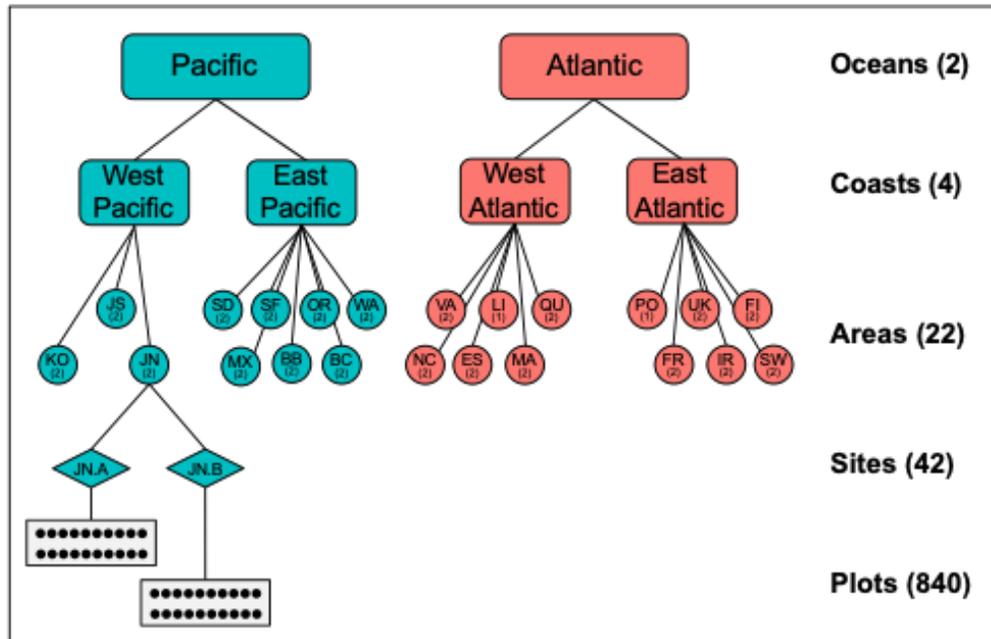


Figure S1. Hierarchical design of the ZEN 2014 seagrass ecosystem survey. Sites are nested in one of 22 areas: KO = South Korea; JS = southern Japan (Seto Inland Sea); JN = northern Japan (Hokkaido); SD = San Diego Bay, US; MX = Mexico (Pacific Baja California); SF = San Francisco Bay, US; BB = Bodega and Tomales Bays, US; OR = Oregon, US, BC = British Columbia, Canada; WA = Washington State, US; NC = North Carolina (Back Sound), US; VA = York River, Virginia, US; ES = Virginia Eastern Shore, US; LI = Long Island, US; MA = Massachusetts, US; QU = Quebec (St. Lawrence Estuary), Canada; PO = Algarve, Portugal; FR = Mediterranean France; UK = Wales, UK; IR = Ireland; FI = Archipelago Sea, Finland; SW = Swedish west coast. Numbers in parentheses indicate the number of sites in a given area.

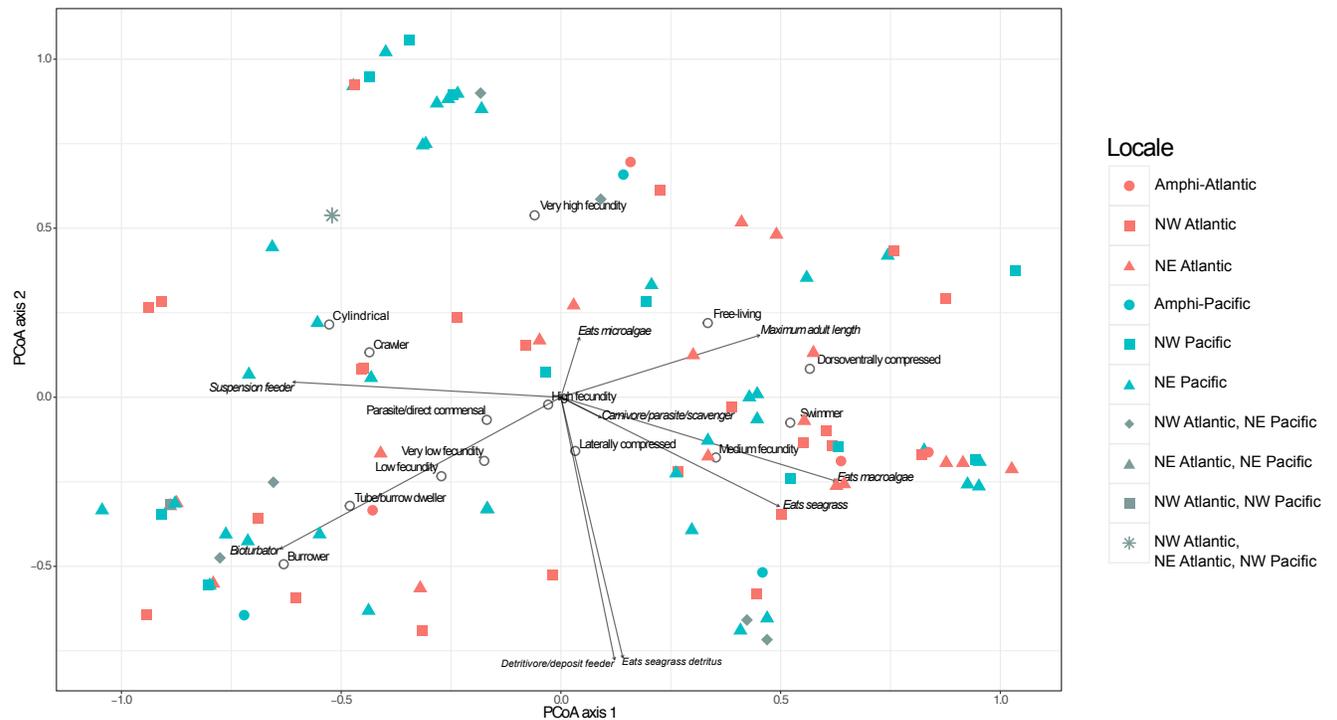


Figure S2. Principal coordinates analysis (PCoA) biplot of peracarid species in our global species pool, based on Gower distances. Solid symbols represent species in trait space, with symbol shape and colour corresponding to where they were found in our samples; hollow symbols represent centroids for categorical traits. Traits were fairly independent, and few were strongly correlated. Additionally, locale was not a significant predictor of where a given species fell in trait space (PERMANOVA; pseudo $F_{9,95} = 0.98$, $p = 0.51$). In other words, there were no traits that were particularly distinct to regions. Amphi-Pacific and Amphi-Atlantic distributions refer to species that occur in both the western and eastern margins of the Pacific and Atlantic Oceans, respectively.

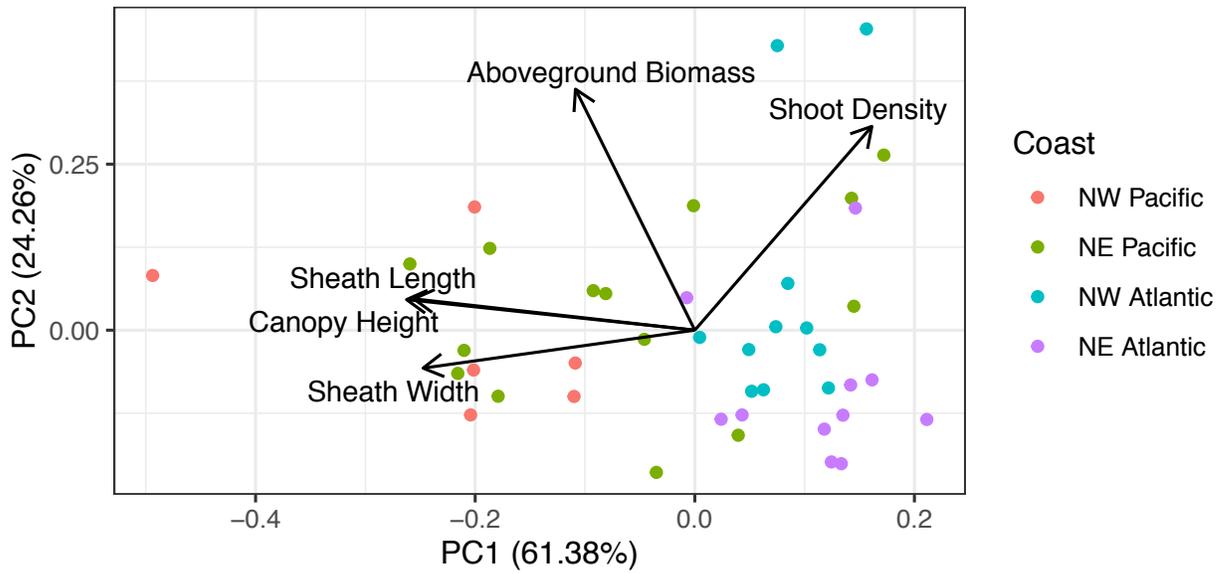


Figure S4. Principal component biplot for eelgrass habitat structure across sites. Most of the variation in eelgrass was between short canopies of dense shoots and taller canopies of sparser shoots. The first two principal components accounted for 85.64% of the total variation in habitat structure at the site level. Eelgrass beds in the Atlantic Ocean were mostly characterized by small, densely packed shoots, while those in the Northwest Pacific contained larger, sparser shoots. Northeast Pacific sites contained both of these bed types.

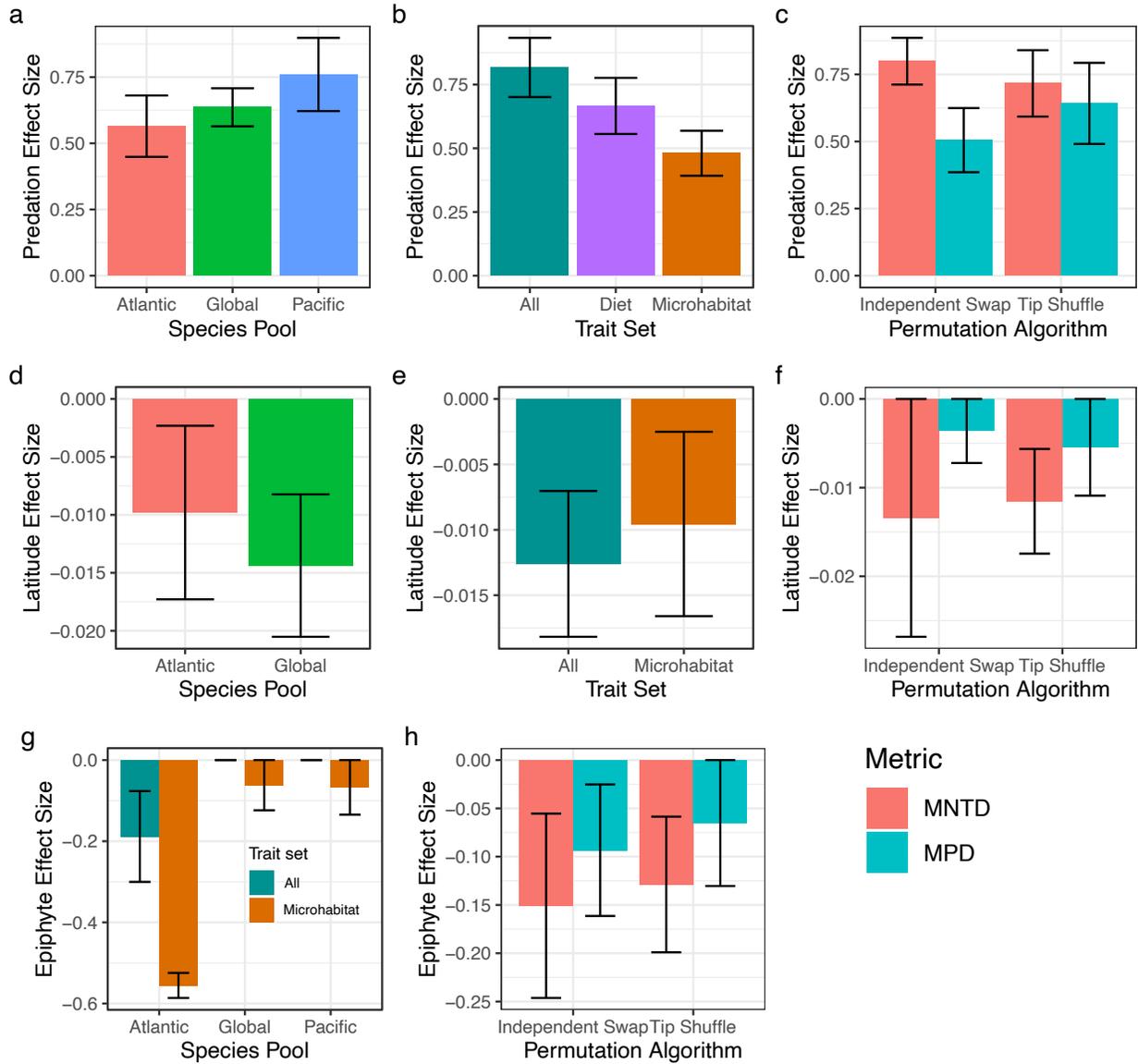


Figure S5. Effects of predation (a-c), latitude (d-f), and epiphyte load (g-h) in best models of site-level trait dispersion (SES values) across three species pools (a, d, g), 3 sets of traits (b, e, g), two permutation algorithms, and two dispersion metrics (c, f, h). Columns show mean effect sizes (across best models selected by AICc) averaged across species pools, trait sets, algorithms, and metrics where appropriate; error bars represent standard errors.

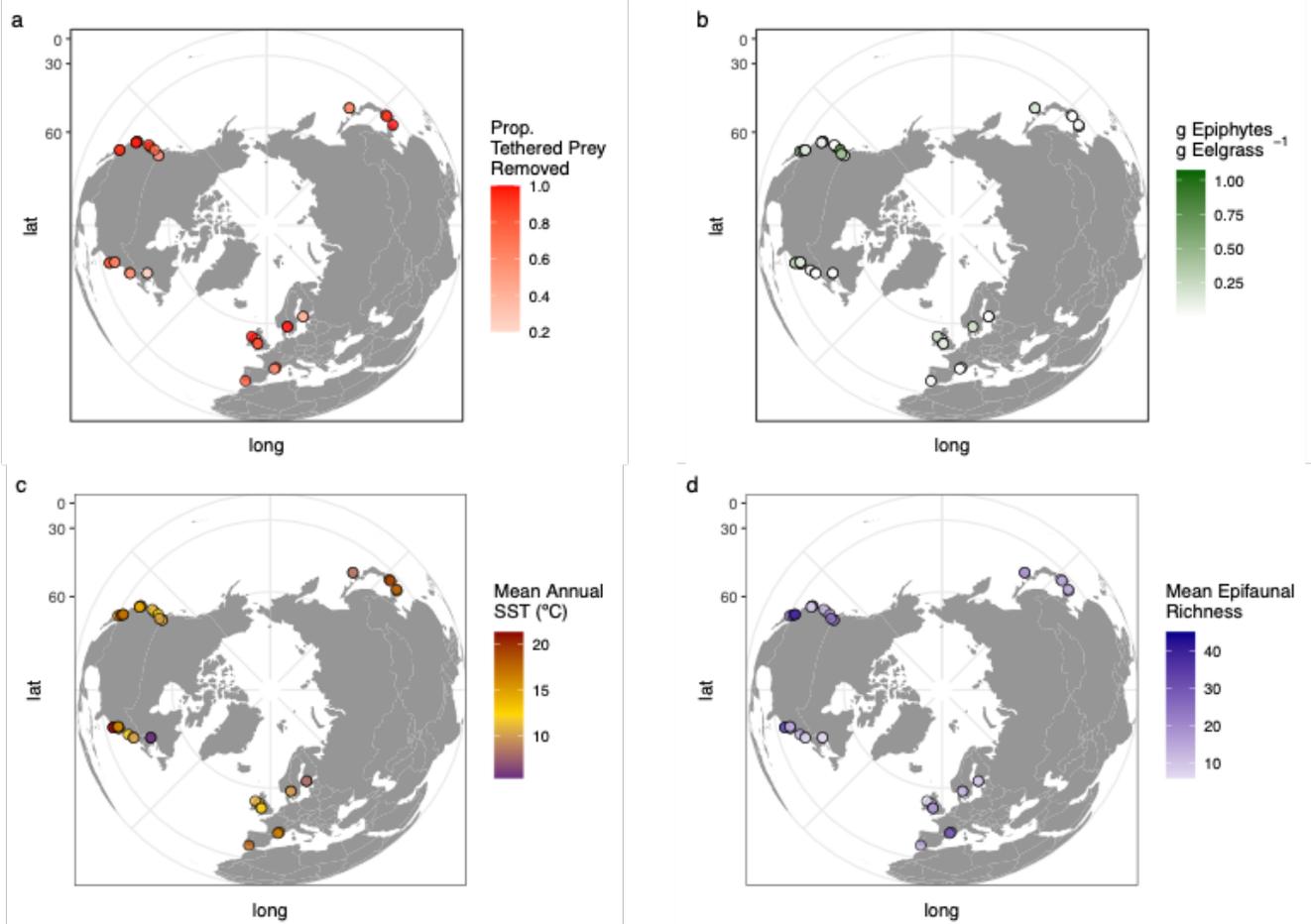


Figure S6. Maps of salinity (a), water column nitrate (b), in-situ temperature (c), and crustacean abundance (d) across sites and ocean basins. Of these predictor, only crustacean abundance was significantly greater in the Pacific ($R^2 = 0.076$, $p = 0.043$). See Fig. S1 for more detailed information about site locations.

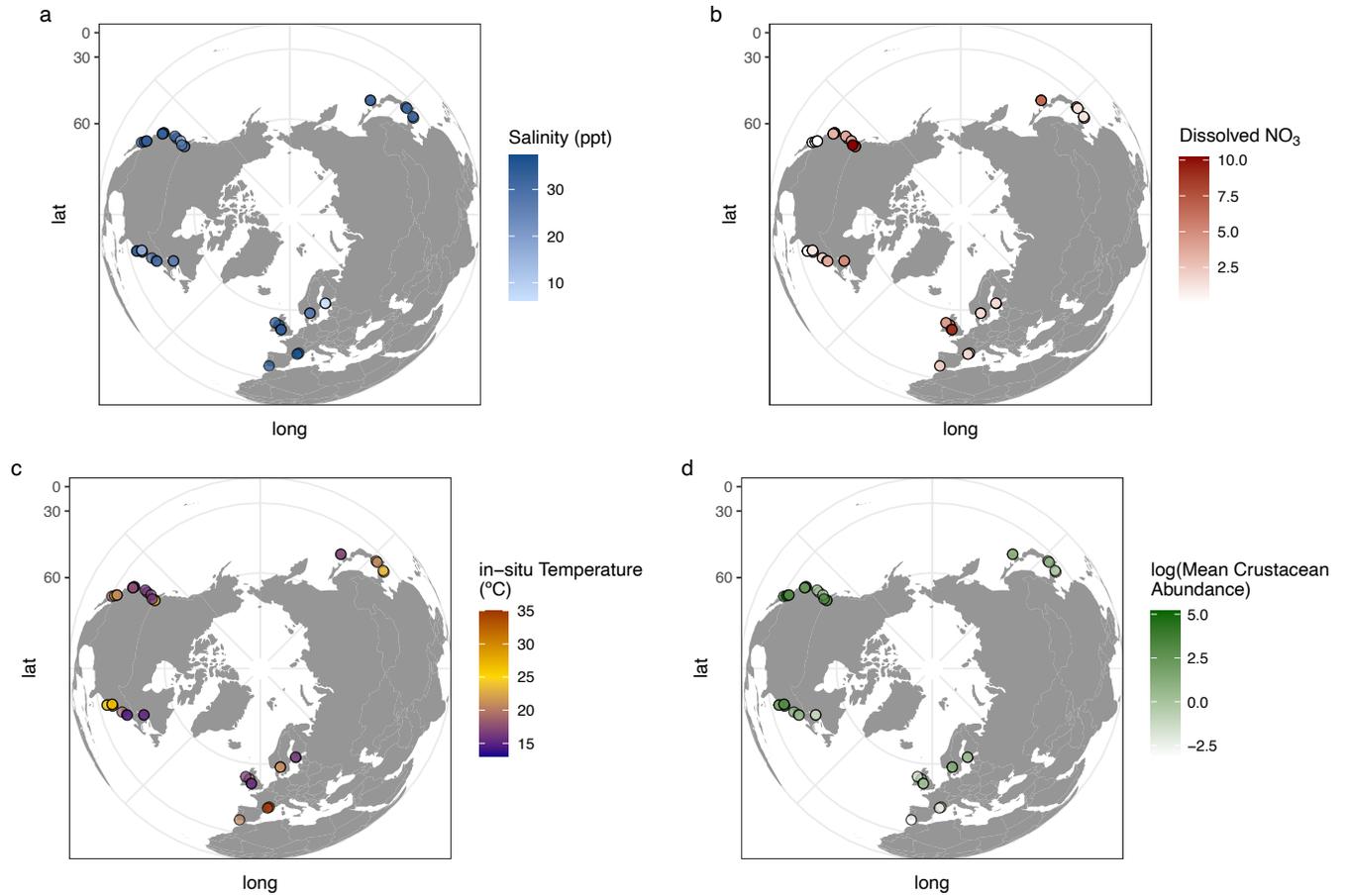


Figure S7. Maps of predation intensity (a), epiphyte load (b), mean annual sea surface temperature (c), and epifaunal species richness (d) across sites and ocean basins. None of these predictors varied significantly by ocean basin. See Fig. S1 for more detailed information about site locations.

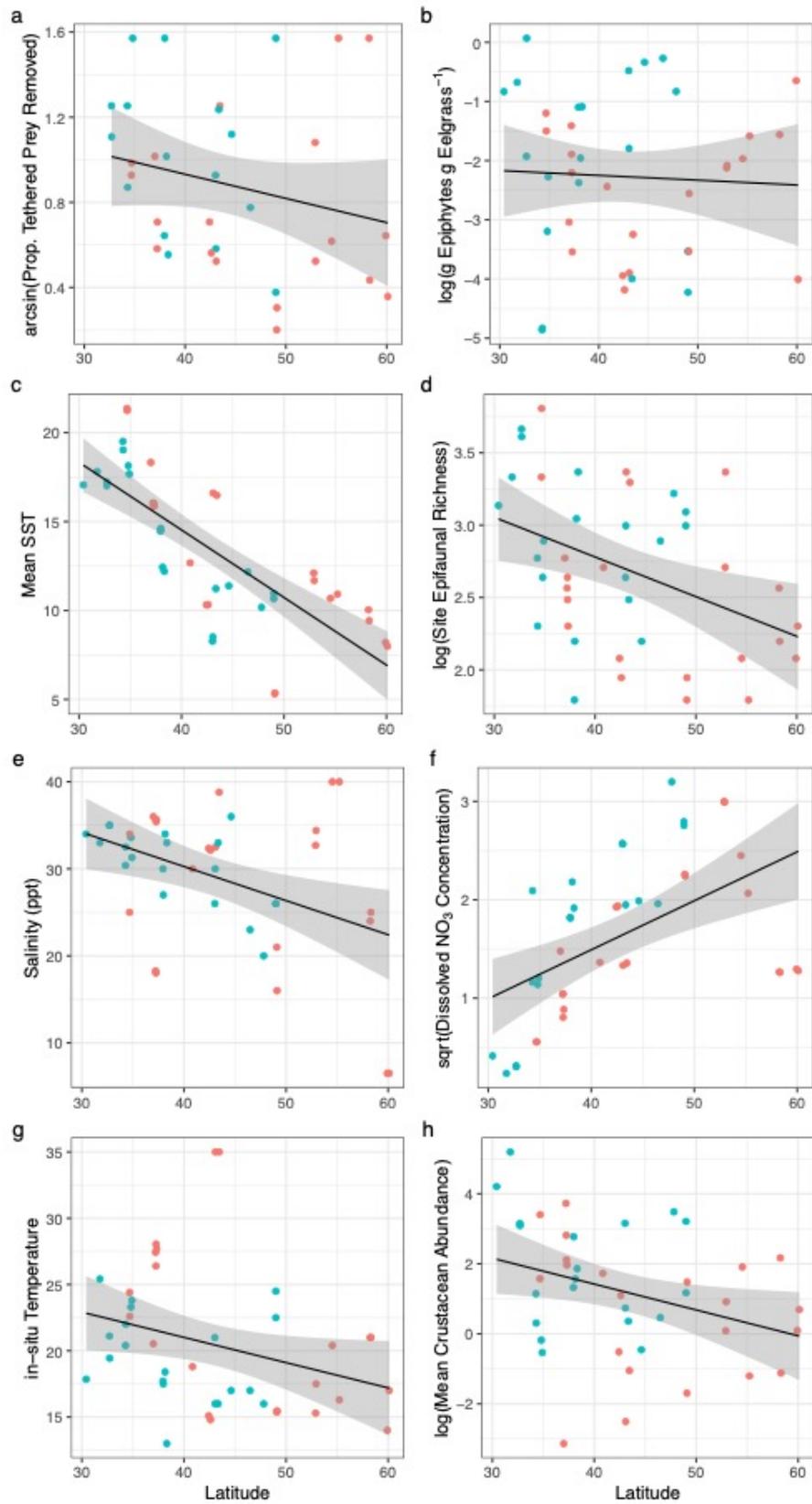


Figure S8. Predictors used in models of dispersion, including predation intensity (a), epiphyte load (b), mean sea surface temperature (c), epifaunal richness (d), salinity (e), water column nitrate (f), in-situ temperature (g), and crustacean abundance (h), plotted against latitude. Without accounting for other variables, latitude was a significant predictor of mean sea surface temperature ($R^2 = 0.58$, $p < 0.0001$), site epifaunal richness (log-transformed; $R^2 = 0.15$, $p = 0.0062$), salinity ($R^2 = 0.16$, $p = 0.0056$), nitrate (square root-transformed; $R^2 = 0.26$, $p = 0.00034$), in-situ temperature ($R^2 = 0.074$, $p = 0.046$), and crustacean abundance (log-transformed; $R^2 = 0.092$, $p = 0.029$). Points represent sites, color-coded by ocean; Atlantic sites are in red, Pacific sites are in blue.