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A Latitudinal Cline in the Taxonomic Structure of Eelgrass Epifaunal Communities is Associated With Plant Genetic Diversity

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ABSTRACT

Aim: Biogenic structural complexity increases mobile animal richness and abundance at local, regional and global scales, yet animal taxa vary in their response to complexity. When these taxa also vary functionally, habitat structures favouring certain taxa may have consequences for ecosystem function. We characterised global patterns of epifaunal invertebrates in eelgrass (*Zostera marina*) beds that varied in structural and genetic composition.

Location: North America, Europe and Asia.

Time Period: 2014.

Major Taxa Studied: Peracarid crustaceans and gastropod molluscs.

Methods: We sampled epifaunal invertebrate communities in 49 eelgrass beds across 37° latitude in two ocean basins concurrently with measurements of eelgrass genetic diversity, structural complexity and other abiotic and biotic environmental variables. We examined how species richness, abundance and community composition varied with latitude and environmental predictors using a random forest approach. We also examined how functional trait composition varied along with community structure.

Results: Total species richness decreased with latitude, but this was accompanied by a taxonomic shift in dominance from peracarid crustaceans to gastropods, which exhibited different sets of functional traits. Greater eelgrass genetic diversity was strongly correlated with both richness and abundance of peracarids, but less so for gastropods.

Main Conclusions: Our results add to a growing body of literature that suggests genetic variation in plant traits influences their associated faunal assemblages via habitat structure. Because peracarids and gastropods exhibited distinct functional traits, our results suggest a tentative indirect link between broad-scale variation in plant genetic diversity and ecosystem function.

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1 | Introduction

Structurally complex foundation species create a variety of microhabitats that can have important influences on diversity in animal communities in both marine and terrestrial systems (Loke and Chisholm 2022; MacArthur and MacArthur 1961). Different animal taxa may coexist by physically partitioning space in these habitats, based on the utility of microhabitats for feeding, avoiding predators or optimising physiological performance (Lindo and Winchester 2013; Lürig, Best, and Stachowicz 2016; Navarro-Mayoral et al. 2020; Schmitz and Suttle 2001). At global scales, these properties of foundation species may contribute to latitudinal diversity gradients, enhancing patterns underlain by biogeographic history, resource availability and other factors (Gaston 2000; Pianka 1966). In habitats composed of monospecific stands of foundation species, intraspecific trait variation can influence foundation species' structural complexity and suitability as habitat for numerous organisms (Crutsinger et al. 2006; Johnson and Agrawal 2005).

Yet, not all taxa respond equally to the same aspects of structural complexity. Diverse trophic guilds in many ecosystems are often composed of distinct lineages of taxa that have converged upon similar diets, despite separate origins (Lefcheck and Duffy 2015; Scheltema 1997). Despite their similarity in one dimension of trait space (e.g., diet), these lineages have distinct morphologies or other traits that may be favoured by different aspects of structural complexity (e.g., Montalbetti et al. 2022). Thus, functionally similar species may differ in being restricted to certain parts of habitat or only facilitated by certain types of foundation species (Lasley-Rasher et al. 2011; da Silva Bomfim et al. 2021). For lineages that are deeply diverged in time, these filters play out on a background of differences in biogeographic or phylogenetic history, differential responses to abiotic environmental filters and other factors that can influence how they are distributed across broad spatial scales (Sanford 2013; Vermeij 1991; Weber et al. 2017). A fuller understanding of the drivers of differences in distributions among otherwise functionally similar taxa should improve our ability to generalise how trait and phylogenetic differences affect species distributions, abundance and community composition.

Worldwide, habitats formed by submerged marine angiosperms (seagrasses) are often composed of clonal individuals of just one or a few species (Duffy et al. 2022; Hughes, Stachowicz, and Williams 2009; Leopoldas, Uy, and Nakaoka 2014; Reusch et al. 2005). In these systems, variation in the number and identity of clonal genotypes and associated variation in shoot density, number of leaves, canopy height and other aspects of structural complexity can affect the composition of epifaunal invertebrate communities (Abbott et al. 2017; Hughes, Stachowicz, and Williams 2009; Reusch et al. 2005). Gastropod molluscs and peracarid crustaceans form an important component of these epifaunal communities around the world (Ha and Williams 2018; Jernakoff and Nielsen 1997; Navarro-Mayoral et al. 2023; Valentine and Duffy 2006). Both are typically included in the 'mesograzer' guild, feeding primarily on epiphytic micro- and macroalgae that foul seagrass blades, as well as detritus, and live seagrass tissue itself (Fong et al. 2018; Jernakoff and Nielsen 1997; Murray, DuBois, and Stachowicz 2024). Yet, gastropods and peracarids are phylogenetically distinct, separated

by more than 550 million years of evolutionary history, and often differ distinctly in their grazing function (Eklöf et al. 2012; Jernakoff and Nielsen 1997; Råberg and Kautsky 2007). In some seagrass systems, they are also differentially susceptible to predation, with peracarids being much more vulnerable to consumption than gastropods at the same sites (Eklöf et al. 2012; Reynolds et al. 2018). Direct development is common to peracarids and when coupled with short generation times can lead to rapid population increases compared to gastropods, which have slower individual growth and more diverse developmental modes. Whether global seagrass communities dominated by gastropods or peracarids are distinct in other ways, including their responses to the structural complexity underlain by seagrass genetic diversity, can have major implications for understanding their broader patterns of distribution and the ability of whole epifaunal communities to promote seagrass growth by suppressing algae (Hughes et al. 2004) and support higher trophic levels (McDevitt-Irwin, Iacarella, and Baum 2016).

Here, using a global dataset of epifaunal invertebrate communities associated with the world's most widespread seagrass species (eelgrass, *Zostera marina*), we investigate how epifaunal community composition, richness and abundance vary with biotic and abiotic environmental predictors including eelgrass habitat structure and genetic diversity, on broad biogeographic scales. We were specifically interested in whether spatial variation in eelgrass habitat structure might correlate with variation in community structure. Given what has been observed relating the genetic diversity of foundation species to associated community structure and ecological interactions (Barbour et al. 2015; Hughes et al. 2008; Whitham et al. 2006), we additionally chose to test the hypothesis that eelgrass genetic diversity predicts the abundance and diversity patterns of its associated epifauna. While the mechanistic explanations remain unresolved, differences among plant genotypes in food value or habitat characteristics can improve performance of individual species by providing diet diversity and habitat complexity and/or enhance diversity by allowing the partitioning of food or habitat resources among species (Abbott et al. 2017; Hughes et al. 2008; Whitham et al. 2006). We focused on spatial shifts in dominance between two major taxonomic groups (peracarid crustaceans and gastropod molluscs) and additionally examined whether communities that differed in their dominant taxon were also distinct in their mean functional traits.

2 | Methods

2.1 | Study Design and Sample Collection

Between May and September 2014, we sampled 49 sites across the range of *Z. marina*, spanning 37° of latitude along the Pacific and Atlantic coasts of Eurasia and North America (30.4°N to 67.3°N; Figure 1; Table S1, Figure S1) to characterise the biological and physical structure of eelgrass beds using standardised measurements. Each site had 20 plots, for a total of 980 plots sampled as part of the *Zostera* experimental network (ZEN). Plots were 1 m² and spaced 2 m apart at each site. We sampled eelgrass biomass and quantified eelgrass habitat structure at the plot level as described by Gross et al. (2022)—briefly, we quantified eelgrass aboveground biomass, shoot density, canopy

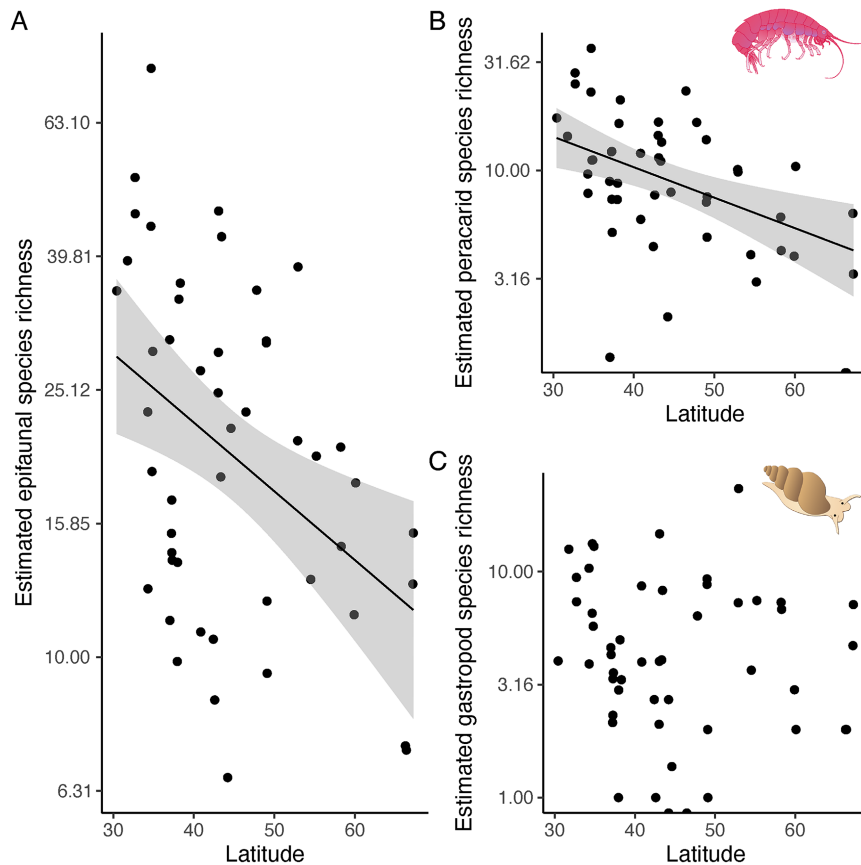


FIGURE 1 | Latitudinal clines in estimated species richness for all epifauna (A), peracarids (B) and gastropods (C) across global eelgrass sites. Plots show asymptotic bias-minimised estimates of richness calculated by modelling how abundances across 20 plots in each site affect observed richness. There was a significant relationship between latitude and estimated species richness for all epifauna ($F_{1,47}=9.91$, $p=0.0029$, $R^2=0.16$) and peracarids ($F_{1,45}=11.40$, $p=0.0015$, $R^2=0.18$) across the Atlantic and Pacific Oceans. Gastropods showed no significant latitudinal richness gradient. Note the logarithmic scale on the y-axes. Peracarid image (*Apherusa cirrus*) by first author, and gastropod image by Dieter Tracey, Waters and Rivers Commission (ian.umces.edu/media-library), used under an Attribution-ShareAlike 4.0 International licence.

height and leaf nitrogen, as well as macroalgal biomass from 20-cm-diameter cores in each plot. We quantified epiphyte load by scraping fouling microalgae from four eelgrass shoots per plot and drying to a constant weight. We additionally quantified eelgrass genotypic richness as the standardised number of genotypes (based on 8, 16 or 24 loci) between 0 (all individuals identical) and 1 (all individuals the same), and allelic richness as the average number of alleles per locus, normalised to 7 genets (Duffy et al. 2022).

2.2 | Abiotic Environmental Variables

To characterise the abiotic environment experienced by epifauna across the range of eelgrass, we measured in situ temperature and salinity at each site at the time of sampling. To characterise the overall abiotic environment of each site, we also retrieved estimates of annual mean sea surface temperature (SST), photosynthetically active radiation (PAR), surface chlorophyll *a* (Chl *a*), salinity and pH from the surrounding region, available in the Bio-ORACLE data set (Tyberghein et al. 2012). These data were taken from monthly readings of the Aqua-MODIS and SeaWiFS satellites at a 9.6 km² spatial resolution from 2002 to 2009. We used the raster package

in R v. 3.6.3 (Hijmans and Etten 2020; R Development Core Team 2022) to extract the annual mean SST, SST range, PAR and Chl *a* from all cells within 10 km of each site and averaged these cell-level estimates to generate site-level predictors. Other water quality parameters, including dissolved nitrate and other nutrients, were spatially interpolated based on surface measurements in the World Ocean Database 2009 (Garcia et al. 2010).

2.3 | Measuring Predation Intensity

To examine how predation intensity related to epifaunal community structure, we used prey tethering units (PTUs)—locally collected prey (shelled gastropods and ‘gammarid’ amphipods) as well as standardised prey types (dried squid and kale) tethered in each plot for 24 h. Data and methods for amphipod and gastropod prey are reported in detail in Reynolds et al. (2018). Standardised squid prey were 1 cm² pieces of dried squid attached by monofilament line to one acrylic rod in each plot (Duffy et al. 2015). Pieces of organic curly leaf green kale measuring approximately 5×3 cm were wrapped around acrylic rods to measure macroherbivory pressure at each site. Each PTU type was deployed in each of the four corners of each plot.

After 24h, we removed the stakes and scored prey as present (uneaten) or absent (eaten); partially consumed prey were considered eaten, and moulted prey were excluded from analyses. We calculated site-level consumption of each prey type by averaging scores across plots.

2.4 | Epifaunal Community Composition

To sample the epifauna associated with the eelgrass blades, we carefully placed an open-mouthed fine-mesh drawstring bag (500 μ m mesh, 18 cm diameter) over a clump of shoots in the centre of the plot so that the mouth of the bag was flush with the sediment surface. We then cut the shoots where they emerged from the sediment and quickly closed the drawstring to capture the shoots and associated animals. We transferred shoots to the lab on ice, rinsed and hand-inspected to dislodge the epifauna. We preserved all epifauna that remained on a 1-mm sieve in 70% ethanol and then identified them to the lowest possible taxonomic level (typically species). We separated epifaunal species into seven coarse taxonomic groups, including peracarid crustaceans (amphipods, isopods, tanaids and mysids), gastropod molluscs, polychaete annelids, bivalve molluscs, decapod crustaceans, anemones and others (including but not limited to barnacles, nemertean worms, echinoderms, ostracods and chironomid midge larvae). Together, peracarids and gastropods comprised the majority of individuals and species in these global epifaunal communities (comprising 32.10% and 56.65% of individuals and 36.34% and 25.11% of species, respectively), and have known functional roles as grazers of eelgrass and associated epiphytes, so we chose to focus subsequent analyses on these taxa, but a full list of species at each site is provided in Table S2.

We scored all peracarid and gastropods identified to species for a common series of functional traits based on information available in the literature, including maximum body size, parental care, developmental mode, tolerance of brackish and freshwater (as our sites spanned a range of salinities), grazer diet components (fresh eelgrass tissue, eelgrass detritus, macroalgae, and microalgae) and alternate nongrazing feeding modes (suspension feeder and carnivore/parasite/scavenger). We also used a series of nested sieves to group individual epifauna into size classes and used these to approximate mean, mode, median and maximum observed sizes for each identified species. We additionally estimated each species' latitudinal range as the difference between the two most extreme point observations regardless of hemisphere (to account for introduced species and others that span the equator), and latitudinal mean as the mean absolute latitude value of point observations, available online from the Ocean Biodiversity Information System (OBIS; Intergovernmental Oceanographic Commission of UNESCO 2023) and the Global Biodiversity Information Facility (GBIF; GBIF 2023). Here, we define functional traits according to the definition provided by Violle et al. (2007): morphological, physiological and behavioural traits that impact organismal fitness, which may also incidentally impact higher-level ecosystem functions. A more detailed discussion of traits including how we defined and measured each, and any transformations we applied prior to analysis is included in Table S3.

2.5 | Functional Trait Ordination and Clustering

To examine how communities dominated by peracarids and gastropods varied across trait space, we calculated continuous community-weighted mean values (CWMs) for traits in each site-level community across its peracarid and gastropod components. For binary and discrete categorical traits (11 traits with 24 categories), continuous CWMs were the average relative abundances of each trait level, while for continuous traits (6 traits), it was the average value—in total, each site had 30 CWM values. We then calculated Bray–Curtis distances among sites based on the CWM-by-site matrix, and visualised sites in trait space using an NMDS ordination.

To examine any geographic signal in the trait composition of these communities, we hierarchically clustered communities in trait space based on average Bray–Curtis distances, separating clusters into discrete groups based on a minimum average distance of 0.1. We then recalculated group-level CWMs by considering individuals from all sites within a group to be part of one community to see how average traits differed across groups.

2.6 | Data Analyses

We first examined how species richness varied across latitude, both for the entire epifaunal community and separately for gastropods and peracarids. Because richness estimates may be biased due to patchy distributions and low abundances, we used asymptotic bias-minimised estimates of richness in our models (Tekwa et al. 2023). Briefly, this method models how abundance and occupancy of species across the 20 plots in each site affect observed richness by estimating the species-level probability of observation across all 20 plots. We additionally examined how the relative abundance per sample bag of each of these two groups varied across latitudes and ocean basins.

We modelled the response of relative abundance of gastropods or peracarids to latitude in generalised linear models as the total proportion of 'successes' (i.e., whether an individual is a gastropod or peracarid vs. other) in each site's pooled sample of individual epifauna with a quasibinomial error distribution and a logit link function, which accounts for overdispersion and uneven epifaunal abundances (van der Kolk et al. 2024; Reynolds et al. 2018). We log-transformed estimated richness as a response to latitude in linear models. We assessed model predictor significance using the Anova() function in the car package (Fox and Weisberg 2019).

To identify candidate predictors of the relative abundance of peracarids and gastropods across sites, we used the log-transformed ratio of peracarid relative abundance to gastropod relative abundance (hereafter log ratio) as the response variable in a random forest model that incorporated both abiotic and biotic environmental predictor variables. Our full list of predictors included ocean basin; the first two principal components of eelgrass morphology (including sheath length, sheath width, longest leaf length, shoot density and aboveground biomass; Figure S2); predation on squid, kale, gastropods and

peracarids; eelgrass genetic diversity; eelgrass morphology; algal abundance; temperature and salinity; light availability, epiphyte load and water column chlorophyll; and water column nutrients (Table S4). We included ocean basin as a categorical predictor that captures broad and difficult-to-capture differences between the Atlantic and Pacific oceans, including age, phylogenetic history and connectivity within basins. When two variables showed a pairwise Kendall's τ correlation value of greater than 0.6, only one was included in the predictor pool (Figure S3). To minimise error rates and maximise computing efficiency, we tuned our random forest model by visually inspecting mean-squared error across all trees in the model and adjusted the number of trees to the smallest number for which error was consistently low. We also used the train function in the R package caret (Kuhn 2008) to find the optimal number of variables tried at each split in each regression tree in the forest. We identified the top 10 predictors of relative abundance from each forest by the degree to which they increased MSE when removed from the model and the total increase in node impurities when removed from the model.

We then performed a model selection procedure to determine the best predictor of the log ratio of peracarids to gastropods. First, we created a set of 10 a priori linear models of the log ratio against the top 10 predictors, which were transformed as appropriate to conform to a normal distribution (Table 1). From here, we selected eight predictors for which the 85% confidence limit of the standardised effect size did not overlap zero, an approach consistent with selection by AICc that permits additional predictors to be tested that may otherwise not be considered (Sutherland et al. 2023). Finally, we included these eight predictors (eelgrass allelic and genotypic richness, in situ temperature, mean eelgrass leaf % C, herbivory, ocean and eelgrass morphology PC1 and PC2) in a full model along with interactions with ocean basin (to account for unmeasured factors that may influence the behaviour of continuous predictors in each ocean—a

total of 16 parameters) and performed automated model selection based on AICc using the dredge function in the MuMIn package (Bartoń 2020). Where two models had a Δ AICc less than 2 units, we selected the model with the fewest parameters for interpretation.

To specifically examine the responses of gastropods and peracarids to aspects of eelgrass habitat composition and structural complexity, we modelled the richness and total abundance of gastropods and peracarids as a function of eelgrass allelic richness, genotypic richness and the first two principal components of eelgrass morphology. To confirm the effect of genetic diversity on the diversity of habitat structure in eelgrass, we examined the significance of modelled relationships between genetic diversity and among-plot variation (as standard deviation) in eelgrass morphology along the first two principal components.

To test whether gastropods and peracarids contributed distinct, nonoverlapping suites of traits to epifaunal communities, we asked whether the log ratio of the two taxa determined the clustering of sites in trait space. We performed a permutational multivariate ANOVA (PERMANOVA) with log ratio as a predictor on the Bray–Curtis distances of CWMs between sites, using 9999 permutations in the vegan package in R (Oksanen et al. 2022). We also investigated whether the volume of trait space occupied by gastropod-dominated (negative log ratio) or peracarid-dominated (positive log ratio) sites differed significantly from each other by measuring the average dissimilarity from individual sites to their group centroid (Anderson, Ellingsen, and McArdle 2006). Because this procedure requires discrete categories across which to compare variances, we assigned sites with positive and negative log ratios to separate groups and compared between them. All statistical analyses were conducted in R v.4.2.2 (R Development Core Team 2022).

TABLE 1 | Top 10 predictors in a random forest model that explained 21.52% of variation in the log ratio of peracarid relative abundance to gastropod relative abundance across global eelgrass sites. Bolded rows indicate predictors included in an initial combined model of log ratio; italicised rows indicate predictors included in the best model selected from the initial combined model.

Predictor	Transformation	% Increase in MSE	% Increase in node impurity
<i>Ocean</i>	<i>None</i>	14.44	12.71
Eelgrass morphology PC1 (62.09%)	None	10.39	16.08
Mean eelgrass leaf % C	None	9.70	13.58
In situ temperature (°C)	None	8.44	11.10
<i>Eelgrass allelic richness (avg. number of alleles per locus, normalised to 7 genets)</i>	<i>Richness²</i>	8.43	14.62
Herbivory (mean presence/absence of kale)	logit	7.66	12.26
Eelgrass morphology PC2 (24.34%)	None	6.50	11.85
Salinity (ppt)	Salinity ⁴ /100,000	6.38	9.10
Mean Water Column Chl <i>a</i>	log	6.05	10.40
Genotypic Richness (effective number of distinct genotypes)	None	5.03	6.72

Note: Richness² represents allelic richness squared, and Salinity⁴ represents salinity raised to the fourth power.

3.1 | Latitudinal Clines in Diversity and Abundance

As is typical for many marine and terrestrial systems, estimated epifaunal species richness declined with increasing latitude ($F_{1,45} = 10.06$, $p = 0.0027$, $R^2 = 0.17$; Figure 1A), and there was no difference in the richness gradient between oceans ($F_{1,45} = 0.33$, $p = 0.57$), although we note that our sampling region includes only temperate latitudes. Peracarid species richness showed a similar latitudinal cline in both ocean basins ($F_{1,45} = 11.40$, $p = 0.0015$, $R^2 = 0.18$; Figure 1B). Gastropods showed no significant latitudinal clines in species richness (Figure 1C). Species richness increased with total abundance for peracarids, but not for gastropods (Figure S2).

We found striking clines in the relative abundance of both peracarids and gastropods across the 37° of latitude surveyed in our study—at high latitudes, gastropods dominated ($\chi^2_1 = 60.55$, $p < 0.001$; Figure 2B), while at lower latitudes, peracarids dominated ($\chi^2_1 = 47.56$, $p < 0.001$; Figure 2A). For peracarids, these patterns also differed by ocean basin—in the Pacific, peracarids dominated (66.42% of epifauna on average) and declined more slowly with increasing latitude than in the Atlantic (27.97% on average; $\chi^2_1 = 7.72$, $p = 0.0055$; Figure 2A). Gastropods did not show significant differences in abundance or latitudinal clines between oceans, but their proportion in the Atlantic (52.70%) was larger on average than in the Pacific (19.43%). There were few sites dominated by other epifaunal taxa, including anemones, mussels and polychaete worms. While this dominance of other taxa did not vary significantly by latitude or ocean basin (Figure 2C), we did find that the relative abundance of decapods declined with latitude ($\chi^2_1 = 26.98$, $p < 0.001$; Figure S5).

3.2 | Predictors of Taxonomic Structure

Our random forest model employed to predict the log ratio of peracarids to gastropods across sites used 3000 trees, testing two variables at each node with an average of 12.03 nodes per tree and explaining 21.52% of the variance in log ratios. Top predictors in this model included eelgrass morphology PC1 and PC2 (positively correlated with shorter leaf lengths and narrower sheath widths, and higher aboveground biomass and shoot density, respectively; Figure S2), ocean basin, eelgrass leaf carbon content, herbivory, in situ temperature, eelgrass allelic and genotypic richness, mean water column Chl *a* and salinity (Table 1, Table S5). In particular, ocean basin, allelic richness, herbivory and genotypic richness had the strongest effects (1.49, 0.47, 0.46 and 0.41 predictor standard deviations per standard deviation of log ratio, respectively; Figure 3A, Table S5), indicating increases in peracarids with increasing genotypic and allelic richness, herbivory and in the Pacific Ocean.

The log ratio of peracarids to gastropods was best explained by an additive model including only eelgrass allelic richness and ocean basin ($F_{2,43} = 13.77$, $R^2 = 0.36$, $p < 0.001$), although the model with the lowest AICc additionally included eelgrass PC2 ($F_{3,42} = 10.94$, $R^2 = 0.40$, $p < 0.001$; Table S5). Log ratios increased (more peracarids relative to gastropods) with eelgrass allelic richness (Figure 3B) and were greater in the Pacific than in the Atlantic Ocean (Figure 3C). Eelgrass allelic richness declined with increasing latitude, while eelgrass allelic richness and morphological variation were greater on average in the Pacific than in the Atlantic (Figure S2, see also Duffy et al. 2022).

Peracarid abundance and richness showed significant responses to eelgrass allelic richness, genotypic richness and the first two principal components of eelgrass morphology—sites with more

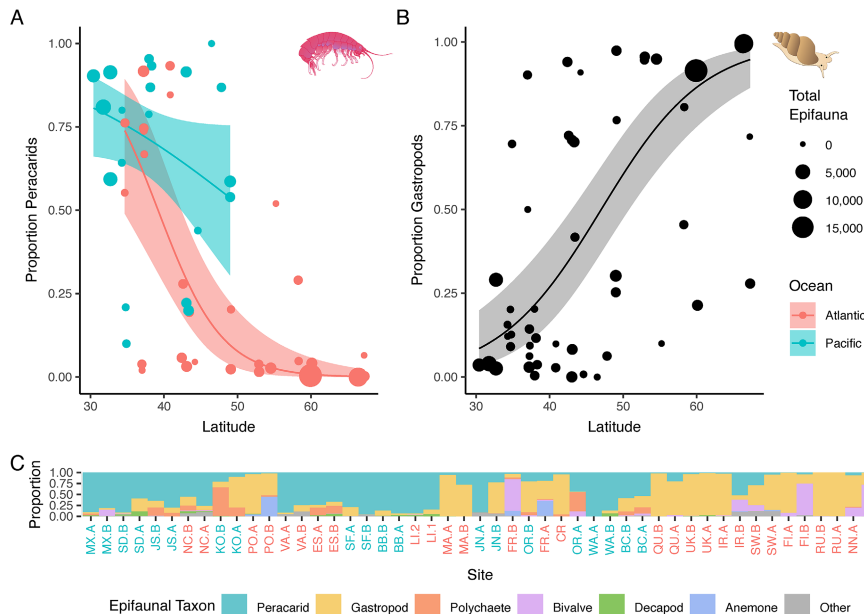


FIGURE 2 | Latitudinal clines in the dominance of peracarid crustaceans (A) and gastropods (B) across global epifaunal communities (C). The relative abundance of each taxon changed significantly with latitude (peracarids $\chi^2_1 = 47.56$, $p < 0.001$; gastropods $\chi^2_1 = 60.55$, $p < 0.001$). For peracarids, the latitudinal clines varied significantly between ocean basins ($\chi^2_1 = 7.72$, $p = 0.0055$). Point sizes in Panels A and B represent the total number of individuals pooled across 20 plots in a site. Site labels in C are coloured according to ocean basin as in Panel A, and arranged from lowest (on the left) to highest latitude (on the right); site locations are shown in Figure S1 and Table S1.

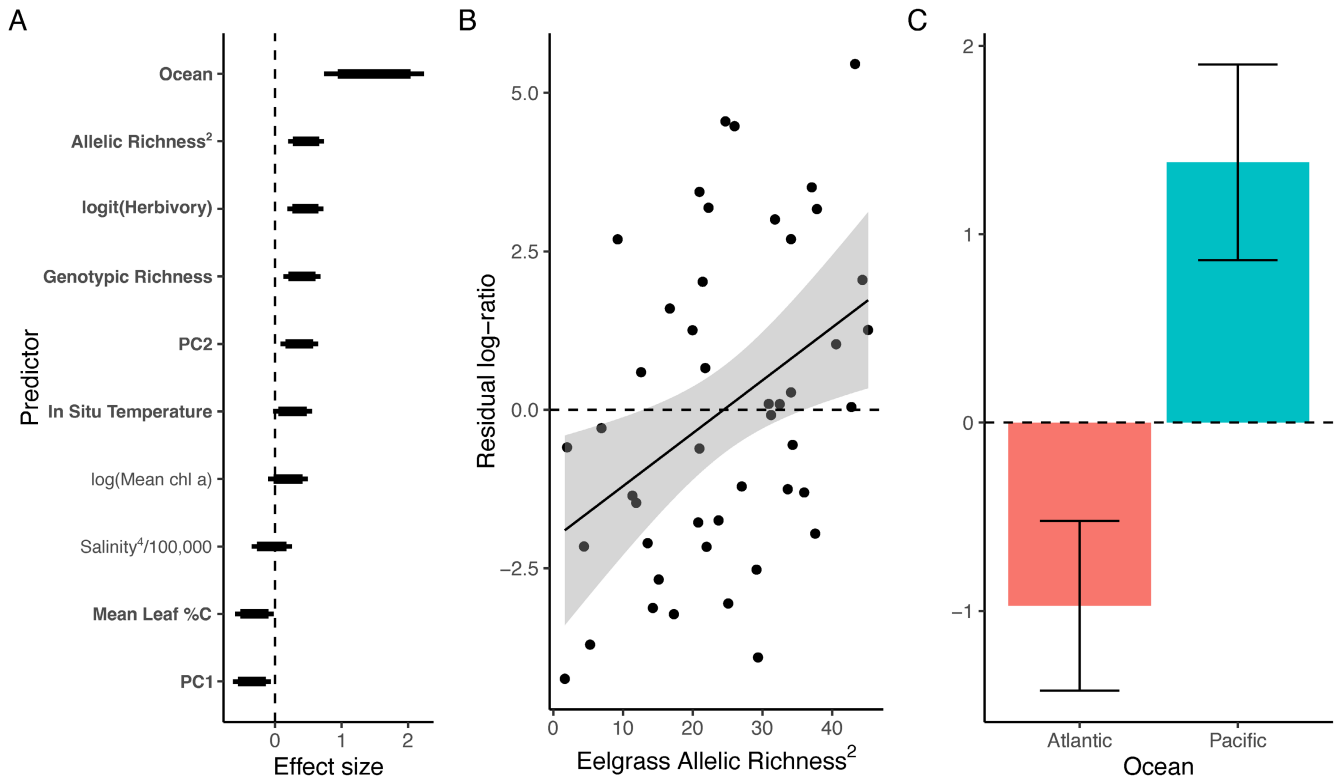


FIGURE 3 | Predictors of the log-transformed ratio of peracarid relative abundance to gastropod relative abundance in epifaunal communities across sites. Of the top 10 predictors identified by an initial random forest model (A), we selected the eight whose 85% confidence interval did not overlap 0 (in bold) for further testing. Log ratios were best explained by an additive model ($F_{2,43} = 13.77$, $R^2 = 0.36$, $p < 0.001$), including eelgrass allelic richness (B) and ocean basin (C); panels show residual variation in log ratio after accounting for the other factor. Communities shifted from being dominated by gastropods to peracarids as eelgrass allelic richness (avg. number of alleles per locus, normalised to seven genets; B; $F_{1,43} = 8.75$, $p = 0.005$) increased. Communities in the Pacific were more peracarid dominated than those in the Atlantic, which were more gastropod dominated (C; $F_{1,43} = 18.80$, $p < 0.001$). In A, thick lines indicate 85% confidence limits for standardised predictor effects, while thinner lines indicate 95% confidence limits. In B and C, the horizontal dashed line indicates a 1:1 ratio of gastropods to peracarids.

genetically diverse eelgrass, eelgrass with wider, longer blades (negative PC1 scores) and higher shoot density and greater aboveground biomass (positive PC2 scores), had more peracarid species and individuals (Tables S6 and S7, Figures S6 and S7). Gastropod species richness showed no positive responses to eelgrass structural complexity or genetic diversity (Table S6, Figure S6), and abundance responded positively only to PC1 (Table S7, Figure S7). Increased eelgrass allelic and genotypic richness was associated with increased eelgrass morphological variation along PC1 and PC2 ($p = 0.0050$ and $p = 0.068$, respectively) and to a lesser extent PC1 ($p = 0.095$ and $p = 0.13$, respectively; see Table S8 for full analysis).

3.3 | Gastropod and Peracarid Effects on Site-Level Trait Structure

Gastropod-dominated epifaunal communities (those with a negative log ratio) occupied a distinctive area of ordination space from peracarid-dominated communities (positive log ratio; pseudo- $F_{1,44} = 14.70$, $p < 0.001$, $R^2 = 0.25$; Figure 4A). Gastropod and peracarid species also occupied distinct regions of trait space (Figure S8). The proportion of other epifaunal taxa did not significantly affect a community's trait assemblage (pseudo- $F_{1,44} = 0.31$, $p = 0.79$, $R^2 = 0.00697$). Despite taxonomic

differences, gastropod-dominated and peracarid-dominated sites did not occupy significantly different volumes of functional trait space ($F_{1,47} = 0.15$, $p = 0.70$, $R^2 = 0.0032$).

Our hierarchical clustering scheme produced five distinct groups of sites with different mean trait values for both peracarids and gastropods (Figure 4B). The first group ('cold Pacific') consisted of cool-temperate Northeast Pacific sites in British Columbia, the outer coast of Washington State (Willapa Bay), Oregon and Northern California, as well as sites in Japan (Hokkaido), South Korea, New York, Portugal and one site in Mediterranean France. The second group consisted of one site in Croatia, where we only found the snails *Bittium reticulatum* and *Hydrobia acuta neglecta*. The third group ('warm sites') consisted of warm-temperate to subtropical sites in Southern California, Mexico (Baja California), Virginia and North Carolina, as well as one site in the Salish Sea (Dabob Bay). The fourth group ('cold Atlantic') consisted of cold temperate sites on both sides of the Atlantic, including New York, Massachusetts, Quebec, France, Ireland, Wales, Sweden, Finland, Norway and Russia (White Sea). The fifth group ('Asia') included sites in Japan and South Korea as well as one site in Southern California (San Diego Bay). Groups varied mostly by mean maximum body length (from the literature; group 1: 24.63 mm; group 5: 11.50 mm), latitudinal range

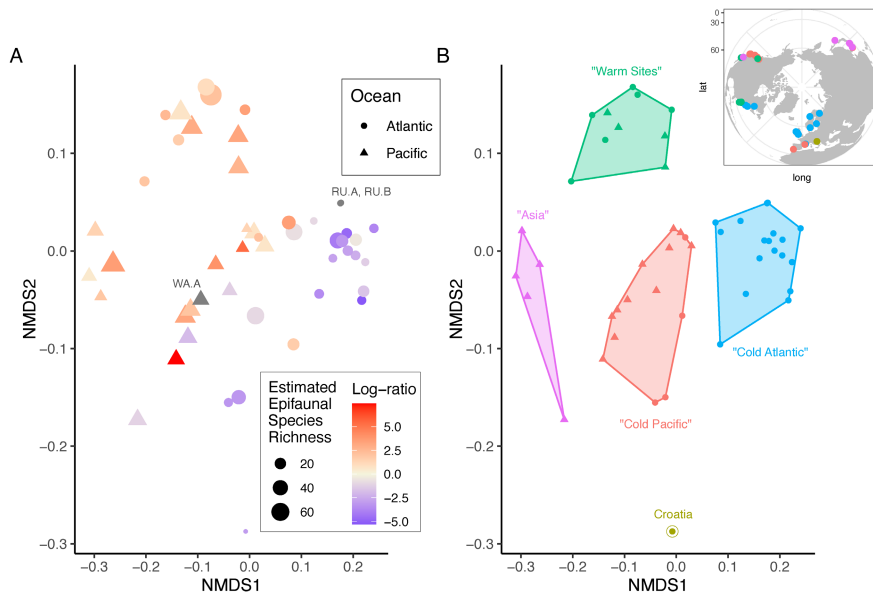


FIGURE 4 | NMDS ordinations of eelgrass epifaunal communities in trait space. Points represent individual sites, and points that fall more closely together are more similar in community-weighted mean trait values. In (A), sites are coloured by the log ratio of the relative abundance of peracarids and gastropods; positive log ratios indicate more peracarids than gastropods, while negative log ratios indicate more gastropods than peracarids. Log ratios significantly predicted sites' positions in trait space (pseudo- $F_{1,44} = 14.70$, $p < 0.001$, $R^2 = 0.25$). In (B), the same sites are coloured according to membership to one of five groups created by hierarchical clustering based on similarities in community-weighted mean trait values; Group 2 circled for visibility. In (A), Site WA.A had no gastropods; Sites RU.A and RU.B had no peracarids. Inset map shows the geographic locations of groups.

(group 2: 68.47°; group 5: 21.64°) and mean latitude (group 4: 52.47°; group 3: 36.32°), while all groups were dominated by microalgal grazers and marine species (Table 2).

4 | Discussion

We found a prominent latitudinal gradient in the species richness of epifaunal invertebrates inhabiting eelgrass, with greater richness at lower latitudes (Figure 1A). Peracarid crustaceans followed this same trend (Figure 1B), but the pattern was not observed for gastropods (Figure 1C). While the decline in species richness with latitude is typical for many terrestrial systems and some marine systems (Gaston 2000; Pianka 1966), evidence increasingly shows that for most marine taxa, richness peaks at mid-latitudes, with a dip near the equator (Arfianti and Costello 2020; Chaudhary, Saeedi, and Costello 2016; Thyrring and Peck 2021). Furthermore, previously published analyses place peaks in gastropod species richness between 25°N and 30°N and peracarid (amphipod) richness between 50°N and 60°N in the northern hemisphere (Arfianti and Costello 2020; Chaudhary, Saeedi, and Costello 2016), in direct contrast with our results. However, those analyses pooled species across multiple nearshore habitat types, including seagrasses, coral reefs, rocky shores and soft sediments. In contrast, our observed peaks in richness at lower latitudes for total epifauna and peracarids are based on a standardised sampling protocol within a single, widespread habitat type. Thus, they likely reflect the responses of these taxa specifically to unique characteristics of eelgrass habitat that overwhelm the influence of broader drivers of species richness.

The composition of epifaunal communities shifted from being peracarid dominated to gastropod dominated at high latitudes,

especially in the Atlantic (Figure 2A,B). As far as we are aware, this latitudinal gradient in taxonomic composition has not been documented elsewhere in the literature, although there is some limited evidence that gastropods may be more abundant in high-latitude seagrass beds than in low-latitude beds (Barnes and Ellwood 2011). This shift in relative abundance appears to derive solely from an increase in peracarid species richness (and abundance) with decreasing latitude (Figure 1B and Figure S4A)—gastropods did not show any latitudinal gradient in species richness (Figure 1C), nor a relationship between species richness and abundance (Figure S4B). The contrast in latitudinal gradients between these taxa, coupled with the consistent effects of eelgrass genetic diversity and habitat structure (Figure 3A, Table S5), suggests that these gradients in richness and relative abundance are not likely driven by processes thought to generate latitudinal diversity gradients, such as temperature. Although we note a positive effect of in situ temperature on the log ratio of peracarids to gastropods, it is overshadowed by the effects of ocean basin and genetic diversity (Figure 3A).

Despite differences in the relative abundances of peracarids and gastropods between the Pacific and Atlantic (Figure 3C), we still observed significant increases in gastropod dominance relative to peracarids with increasing latitude in Pacific sites, suggesting additional mechanisms acting within ocean basins to drive the latitudinal pattern. Notably, relative dominance of peracarids increased with eelgrass allelic richness, an effect that persisted after accounting for ocean basin (Figure 3B). Eelgrass genetic diversity and variation in morphology are both greater in the Pacific than in the Atlantic, the result of bottlenecks that occurred during its colonisation of the Atlantic via the Arctic (Duffy et al. 2022; Olsen et al. 2004; Yu et al. 2023; Figure S2A). The response of epifaunal communities to structural complexity

TABLE 2 | Mean trait values of the peracarid and gastropod community in five a posteriori groups of eelgrass sites created by hierarchical clustering based on similarities in site-level community-weighted mean trait values. Dominant values for binary and categorical traits are shown, while group-level community-weighted means are supplied for continuous traits. Observed sizes are derived from sieved epifaunal samples. Latitudinal range and mean latitude are derived from observations gathered from GBIF and OBIS.

Group	Diet	Parental care	Developmental mode	Mode			Mean		Lat. range	Lat. mean	Salinity
				Obs. size (mm)	Max Obs. size (mm)	Obs. size (mm)	Max Lit. size (mm)				
1—'Cold Pacific'	Microalgal grazer	Brooder	Direct development	2.528	5.461	2.354	24.628	32.130	46.635	Marine	
2—Croatia	Microalgal grazer, detritivore	Broadcast spawner	Lectithotrophic	2.800	8.000	2.364	15.000	68.471	52.156	Marine, Brackish	
3—'Warm Sites'	Microalgal grazer	Brooder	Direct development	1.417	4.710	1.595	11.781	38.075	36.316	Marine	
4—'Cold Atlantic'	Microalgal grazer, detritivore	Lays egg case	Direct development	1.574	3.814	1.552	12.648	45.854	52.467	Marine, Brackish	
5—'Asia'	Microalgal grazer, detritivore	Brooder	Direct development	1.661	4.924	1.755	11.502	21.643	38.111	Marine	

in eelgrass is well characterised (Carr, Boyer, and Brooks 2011; Lürig, Best, and Stachowicz 2016; Orth 1992), particularly as refuge from predators. Experimental studies within a single location show that eelgrass genetic diversity affects the abundance and richness of epifaunal mesograzers and that genetic diversity is associated with eelgrass trait diversity (Abbott et al. 2017; Hughes, Stachowicz, and Williams 2009; Reusch et al. 2005; Figure S2B,C). We did find some evidence that genetic diversity (especially allelic richness) was associated with variation in eelgrass morphology in our dataset (Table S8), suggesting a potential link between genetic variation and structural complexity. Differences in shoot density, width and length as a result of genetic differentiation may potentially create a greater variety of microhabitats that support more peracarid species and individuals—for example, longer leaves create horizontal 'canopies' that are distinct from vertical 'stem' habitats (Lürig, Best, and Stachowicz 2016; Navarro-Mayoral et al. 2023).

Eelgrass PC2 and PC1 were top predictors of peracarid dominance in our random forest model, indicating that aspects of eelgrass morphology, notably shoot density, leaf length and sheath width are also associated with epifaunal log ratios (Table 1). Our previous work found that these (and other) aspects of plant morphology are associated with genetic composition rather than diversity, suggesting a link among eelgrass genetics, structural complexity and animal communities (Duffy et al. 2022). Furthermore, genetic measures here are from noncoding microsatellite DNA markers, and thus any link between plant genetics and function is necessarily correlative only (although we note that we recover similar patterns of geographic variation in genetics with whole-genome sequencing, albeit at fewer locations [compare Duffy et al. 2022 and Yu et al. 2023]). Eelgrass genetic diversity thus may be correlated with other factors that could drive differences in log ratios, whether through plant morphology or other pathways, but we did not recover these in our analyses.

Log ratios showed a significant positive relationship with peracarid species richness, but no relationship with gastropod richness (Figure S4). If peracarid species are functionally distinct, the greater richness and abundance of peracarids at lower latitudes suggest that they occupy a greater volume of trait space in these sites and may competitively exclude gastropods, particularly if peracarids are also facilitated by greater eelgrass structural complexity (Figure S6, Table S6). Yet, our ordinations (Figure 4, Figure S8) point to distinctions between the traits of gastropods and peracarids, rather than overlap. However, the limited number of comparable traits we were able to assemble for both gastropods and peracarids may reflect niche differences that promote stabilising coexistence rather than fitness differences (sensu Chesson 2000; Mayfield and Levine 2010), obscuring potential interactions between these two taxa that may lead to competitive exclusion. For example, in many cases, gastropods and peracarids differ in their feeding rates on microalgae, macroalgae or detritus (Graça, Newell, and Kneib 2000; Råberg and Kautsky 2007; Sampaio et al. 2017), which may lead to competitive exclusion if multiple species focus on the same food source. Peracarids tend to be more selective grazers than gastropods, and greater richness of peracarid species with nonoverlapping diets may contribute to the exclusion of gastropods (Duffy and Harvilicz 2001;

Jernakoff and Nielsen 1997). An increase in herbivory with increasing dominance of peracarids (Figure 3A) could indicate that peracarids are monopolising algal food sources to the detriment of gastropods. Peracarids may also dislodge or even prey upon small molluscs (Lefcheck et al. 2014). It seems unlikely that these behaviours would have a major effect on global distributions of the two taxa, but this remains to be tested.

Latitudinally, our network is notably biased in its sampling of eelgrass epifauna in the Atlantic and Pacific Oceans. Our 29 Atlantic sites span nearly 33° of latitude—nearly the full latitudinal range of eelgrass in the Atlantic (Green and Short 2003; den Hartog 1970)—and include 14 of our highest-latitude sites (Figure 2C). In the Pacific, the remaining 20 sites span 18.6° of latitude, excluding higher-latitude areas in Alaska, British Columbia and the Sea of Okhotsk where eelgrass is known to occur. The latitudinal shift in dominance from peracarids to gastropods thus seems to be in part driven by high-latitude gastropod-dominated Atlantic sites at one extreme, and low-latitude peracarid-dominated Pacific sites at the other (Figures 2 and 3C). However, the trend, while weaker, is still observable in the limited latitudinal range of our Pacific sites (Figure 2), and we have anecdotal evidence to support that gastropods are more abundant than peracarids in Pacific sites up to 59°N (Duffy et al. 2015a; Aoki et al. 2024).

In many of the high-latitude Northeast Atlantic sites that strongly contribute to the latitudinal dominance pattern, we observed that peracarids have declined dramatically in abundance because of overfishing and mesopredator release (Baden et al. 2012; Synnes et al. 2023). The dominance pattern may instead reflect geographic variation in human impacts more than a legacy effect of eelgrass range expansion and genetic diversity. Of note here is the fact that the mean and maximum observed sizes of epifauna (gastropods and peracarids) are the smallest in the ‘Cold Atlantic’ group of sites, which contrasts with the general trend for increased body size in colder environments (Atkinson and Sibly 1997), but might be expected under heavy predation pressure. However, past work (Reynolds et al. 2018) shows that even if predation on peracarids has increased recently in these northern sites, it is still lower than those at the southern end of *Z. marina*’s distribution, and that the recent reductions in peracarid abundance in the north may strengthen the underlying pattern of taxonomic dominance. Furthermore, the effects of fishing are hardly limited to one geographic region.

Regardless of the proximate mechanisms behind the latitudinal shift of taxonomic composition we observed, they ultimately contribute to significant, large-scale differences in the functional trait structure of global eelgrass communities. Gastropod-dominated sites were not only geographically distinct but also occupied a distinct area of trait space from communities dominated by peracarids (Figure 4A). Sites with ally similar mesograzers appeared to group according to similar latitudes within but rarely between ocean basins (Figure 4B), emphasising the role of distinct ocean basins as well as correlated aspects of eelgrass habitat structure in affecting the structure of epifaunal communities (Figure 3A,C). Epifaunal mesograzer communities in seagrass beds play a critical role in

linking the primary production of algae and seagrass to populations of larger predators, including juveniles of economically important fishery species (Bandon and zu Ermgassen 2014; Heck, Hays, and Orth 2003; McDevitt-Irwin, Iacarella, and Baum 2016). Because epifauna vary in their ability to consume fouling epiphytes, feed directly on seagrass tissue and their palatability to predators (Jernakoff and Nielsen 1997; Lewis and Anderson 2012; Reynolds et al. 2018), understanding the functional consequences of variation in taxonomic structure across broad biogeographic regions may help us begin to predict the otherwise idiosyncratic and geographically variable dynamics of seagrass ecosystem function (Duffy, Hughes, and Moksnes 2014).

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Our data and code have been privately uploaded to the Dryad data repository for peer review: https://datadryad.org/stash/share/Ki8V0vhJdq2j_hgtgWNxOtjISdKQppSAv_oZ2XDhPOE. Upon acceptance, data and code will be made available publicly on Dryad.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.