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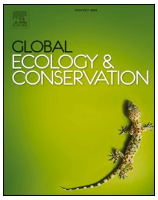

Original research article

Increasing nutrients negatively impact seagrass-associated biodiversity

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ABSTRACT

Seagrass meadows are globally important coastal habitats support high biodiversity and underpin key ecological functions, yet they are increasingly threatened by eutrophication. While the impacts of nutrient enrichment on seagrass condition and productivity are well established, its influence on the structure of associated epifaunal communities remains less clearly understood, particularly across broad spatial scales. In this study, we examined epifaunal assemblages associated with *Zostera marina* meadows at 16 sites spanning lagoon, estuarine, coastal, and island environments around the British Isles. Using standardised field sampling in combination with mixed-effects modelling, we investigated how variation in environmental setting within the seascape, seagrass morphological traits, and leaf tissue nutrient concentrations (nitrogen and phosphorus) shaped patterns of epifaunal abundance, richness, and community composition. Epifaunal assemblages exhibited strong spatial heterogeneity, with local site-level environmental conditions explaining a large proportion of variation in community structure. While broader habitat categories provided some explanatory value, seascape-level fine-scale environmental context consistently emerged as an additional driver. Seagrass morphological traits, including leaf length, width, biomass, and epiphyte cover, had limited influence on epifaunal richness and abundance, suggesting that small-scale habitat complexity was not the primary determinant of biodiversity within these meadows. In contrast, nutrient availability, particularly nitrogen enrichment, had a marked effect on epifaunal diversity. Higher nitrogen concentrations were generally associated with reduced epifaunal abundance and richness when standardised by leaf area, consistent with detrimental ecological effects of eutrophication. However, these relationships varied among habitat types: moderate nitrogen levels corresponded with increased diversity in estuarine and island sites, whereas coastal and lagoon meadows showed stronger declines under enhanced enrichment. Phosphorus exhibited especially negative effects in lagoon environments. These findings demonstrate that elevated nutrient concentrations alter seagrass-associated biodiversity in context-dependent ways. Effective management and restoration will therefore require site-specific nutrient reduction and monitoring strategies that reflect local ecological conditions rather than uniform regional targets.

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1. Introduction

Seagrass meadows are highly productive ecosystems, supporting diverse communities of organisms, shaped by the broad range of environments in which they occur. They span all climatic zones from the warm tropics of the Caribbean and Indo-Pacific, through cooler Atlantic and Pacific coasts, all the way to the Arctic north and the fringes of the Southern Ocean (McKenzie et al., 2020; Short et al., 2007). Despite these environmental differences, seagrass meadows often exhibit similar food web structures, with epifaunal organisms playing central roles as intermediaries in trophic transfers (Coll et al., 2011; Park et al., 2013). Temperate seagrass ecosystems typically support lower species richness, but strong seasonal dynamics and high endemism, often dominated by a few foundation species (Short et al., 2007). Tropical seagrass meadows host far greater biodiversity, with complex food webs, continuous productivity, and close ecological coupling to coral reefs and mangroves (Mishra et al., 2025).

Epifauna, inhabiting seagrass shoots and leaves, sediments, and hard substrates, are integral to biodiversity and ecological function. They facilitate nutrient cycling and serve as prey for higher trophic levels, underscoring their importance in seagrass ecosystem dynamics (Cui et al., 2021).

Ecosystem resilience is enhanced through top-down trophic interactions, whereby predators regulate lower trophic-level organisms, maintaining balance and mitigating environmental stressors (Field et al., 2006; Fortuna et al., 2024; Unsworth et al., 2015). For example, in Northern Baltic Sea eelgrass meadows, Gagnon et al. (2021) demonstrated that top predators regulate mesograzers such as crustaceans and gastropods. These mesograzers reduce algal overgrowth caused by nutrient enrichment, and their functional redundancy, where one group can compensate for the loss of another, provides further resilience (Vierucci, 2009). Such redundancy ensures that eelgrass meadows remain robust against stressors, including nutrient-driven algal blooms and trophic disruptions.

Broad-scale analyses across the Northern Hemisphere show that latitudinal gradients strongly influence seagrass epifauna composition and biodiversity (Duffy et al., 2022; Whalen et al., 2020). Species richness and abundance generally decline with latitude, reflecting interactions between environmental conditions and habitat complexity (Gross et al., 2022, 2024; Reynolds et al., 2018). Reynolds et al. (2018), for instance, found that predation intensity in eelgrass meadows decreased with latitude, with temperature acting as a key predictor. Higher shoot densities also reduced predation, likely due to the shelter provided. These results indicate that cooler, higher-latitude meadows support distinct epifaunal communities shaped by reduced predation pressure and increased structural complexity.

Similarly, Gross et al. (2022) examined crustacean communities across latitudinal gradients in the Pacific and Atlantic. They reported stronger predation pressures at lower latitudes, with Pacific assemblages showing greater trait diversity compared to the more clustered traits of Atlantic communities. Higher epiphyte loads were linked to increased trait clustering, influencing epifaunal interactions. Together, these studies highlight how biogeographic gradients and species interactions shape community structure.

While broad-scale studies emphasise latitudinal influences, they often overlook smaller-scale environmental variation. Seagrass meadows are found in estuaries, coastal margins, islands, and lagoons, each with distinct conditions that influence community composition (Olsen et al., 2004). In the British Isles, eelgrass (*Zostera marina*), the dominant species of the Northern Hemisphere, thrives in settings ranging from the turbid, muddy waters of the Severn estuary to the clear, deeper waters around oceanic islands (Davison and Hughes, 1998). Across these habitats, factors such as hydrodynamics, intertidal emersion, light, nutrients, and salinity vary considerably, shaping sediment type and site biogeochemistry (Gerbersdorf and Wieprecht, 2015). Although some effects on plants are known, for example on primary production (Collier et al., 2017), root stability (Carr et al., 2012) and growth (Cognat et al., 2018) our understanding of how these pressures influence seagrass-associated biodiversity and food webs remains incomplete.

Different environments impose contrasting constraints on epifauna. Estuaries, with high nutrient input from terrestrial runoff, promote epiphyte growth that supports epifaunal consumers (Whitfield et al., 2022). Yet turbidity, fluctuating salinity, and variable temperatures impose stress, fostering adaptive communities (Wołowicz et al., 2007). Islands provide clearer waters and stable salinity favourable for seagrass growth, but limited nutrients may constrain epifaunal diversity (Gil et al., 2006). Coastal habitats, with moderate nutrient levels and wave action that enhances clarity, support diverse epifauna, though high energy can uproot seagrass and disrupt communities (Reise, 2002). Lagoons, by contrast, offer shelter and habitat stability, but nutrient build-up can drive eutrophication and hypoxia, potentially threatening seagrass and epifauna (Han and Liu, 2014).

Understanding how such local environmental variations shape epifaunal composition is crucial, as they strongly influence habitat quality, resource availability, and species interactions, factors often obscured in broad-scale analyses (Ackerly, 2003). For instance, estuarine stressors such as turbidity and salinity fluctuation may select for stress-tolerant taxa, whereas nutrient-limited island meadows favour different communities. Coastal systems may support generalist species, while lagoons, despite their stability, are vulnerable to episodic biodiversity collapse from nutrient enrichment.

This study investigates how seascape and habitat level environmental variation influences epifaunal biodiversity in seagrass habitats across the British Isles. Using multivariate analyses of eelgrass communities across diverse environments, it aims to assess how seascape characteristics drive differences in richness and community structure. By linking seascape and habitat variation to biodiversity patterns, this work will improve predictions of how changing conditions alter epifaunal diversity and the resilience of seagrass ecosystems. Such understanding is essential for conservation and management, as it highlights the need for habitat-specific approaches to protect seagrass meadows and their associated biodiversity.

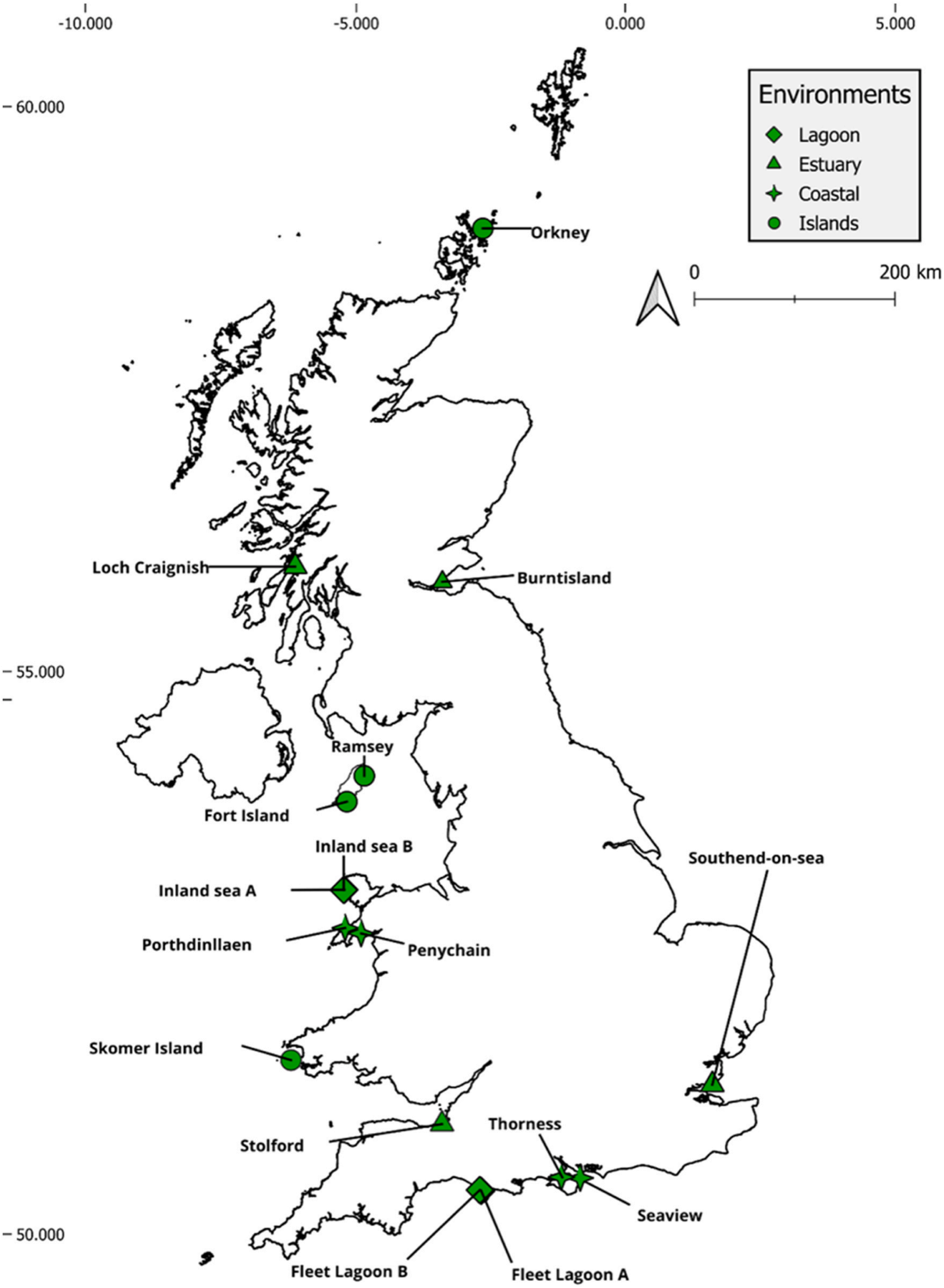

Fig. 1. Map of all the sample sites across the British Isles, categorized by environmental type. Seagrass and associated biodiversity data were collected from 16 distinct sites, classified into four environments: Lagoon (diamond), Estuary (triangle), Coastal (star), and Island (circle).

2. Methods

2.1. Study site

The British Isles seascape lies within the temperate North Atlantic seagrass bioregion, which supports the lowest seagrass diversity globally (Short et al., 2007). This bioregion contains six seagrass species, of which four occur in British Isles waters: *Zostera marina, NanoZostera noltii, Ruppia maritima* and *Ruppia cirrhosa*. The coastline of the British Isles encompasses a range of distinct environments. For this study, we selected four broad habitat categories: lagoon, estuary, coastal, and outer island to assess variation in epifaunal assemblages.

In total, 16 sites were surveyed (four per habitat type), selected from established seagrass meadows documented through SeagrassSpotter (Jones et al., 2025). Some classifications required justification. For example, Loch Craignish was considered an estuary site, despite exhibiting coastal features, due to its inland position relative to other coastal sites (Fig. 1). Similarly, the Inland Sea (sites A and B) was classified as lagoonal. While not true lagoons, these sites share key lagoonal characteristics and were included to increase sampling representation, given that Fleet Lagoon is the only true UK lagoon supporting seagrass. Two Isle of Wight sites (Thorness and Seaview) were categorised as coastal. Although island-based, their characteristics aligned more closely with coastal environments than with outer island sites elsewhere in the British Isles.

2.2. Study design

The study design followed protocols from the Zostera Experimental Network (ZEN) handbook (Sections II.A.3 and B.3; (Reynolds et al., 2018)) covering field surveys of epifauna and seagrass collection, as well as laboratory sample processing. We extended these methods to include measurements of seagrass functional traits and tissue nutrient content to examine how epifaunal diversity varied across environments.

While the ZEN handbook recommends 20 samples per site, we conducted a statistical power analysis using existing ZEN datasets ($\alpha = 0.05$, power $= 0.8$). Results indicated that reducing sampling effort to 10 replicates per site retained sufficient statistical power, thereby optimising survey efficiency.

2.3. Data collection

Sampling began at the first point of seagrass contact along a shore-perpendicular transect. At 1 m intervals, a 0.25 m^2 quadrat was placed and five shoots were cut just above the meristem. If the meristem was below the sediment surface, shoots were cut at sediment level, but below the sheath tip to avoid uprooting. A 200 μm mesh bag was slipped over the blades to capture epifauna before sealing and labelling the sample. Samples were processed as soon as possible to minimise tissue alteration. Seagrass morphometric traits were measured immediately, while epifauna were preserved in 70% ethanol for laboratory identification (Shian et al., 2016).

2.4. Habitat and environmental data

Sheath length was measured from the cut point (just above the meristem) to the highest intact leaf sheath (Gaeckle et al., 2006). The number of leaves per shoot, maximum leaf length, and maximum leaf width were recorded to estimate shoot surface area, providing indicators of seagrass growth, condition, and stress response.

Leaf tissue nitrogen (N) and phosphorus (P) values were measured by drying seagrass samples at 50°C for 24 h, grinding to a fine powder, and submitting to OEA Laboratories Ltd (Exeter, EX2 4 AN, UK) for elemental analysis. Epiphyte load was visually estimated (% cover) (McKenzie et al., 2000), as high epiphyte abundance typically indicates nutrient enrichment and can negatively impact seagrass through shading and oxygen depletion (Brodersen et al., 2015; Ralph et al., 2007).

2.5. Species identification

Epifaunal specimens were identified using dichotomous keys in Handbook of the Marine Fauna of North-West Europe (Hayward Ryland, 2017). Identification proceeded from higher taxonomic levels (class, order, family) to species, with confirmation through comparisons to published distribution ranges, habitat preferences, and reference images. Final identifications were validated using the World Register of Marine Species (WoRMS) to ensure nomenclatural accuracy.

2.6. Data analysis

To evaluate patterns in seagrass epifaunal communities, we first calculated epifaunal species abundance and richness for each sample and summarised these metrics across habitats (coastal, estuarine, lagoon, island). We then assessed community structure, at the site level, using non-metric multidimensional scaling (NMDS) based on Bray–Curtis dissimilarities of Hellinger-transformed species abundance data. Species abundances were averaged within sites prior to analysis, and empty sites and taxa were removed. Ordination was performed using the *vegan* package for R (Oksanen J et al., 2024), with stress values inspected to verify low-dimensional fit. Next, we tested for multivariate differences in community composition using permutational multivariate analysis of variance (PERMANOVA; 999 permutations) implemented the *vegan* package for R. Two complementary models were fitted. In the first model, differences among environments were tested with permutations restricted within sites to account for site-level non-independence among samples. In the second model, environment and site nested within environment were included as fixed effects to explore the relative contribution of variation among environments and among sites within environments.

Next, to assess whether seagrass structural traits influenced epifaunal assemblages, we fit mixed-effects models relating total abundance and species richness to measured seagrass shoot-level traits (e.g., leaf width, leaf length, sheath length, number of leaves per shoot, epiphyte cover, and dry biomass). As our samples included numerous true zeros (samples where shoots had no epifauna), we modelled abundance with negative binomial error structures and richness with a Poisson structure using the *glmmTMB* package for R (Brooks et al., 2017). Because our sampling method involved directly sampling shoots (Reynolds et al., 2018), rather than all shoots within a defined area (e.g., a quadrat), models were subsequently refit using leaf area as an offset term to account for variation in available habitat surface area; since seagrass shoot size can influence epifaunal colonisation. Site was included as a random effect to account for spatial non-independence.

Because leaf traits had limited impact, we conceptualised two final models relating total abundance and species richness to measured nutrient availability and environment. Nutrient availability was incorporated as fixed effects using leaf tissue nitrogen (N) and phosphorus (P) concentrations, with environment (categorical) and its interactions with nutrient variables included to test for habitat-specific responses. Site was again included as a random effect to account for spatial non-independence, and leaf area was included as an offset term to account for variation in available habitat surface area. We modelled abundance with negative binomial error structures and richness with a Poisson structure. For each selected model, we extracted effect estimates, confidence intervals, and significance values, and reported marginal and conditional R^2 (variance explained by fixed effects alone and by the full model, respectively) using the *MuMIn* package for R (Bartoń 2024). All statistical analyses were conducted in R (R Core Team, 2024).

3. Results

Abundance and richness of seagrass epifaunal communities varied among sites and habitats across the British Isles, highlighting potential influences of local environmental contexts on community structure. Across all sampled sites, 50 distinct species were identified. Island sies showed the highest abundance and richness with a total of 185 ± 18 individuals and 21 ± 0.5 species, where *Dynamene bidentate* (an isopod) and *Apherusa cirrus* (an amphipod) contributed to 65% (120 individuals) of the species observed. Coastal sites had the lowest animal abundance, totalling 40 ± 4 individuals with a richness of 16 ± 0.4 species. Estuarine sites had moderate species abundance and the highest richness with 93 ± 5 individuals and 24 ± 0.5 species. Lagoon sites showed the lowest species richness with 13 ± 0.5 species with 79 ± 9 individuals. *Dexamine spinosa* (an amphipod)*, Pullilina sarsii* (Gastropod), and *Idotea chelpes* (an isopod) were the most widespread species. *Pusillina sarsii* was the only species found across each environmental type as shown in (see Appendix 1).

Using a site-level NMDS ordination of epifaunal communities, we reveal clustering of sites by environment (Fig. 2; stress = 0.1419), indicating modest two-dimensional representation of community dissimilarity. Moreover, the broad habitat categories we used (environment) explained a modest but significant proportion of variation in epifaunal community composition (PERMANOVA with

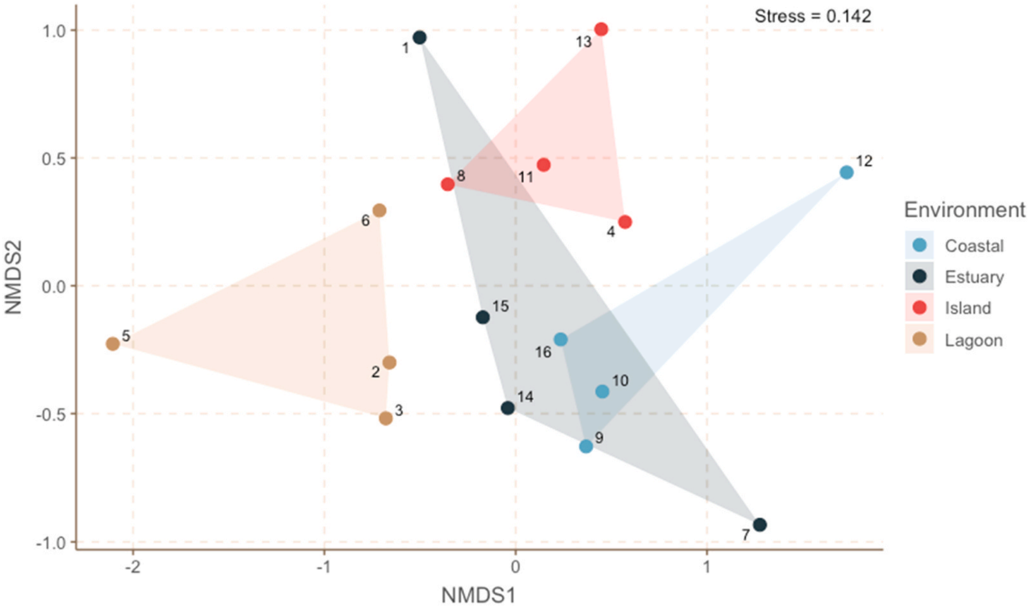

Fig. 2. Non-metric multidimensional scaling (NMDS) ordination of epifaunal community composition, based on Bray–Curtis dissimilarities, across 16 seagrass sites in the British Isles. Each point represents a site-level replicate (average of 10 within-site samples), coloured by environment: coastal, estuary, lagoon, or island. Convex hulls indicate the observed multivariate extent of samples within each environment. Stress = 0.1419.

permutations restricted within sites: $R^2 = 0.13$, $F = 7.45$, $p < 0.001$), indicating that differences among environments contribute to, but do not fully explain, observed patterns in assemblage structure. In a complementary fixed-effects PERMANOVA including environment and site nested within environment, a large proportion of the remaining variation was attributable to differences among sites within environments (site[environment]: $R^2 = 0.44$, $F = 5.25$, $p < 0.001$), highlighting pronounced site-level heterogeneity. These results likely indicate that epifaunal communities are highly site-specific, suggesting that local site-level conditions may play an important role in structuring epifaunal assemblages, potentially outweighing broad environmental categorisation.

Despite the well-established role of seagrass leaf traits in shaping biodiversity–ecosystem functioning, we found limited evidence for any significant relationships between epifaunal abundance (marginal $R^2 = 0.12$; conditional $R^2 = 0.54$) or richness (marginal $R^2 = 0.04$; conditional $R^2 = 0.28$) and the fine-scale site-level seagrass morphological traits measured. None of the predictors, including leaf width, leaf length, sheath length, dry biomass, number of leaves per shoot, or epiphyte cover, were statistically significant (all $p > 0.05$). While the direction of some effects (e.g. a weak positive association with dry biomass and leaf width) suggested potential trends, these were highly uncertain. Overall, we found that seagrass epifaunal communities across the British Isles were not strongly structured by variation in seagrass leaf traits at the scales measured.

Because individual leaf traits had limited influence, we then used leaf area as an offset to control for variation in the size of seagrass shoots sampled (potential surface area as epifaunal habitat) at each site and examined the effects of nitrogen (N), phosphorus (P), and environment on epifaunal abundance and richness. Using generalised mixed effects models (Fig. 3), we found that N had a significant negative overall effect on epifaunal abundance (Fig. 4A; estimate = –2.32, $p < 0.05$), meaning that, per unit leaf area, higher nitrogen availability generally corresponded to lower epifaunal abundance; an increase of 1 unit of N corresponds to approximately 90% decrease in abundance per cm^2 leaf area. However, we found that this effect was reversed in estuarine and island habitats due to positive N × environment interactions (N × estuary: 2.85, $p < 0.05$; N × island: 2.64, $p < 0.05$), indicating that in these habitats, higher N was associated with higher abundance compared to the coastal baseline (Fig. 4B). In contrast, P did not show significant main or interactive effects. Some environment categories showed marginally significant differences compared to the reference coastal environment (e.g., lagoon: $p \approx 0.068$), indicating that local habitat context also influences epifaunal abundance.

For epifaunal species richness, we observed a similar pattern to that observed for epifaunal abundance (Fig. 3). Nitrogen had a significant negative overall effect (Fig. 5A; –1.94, $p < 0.05$), but again the negative effect was mitigated or reversed in estuarine habitats (Fig. 5C; N × estuary: 2.88, $p < 0.05$). Phosphorus did not have a significant main effect but was strongly negative in lagoons (Fig. 5; P × lagoon: –20.63, $p < 0.05$). Environmental effects mirrored the abundance model: richness was lower in estuaries (–2.65, $p < 0.05$) and higher in lagoons (8.69, $p < 0.05$) compared to coastal baseline sites (Fig. 5B), whereas island environments did not differ. By including leaf area as an offset, these models reveal that nutrient availability and environment context structure epifaunal

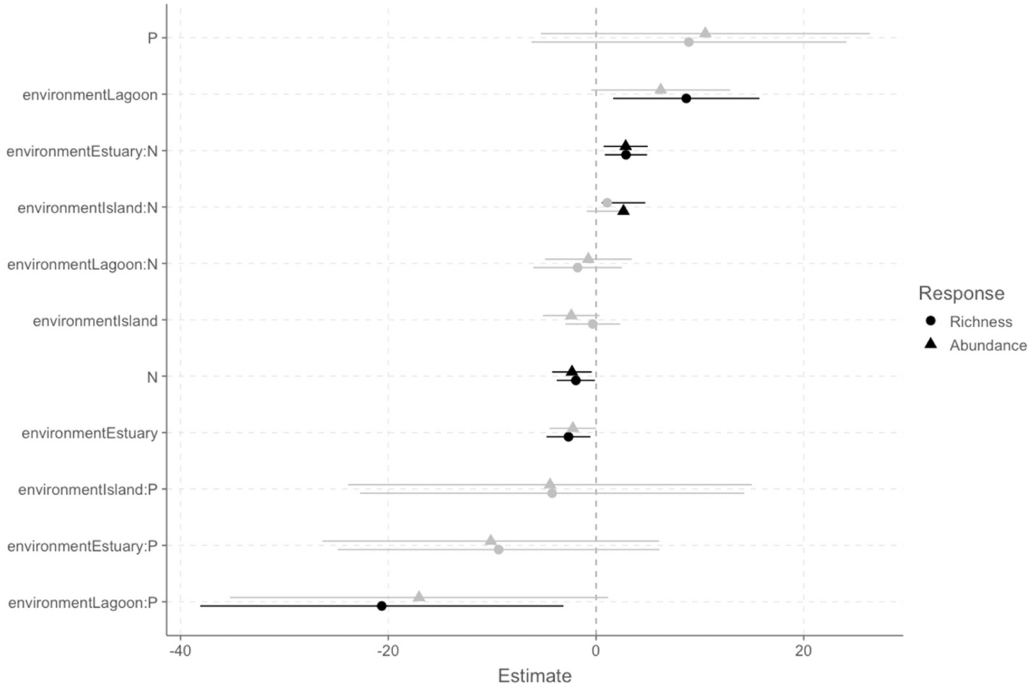

Fig. 3. Estimated regression coefficients from negative binomial mixed-effects models of epifauna richness and abundance. Points represent model coefficients for each predictor with 95% confidence intervals. Shapes indicate the response variable (● = richness, ▲ = abundance). Coefficients are displayed on the log scale, such that values above zero indicate a positive association, and values below zero indicate a negative association. Black symbols and lines denote significant effects ($p < 0.05$), while grey symbols and lines denote non-significant effects ($p \geq 0.05$). Models included a random intercept for site and an offset for seagrass leaf area.

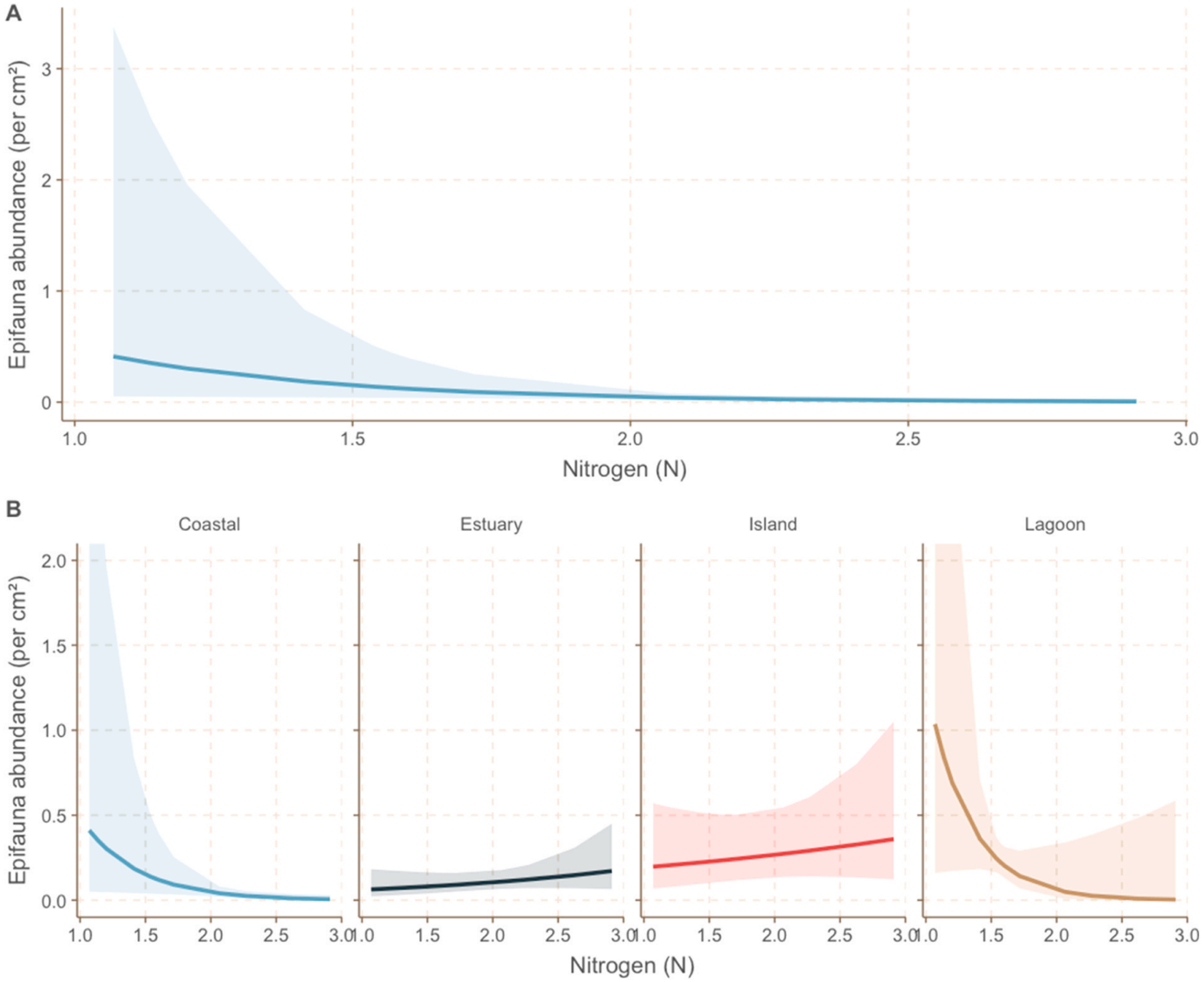

Fig. 4. Significant predictors of epifauna abundance per cm^2 leaf area. Panel A shows the marginal effect of Nitrogen (N), and B shows the interaction between Environment and N. Shaded areas or error bars represent 95% confidence intervals. Predictions were calculated holding other covariates at their mean values.

abundance and richness independently of seagrass habitat complexity, and that the effect of N can vary strongly among habitats, even reversing from negative in coastal sites to positive in estuaries and islands.

Finally, variability among sites was considerable (variance = 0.058 for abundance, 0.054 for richness), highlighting the role of local conditions not captured by measured seagrass traits or nutrient levels. Combined, these results suggest that while seagrass leaf morphology alone is a poor predictor of epifaunal communities, nutrient availability and habitat type interact to shape both abundance and richness, with the strength and direction of these effects varying spatially across the British Isles.

4. Discussion

We have now transgressed seven of the nine *so called* Planetary Boundaries, including the biogeochemical flows of nitrogen and phosphorus (Sakschewski and Caesar, 2025). Nutrient enrichment remains one of the most pressing environmental challenges in coastal waters, particularly with regard to biodiversity loss (Smith, 2003).

Yet, surprisingly few studies have examined the impacts of elevated nutrient levels on biodiversity across large spatial scales (Duprey et al., 2016). Within seagrass systems, research has predominantly focused on plant level habitat degradation (Schmidt et al., 2012) or food web interactions (Cui et al., 2021), with comparatively limited attention to associated faunal communities, with many such investigations being laboratory-based (Peixoto Dias et al., 2025). Our study, therefore, provides a novel large-scale assessment of seagrass-associated biodiversity across temperate settings, revealing a clear negative influence of increasing nitrogen on epifaunal richness, abundance, and community composition.

Epifaunal assemblages in *Zostera marina* meadows were highly site-specific, with strong spatial variation in both abundance and richness. While the seascape setting explained some of the observed ecological community structure, site identity (i.e., its local

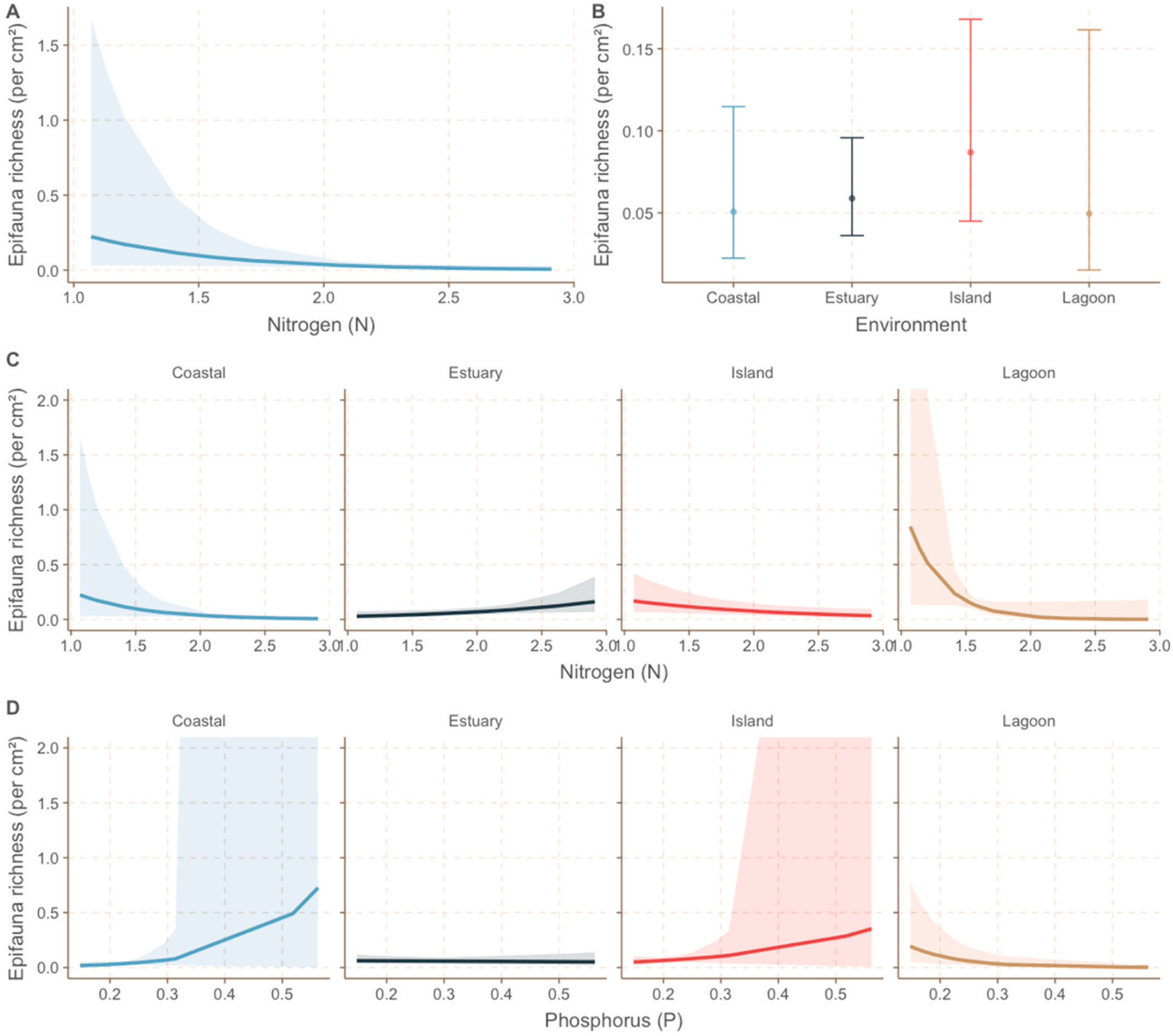

Fig. 5. Significant predictors of epifauna richness per cm^2 leaf area. Panel A shows the marginal effect of Nitrogen (N), B shows the marginal effect of Environment, C shows the interaction between Environment and N, and D shows the interaction between Environment and Phosphorus (P). Shaded areas or error bars represent 95% confidence intervals. Predictions were calculated holding other covariates at their mean values.

environmental conditions) accounted for the majority of differences. This finding supports earlier work showing that localised factors, including hydrodynamics, sediment type, and nutrient regimes, are likely key determinants of seagrass-associated communities (Bowden et al., 2001; Rodil et al., 2021; Saunders et al., 2003). However, our results contrast with basin-wide studies that identified latitude and temperature as dominant drivers in low nutrient seagrass systems (Duffy et al., 2022; Whalen et al., 2020). We hypothesise this difference to be due to the relatively limited variability in that dataset with respect to nutrient conditions, as the majority of the sites examined were relatively ‘healthy’. Seagrass meadows in the UK are known to be highly nitrogen-rich, with some sites exhibiting values higher than previously recorded anywhere in the World (Jones and Unsworth, 2016), creating a ready test ground for understanding these factors.

Patterns of epifaunal diversity changed with respect to the seascape setting. Species abundance and richness peaked at island sites and were lowest in coastal meadows, diverging from studies in the United States that reported no clear relationships with environmental variables (Murphy et al., 2021). Lower diversity and abundance in coastal sites may be a result of complex anthropogenic stressors such as boating disturbance, and habitat fragmentation (Green et al., 2021; Jones and Unsworth, 2016; Jones et al., 2025), but also an interaction with elevated nutrient levels (Gil et al., 2006). While reduced anthropogenic pressure may benefit faunal populations, it can also increase competitive dynamics and destabilise food webs under weak top-down control (Coll et al., 2011; Morozov et al., 2012; Ritchie and Johnson, 2009). These findings echo Jephson et al. (2008) who showed that both nutrient enrichment and trophic interactions regulate grazer populations in seagrass systems.

Seagrass meadows are recognised as ecosystems where biodiversity underpins nutrient cycling, secondary production, and carbon storage (Duarte et al., 2025; Duffy, 2006). Sites with higher richness also often supported greater overall abundance, particularly island meadows, consistent with evidence that diverse assemblages partition resources and stabilise trophic interactions (Duffy et al., 2003; Gamfeldt et al., 2015). However, the lack of strong links between seagrass morphology and faunal richness suggests that biodiversity is not a simple function of habitat complexity. Instead, nutrient regimes and site-specific conditions appear more important in regulating ecosystem functioning.

Seagrass structural traits, including leaf width and biomass, showed only weak and uncertain relationships with epifaunal diversity. Previous studies have emphasised the role of shoot density and leaf length in providing refuge and colonisation surfaces (Bostrum and Mattila, 1999; Heck and Orth, 1980) but our findings suggest that UK meadows fall within a threshold of structural suitability, with environmental and community drivers exerting stronger influences (Murphy et al., 2021). Nutrient availability, particularly nitrogen, emerged as a more consistent driver. Nitrogen enrichment reduced both abundance and richness when standardised by leaf area, reflecting its role in promoting epiphyte overgrowth and reducing seagrass health (Burkholder et al., 2007). With increased epiphyte load from higher nitrogen, it might be expected that many of the grazing epifauna proliferate, as studies from Sweden have revealed strong negative correlations between the two (Jephson et al., 2008). However, there is strong evidence that these populations are in fact structured far more by top-down (i.e., predation) rather than bottom-up processes (algae) (Reynolds et al., 2018). Predatory fish populations around the coasts of the British Isles remain depleted (Hunt et al., 2024; Kelly et al., 2006), likely leading to increased secondary consumers (e.g., fifteen-spined stickleback) (Moksnes et al., 2008) that are likely to control grazer abundance and known to be abundant in seagrass within the region (Bertelli and Unsworth, 2014). However, context-dependent effects were evident: in estuarine and island systems, moderate enrichment appeared to enhance food availability, while in nutrient-impacted coastal sites further enrichment exacerbated biodiversity loss. Phosphorus showed particularly strong negative effects in lagoon systems, consistent with their limited flushing capacity and vulnerability to nutrient enrichment (Tett et al., 2003). These findings highlight the interplay between nutrient enrichment and local conditions in shaping biodiversity (Bertelli et al., 2021; Vieira et al., 2022, 2024).

The high levels of unexplained variance among sites underscores the complexity and the knowledge gaps in our understanding of seagrass–epifauna interactions and the drivers of coastal biodiversity. Such knowledge gaps also exist for seagrass-infauna relationships (Riera et al., 2025). We hypothesise that the spatial configuration of the seascape connectivity (Preston et al., 2025), predator pressure (Reynolds et al., 2018) and historical disturbance altering within habitat connectivity (Grech et al., 2018), likely have far bigger roles than we appreciate. We also recognise that stochastic recruitment events may also influence the relative abundance of these communities (Bulleri, 2005). Management approaches must therefore go beyond morphological monitoring, integrating nutrient status and site-specific pressures.

Overall, British Isles *Zostera marina* meadows exhibit fine-scale ecological heterogeneity. Although habitat type and nutrient dynamics shape broad patterns, local site conditions dominate faunal community structure. Conservation and restoration efforts should be tailored to these contexts, with adaptive strategies that account for both the risks of nutrient enrichment and the potential for moderate nutrient concentrations to sustain biodiversity in certain environments. As seagrass meadows gain recognition for their biodiversity and climate mitigation roles, nuanced understanding of these drivers is essential for effective protection and restoration.

Author contributions

Project inception and design (all authors); Project planning, delivery and fieldwork (MH and RU); Laboratory analysis (MH); Statistics (BJ and RU); Writing and reviewing (all authors).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data archiving

All data will be archived within the MEDIN (UK) system linked to GBIF and OBIS.

Appendix A. List of species that were found across all sample sites. Each species is categorised under Class, then Order, and then species name and is shown which environments they were found with the labels *I* (Island), *C* (Coastal), *E* (Estuary), and *L* (Lagoon). Species that were unidentified due to genetics analysis needed (nematode ssp.) or damaged samples have been excluded from this list

Class: Bivalve

- **Order:** Cardiida

o *Abra tenuis* (Montagu, 1803) (*C*)
o *Cerastoderma edule* (Linnaeus, 1758) (*E*)

Class: Enteropneusta

- **Order:** Enteropneusta *incertae sedis*
- *Saccoglossus ruber* (Tattersall, 1905) (*I*)

Class: Gastropoda

- **Order:** Archaeogastropoda
- *Patella pellucida* (Linnaeus, 1758) (*E, I*)
- **Order:** Aplysiida
- *Aplysia punctata* (Cuvier, 1803) (*I*)
- **Order:** Caenogastropoda
- *Bittium reticulatum* (da Costa, 1778) (*C, E*)
- **Order:** Littorinimorpha
- *Alvania puncture* (Montagu, 1803) (*C*)
- *Cingula trifasciata* (J. Adams, 1800) (*C*)
- *Ecrobia ventrosa* (Montagu, 1803) (*L*)
- *Hydrobia acuta neglecta* (Muus, 1963) (*E*)
- *Lacuna crassior* (Montagu, 1803) (*C*)
- *Lacuna vincta* (Montagu, 1803) (*E*)
- *Littorina littorea* (Linnaeus, 1758) (*E, I*)
- *Littorina obtusata* (Linnaeus, 1758) (*C*)
- *Littorina saxatilis* (Olivi, 1792) (*C, E, L*)
- *Melarhaphe neritoides* (Linnaeus, 1758) (*C*)
- *Obtusella intersecta* (S. V. Wood, 1857) (*E*)
- *Peringia ulvae* (Pennant, 1777) (*E*)
- *Potamopyrgus antipodarum* (J. E. Gray, 1843) (*E*)

Pusillina sarsii (Lovén, 1846) (*C, E, I, L*)

- Rissoa membranacea (J. Adams, 1800) (C, E, L)
- Rissoella opalina (Jeffreys, 1848) (I)
- **Order:** Trochida
- Steromphala pennanti (R. A. Philippi, 1851) (I)
- Steromphala umbilicalis (da Costa, 1778) (C, E, I)

Class: Hexacorallia

- **Order:** Actiniaria
- *Anemonia viridis* (Forsskål, 1775) (*C, E*)

Class: Malacostraca

- **Order:** Amphipoda
- *Apherusa cirrus* (Spence Bate, 1863) (*I*)
- *Corophium arenarium* (Crawford, 1937) (*L*)
- *Corophium multisetosum* (Stock, 1952) (*L*)
- *Dexamine spinosa* (Montagu, 1813) (*E, I, L*)
- *Ericthonius difformis* (H. Milne Edwards, 1830) (*I, L*)
- *Gammarus locusta* (Linnaeus, 1758) (*I*)
- *Gammarus zaddachi* (Sexton, 1912) (*E*)
- *Leptocheirus pilosus* (Zaddach, 1844) (*L*)
- *Microprotopus maculatus* (Norman, 1867) (*C, I*)
- *Nototropis swammerdamei* (H. Milne Edwards, 1830) (*E, I*)
- *Nototropis vedlomensis* (Spence Bate & Westwood, 1862) (*E*)
- **Order:** Decapoda
- *Eualus gaimardii* (H. Milne Edwards, 1837) (*E*)
- *Rhithropanopeus harrisii* (Gould, 1841) (*E*)
- **Order:** Isopoda
- *Cleantis prismatica* (Risso, 1827) (*E, I, L*)
- *Dynamene bidentata* (Adams, 1800) (*I*)
- *Idotea balthica* (Pallas, 1772) (*I*)
- *Idotea chelipes* (Pallas, 1766) (*E, L*)
- *Idotea linearis* (Linnaeus, 1767) (*I*)
- *Idotea neglecta* (G. O. Sars, 1897) (*E*)
- *Idotea pelagica* (Leach, 1816) (*E*)
- *Lekanesphaera rugicauda* (Leach, 1814) (*L*)

Class: Polychaeta

- **Order:** Eunicida
- *Hyalinoecia tubicola* (O.F. Müller, 1776) (*I, L*)
- **Order:** Terebellida
- *Nicolea zostericola* (Örsted, 1844) (*I*)
- **Order:** Phyllodocida
- *Parexogone hebes* (Webster & Benedict, 1884) (*I*)

Data availability

Data will be made available on request.

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