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ARTICLE

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Mapping benthic biodiversity to facilitate future sustainable development

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Abstract

Human activities in the marine environment are expanding rapidly, with much of the growth in the Northeast Atlantic driven by offshore wind development. While offshore wind is critical for achieving net zero carbon targets, planning decisions must also address the twin challenge of conserving and restoring biodiversity. We combined open-access data from hundreds of grab and core surveys with random forest modeling to provide new insights into patterns of benthic biodiversity across the Northeast Atlantic continental shelf. Multiple dimensions of biodiversity were mapped using Hill numbers ($q = 0$, 1, 2) and raw abundance, assessed within the Whittaker framework (alpha-, beta-, and gamma-diversity) to reveal patterns at different spatial scales. These metrics were synthesized into a single biodiversity map using clustering, delineating areas of seabed with shared biodiversity characteristics. This analysis offers an evidence-based framework for safeguarding benthic biodiversity and informing management decisions in an era of rapidly expanding offshore development. Our results also highlight key environmental drivers, with higher biodiversity consistently associated with greater gravel coverage and moderate to high current speeds.

KEYWORDS
benthic macrofauna, biodiversity, clustering, random forest, seabed

INTRODUCTION

Human activities in the marine environment are rapidly increasing (Halpern et al., 2015; Jouffray et al., 2020), with much of the recent growth associated with net zero targets and the expansion of the offshore wind industry (Birchenough & Degraer, 2020; IEA, 2019; Korpinen et al., 2021). Adopting more sustainable and restorative ways of conserving biodiversity is now a global priority (Hooper et al., 2021; Maron et al., 2016; United Nations, 2023). Yet, offshore wind projects are associated with various benthic effects, with implications for biodiversity (Dannheim et al., 2020; Li et al., 2023). Thus, to be sustainable, such development must be cognizant of the twin challenges of climate change and biodiversity loss (Arneth et al., 2020; Bellard et al., 2012), and the role of the benthos in both (Solan et al., 2020). Biodiversity loss impairs ecosystem services and negatively impacts humanity (Cardinale et al., 2012; Naeem et al., 2016; Worm et al., 2006). Improving understanding of spatial

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and temporal patterns in seabed biodiversity is key to sustainable development (Clare et al., 2022; Kunzig, 2008; Magurran, 2021; Pauly, 1995) and can help ensure that future licensed activities avoid areas of importance.

Marine benthic fauna are critically important for both ecosystem and human health, providing a range of functions including ecosystem stability and resilience (Duncan et al., 2015; Galparsoro et al., 2014; Snelgrove et al., 2018). Despite its importance, marine benthic biodiversity is changing (Sala & Knowlton, 2006; Thompson et al., 2020) because of factors including habitat destruction (Harris, 2020), demersal fishing (Kaiser et al., 2000), pollution (Hale et al., 2018), climate change (Weinert et al., 2021), and the introduction of non-native species (Snelgrove, 1997). The challenge therefore is how to conserve biodiversity and, where degraded, recover it while simultaneously accommodating ever-increasing human activities in the marine ecosystem.

A range of measures have been implemented to address this paradoxical tension, including the establishment of marine-protected areas (MPAs) (Kriegl et al., 2021; Roberts et al., 2017; Sala et al., 2021), restrictions on fishing effort (Hiddink et al., 2006), and "net gain" policies (Hooper et al., 2021), achieved through initiatives like "building with nature" (de Vriend & Van Koningsveld, 2012), restoration (Abelson et al., 2016; Cooper et al., 2007; Cuvelier et al., 2018) and nature-based solutions (Solan et al., 2020). A growing number of authors argue that MPAs alone will not be sufficient to protect biodiversity (Santangeli et al., 2023; Weinert et al., 2021). Therefore, new approaches are needed to ensure decision-making adopts a more ecosystem-wide perspective, aiming for human activities to result in no net loss or, ideally, a net gain in biodiversity. Such an approach will require improved understanding of the benthos and its interactions with other components of the system. One aspect of the benthos that remains poorly understood is spatial biodiversity patterns, with existing knowledge largely derived from limited data and simple metrics (Barrio Froján et al., 2012; Reiss et al., 2010) or from physical habitat proxies such as the European Nature Information System (EUNIS) marine habitat classification (Davies et al., 2004). Enhancing our understanding of benthic biodiversity at management-relevant scales can aid in marine licensing, ensuring that developments avoid impacting critical areas and informing decisions on biodiversity recovery and conservation (Kunzig, 2008).

The abstract concept of biodiversity, defined as the "variety of life" (Gaston, 1996), cannot be captured by a single measure (Santini et al., 2017; Warwick & Clarke, 1995). Building on this idea, Magurran (2021) identifies two key facets of biodiversity assessment. The first focuses on numbers of species, with different commonly used metrics effectively "turning the dial" on relative abundance. Accounting for abundance is important, as given the same number of species, locations with a more even spread of individuals between species are considered more diverse than those where abundance is dominated by a small number of taxa (Gotelli & Chao, 2013). Hill numbers (Hill, 1973) provide a convenient set of three such metrics within the same statistical framework, with Hill (number) 0 being species richness, Hill 1 the exponential form of Shannon diversity, and Hill 2 the reciprocal form of Simpson diversity. Hill 1 and 2 can be interpreted, respectively, as the effective number of frequent and highly frequent species in the assemblage (Chao et al., 2023). Differences between these metrics provide information on whether any change is driven by rare or more abundant taxa. The second important facet takes account of taxon identity, recognizing that two areas can have the same number of species yet share none in common. In this scenario, it could be misleading to suggest that the biodiversity of these locations is the same. This issue is addressed by Whittaker (1960, 1972), who partitioned biodiversity into alpha, beta, and gamma components. We define alpha-diversity as sample-level species richness, gamma-diversity as regional species richness estimated from a collection of samples, and beta-diversity as the effective number of communities within a region (i.e., gamma-diversity divided by mean alpha-diversity), thereby capturing changes in species richness and composition across spatial scales (Wang & Loreau, 2014). Whilst there are other approaches for quantifying biodiversity (e.g., Taxonomic Distinctness, Clarke & Warwick, 1998; Phylogenetic diversity, Cardillo, 2023; Biological Traits, Bremner et al., 2006; Rao's Quadratic Entropy, Botta-Dukat, 2005), we focus on classic metrics as a starting point from which the approach taken in this paper can be developed in the future.

Biodiversity and its patterns in the marine benthos have been extensively studied across various geographical regions and spatial scales (e.g., Barrio Froján et al., 2012; Bolam et al., 2008; Heip et al., 1992; Rees et al., 1999; Reiss et al., 2010; Renaud et al., 2009; Thompson et al., 2020). The majority of these studies focus on alpha-diversity (Vassallo et al., 2020), namely, the variety of species found in the sampling device (e.g., grab), using metrics like Shannon–Wiener (H') and Margalef's diversity. Far fewer studies have considered beta-diversity, either in isolation or in combination with alpha-diversity (Ellingsen & Gray, 2002), or alpha- and gamma-diversity (Barros et al., 2014). The inability to integrate outcomes from studies using different biodiversity scales and metrics currently hampers our understanding of benthic biodiversity across large spatial scales. This, in turn, hinders effective marine management decisions regarding the potential ecological risks posed by future offshore developments.

Improved access to data, together with new data science techniques, like machine learning, makes it possible to create high-resolution maps reflecting different aspects of the benthos (e.g., Bolam et al., 2023; Cooper et al., 2019; Mazor et al., 2017). In this study, we use open benthic data (see *OneBenthic*, https://rconnect.cefas.co.uk/onebenthic_portal/), along with multiple environmental raster predictor layers to map various aspects of biodiversity using a random forest approach. This mapping is based on Hill numbers, abundance, and the Whittaker framework. Our aim was to develop an approach to synthesize complex, multidimensional biodiversity information into a single, holistic integrated assessment that can be more readily used, particularly by decision-makers who need clear guidance on priority areas. While individual

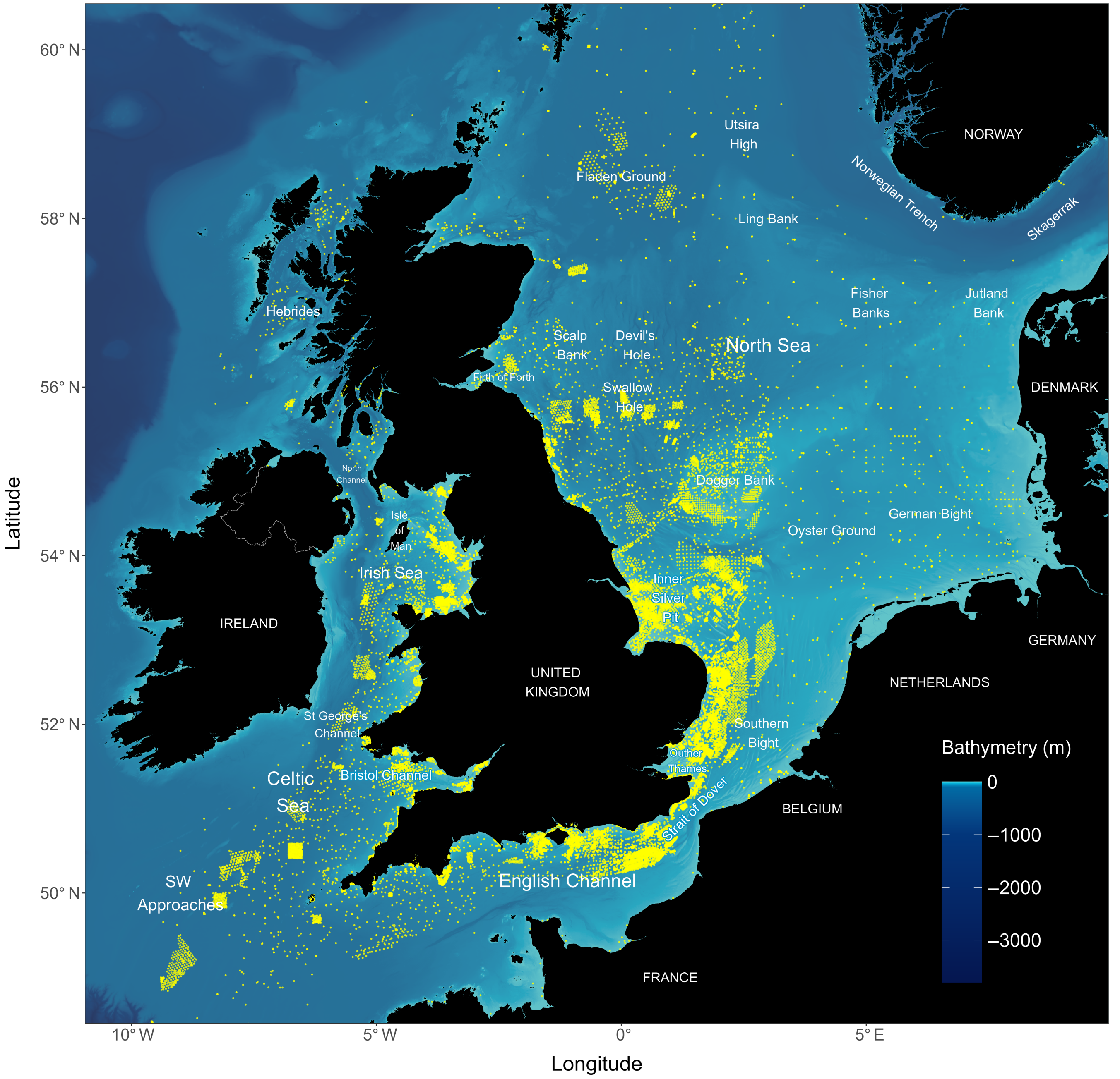

FIGURE 1 Locations (in yellow) of 0.1-m^2 grab or core samples from *OneBenthic*. Although depth was not found to be a significant factor in this study, the bathymetric map (source: GEBCO Grid; GEBCO Compilation Group, 2023) provides context for the seabed sampling locations. Note that the data are disparate and not evenly distributed in space and time, which is a limitation of the dataset.

TABLE 1 Equations used in this study for calculation of biodiversity metrics.

Metric	Description	Equation	No.
Hill no. (^0D)	Species richness (S) where S: total no. species; q: sensitivity to relative abundance; p_i: proportion of species belonging to ith species	$^qD = \left(\sum_{i=1}^{S} {p_i}^q\right)^{\frac{1}{1-q}}, q = 0$	(1)
Hill no. (^1D)	Exponential of Shannon entropy (e^H)	$^qD = \left(\sum_{i=1}^{S} {p_i}^q\right)^{\frac{1}{1-q}}, q = 1$	(2)
Hill no. (^2D)	Reciprocal of Simpson index $\left(\frac{1}{d}\right)$	$^qD = \left(\sum_{i=1}^{S} {p_i}^q\right)^{\frac{1}{1-q}}, q = 2$	(3)
Abundance (N)	No. individuals summed over all taxa	$N = \sum(n)$	(4)
Alpha-diversity (α)	Sample-level species richness where Z: species abundance	$^qD_\alpha = \frac{^qD_{\text{joint}}}{N} = \frac{1}{N}\left\{\sum_{i=1}^{S}\sum_{k=1}^{N}\left(\frac{Z_{ik}}{Z_{++}}\right)^q\right\}^{\frac{1}{1-q}}, q \neq 1.$	(5)
Beta-diversity (β)	Effective no. communities	$^qD_\beta = \frac{^qD_\gamma}{^qD_\alpha}, q \geq 0.$	(6)
Gamma-diversity (γ)	Regional species richness	$^qD_\gamma = \left(\sum_{i=1}^{S}\left(\frac{Z_{i+}}{Z_{++}}\right)^q\right)^{1/(1-q)} = \left(\sum_{i=1}^{S} p_{i+}^q\right)^{1/q \neq 1}, q \neq 1.$	(7)

biodiversity metrics provide valuable, but sometimes contrasting, perspectives (e.g., alpha- vs. beta-diversity), integrating them helps highlight areas where multiple dimensions of biodiversity are consistently high. This synthesis is intended to support marine spatial planning by providing an accessible, practical output that complements the underlying detailed metrics. Understanding where biodiversity is high—and thus where environmental protection may be most warranted and effective—is vital for future sustainable development. This study provides a data-driven perspective based on classic biodiversity metrics, an approach which can inform marine spatial planning and management decisions in the United Kingdom and in other regions facing similar challenges.

METHODS

Our goal was to produce a single, holistic map of benthic biodiversity to support marine spatial planning and licensing. This map integrates multiple spatially explicit metrics, synthesizing complex, multidimensional information into a clear, reproducible output that guides prioritization of protection or mitigation. Given the length and complexity of the methods, this section provides a high-level overview; full details are available in Appendix S1. All analyses were conducted in R (R Development Core Team, 2024), which provided a flexible and reproducible environment for data processing, statistical modeling, and map generation.

TABLE 2 Matrix of biodiversity metrics.

	Whittaker framework		
Metric	**α**	**β**	**γ**
Hill no. (^0D)	$^0D_\alpha$	$^0D_\beta$	$^0D_\gamma$
Hill no. (^1D)	$^1D_\alpha$	$^1D_\beta$	$^1D_\gamma$
Hill no. (^2D)	$^2D_\alpha$	$^2D_\beta$	$^2D_\gamma$
Abundance (N)	N	N_{cv}	N_{tot}

Abbreviations: $^0D_\alpha$, Hill 0 alpha; $^0D_\beta$, Hill 0 beta; $^0D_\gamma$, Hill 0 gamma; $^1D_\alpha$, Hill 1 alpha; $^1D_\beta$, Hill 1 beta; $^1D_\gamma$, Hill 1 gamma; $^2D_\alpha$, Hill 2 alpha; $^2D_\beta$, Hill 2 beta; $^2D_\gamma$, Hill 2 gamma; N, abundance; Ncv, abundance cv; N_{tot}, abundance total.

Dataset

Macrofaunal data were sourced from the *OneBenthic* Grab and Core database (https://rconnect.cefas.co.uk/onebenthic_portal/), which compiles publicly available survey data on macrofaunal abundance, biomass, and sediment particle size. Taxonomic nomenclature in the database was standardized using the World Register of Marine Species (WoRMS Editorial Board, 2024), with each taxon linked to its AphiaID; colonial taxa were assigned a nominal abundance of 1. We retained all comparable samples—collected with a 0.1-m^2 grab or core and processed with a 1-mm sieve—spanning 1985–2023, yielding 37,909 samples. More than 90% of these were collected between 2000 and 2023, ensuring the dataset largely reflects contemporary conditions. Samples with metadata or survey notes indicating localized,

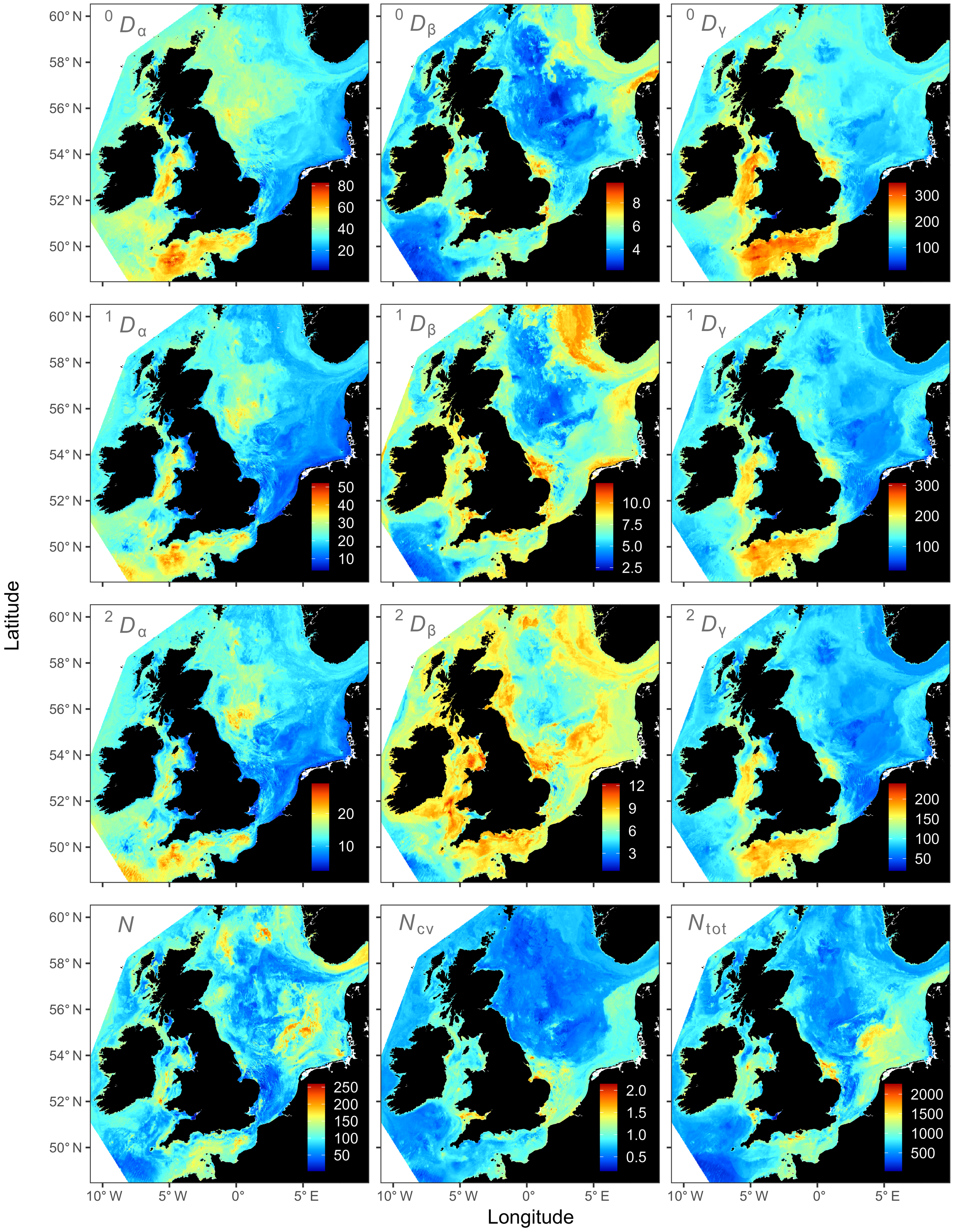

FIGURE 2 Legend on next page.

nonrepresentative impacts (e.g., dredged material disposal sites, aggregate extraction zones) were excluded. Widespread activities such as demersal fishing, which affect much of the region, were not grounds for exclusion, as our aim was to remove only samples associated with clear, localized acute impacts. Records used in biodiversity metrics were restricted to species, genus, or family level. While inclusion of higher level identifications may overlap with species entries, many benthic taxa cannot be resolved further. Limiting records to family level and below was therefore adopted as a practical compromise, minimizing double counting while retaining meaningful taxonomic information. To reduce spatial autocorrelation, samples closer than 50 m to any other were excluded (following Cooper et al., 2019), leaving 22,793 samples for analysis (Figure 1).

Biodiversity metrics

We calculated biodiversity metrics based on Hill numbers ($q = 0, 1, 2$) and abundance within the Whittaker framework (α-, β-, γ-diversity), producing 12 core metrics. Hill 0 corresponds to species richness, Hill 1 to the exponential of Shannon entropy, and Hill 2 to the inverse of Simpson diversity, capturing differences in the influence of rare versus common species. Alpha-diversity quantifies diversity within individual samples; beta-diversity describes compositional turnover among samples within a region; and gamma-diversity estimates regional diversity from multiple samples.

Abundance was assessed independently, while species-based metrics were statistically standardized to control for variation in sample counts following Thompson et al. (2020), with rarefaction and extrapolation implemented in the *iNEXT* package in R (Hsieh et al., 2016). Alpha-diversity was standardized to a single grab sample, while beta- and gamma-diversity were based on six grab samples drawn from within a 75-km radius and ±182 days of each focal cell.

Detailed equations for metric calculation are provided in Table 1, and the full list of calculated metrics is summarized in Table 2. Technical steps for data pretreatment (e.g., outlier handling, transformations) and preparation of metrics for clustering (e.g., covariance assessment) are provided in Appendix S1: *Outlier removal*, *Data transformation*, and *Covariation assessment and selection of metrics*.

TABLE 3 Mean and SD of model validation statistics over 10 random split sample runs.

Model	*n*	R^2
${}^0D_\alpha$	15,944	0.49 ± 0.01
${}^1D_\alpha$	14,252	0.39 ± 0.01
${}^2D_\alpha$	14,123	0.32 ± 0.01
${}^0D_\beta$	15,755	0.51 ± 0.01
${}^1D_\beta$	14,310	0.50 ± 0.01
${}^2D_\beta$	12,585	0.41 ± 0.01
${}^0D_\gamma$	15,891	0.69 ± 0.01
${}^1D_\gamma$	12,955	0.69 ± 0.01
${}^2D_\gamma$	11,469	0.69 ± 0.01
N	15,012	0.32 ± 0.02
N_{cv}	15,834	0.47 ± 0.01
N_{tot}	14,876	0.48 ± 0.02

Abbreviations: ${}^0D_\alpha$, Hill 0 alpha; ${}^0D_\beta$, Hill 0 beta; ${}^0D_\gamma$, Hill 0 gamma; ${}^1D_\alpha$, Hill 1 alpha; ${}^1D_\beta$, Hill 1 beta; ${}^1D_\gamma$, Hill 1 gamma; ${}^2D_\alpha$, Hill 2 alpha; ${}^2D_\beta$, Hill 2 beta; ${}^2D_\gamma$, Hill 2 gamma; N, abundance; Ncv, abundance cv; N_{tot}, abundance total.

Biodiversity clusters

To synthesize the multidimensional biodiversity metrics into a single, usable classification, we applied k-means clustering. This approach groups samples with similar biodiversity characteristics across multiple metrics, helping to highlight regions where multiple aspects of biodiversity are consistently high. The number of clusters was determined using an elbow plot criterion. This synthesis is intended to support decision-makers by simplifying complex information into a form that can be directly used in planning, while retaining access to the underlying metrics for detailed ecological interpretation. Technical steps for clustering procedures are provided in Appendix S1: *Clustering procedure*.

Spatial modeling

We used random forest models (Breiman, 2001) to predict the spatial distribution of biodiversity metrics and cluster groups across the study area, applying regression for continuous metrics and classification for cluster groups. Models were trained and validated using repeated cross-validation, with performance assessed using

FIGURE 2 Random forest models for a range of biodiversity metrics (${}^0D_\alpha$, Hill 0 alpha; ${}^0D_\beta$, Hill 0 beta; ${}^0D_\gamma$, Hill 0 gamma; ${}^1D_\alpha$, Hill 1 alpha; ${}^1D_\beta$, Hill 1 beta; ${}^1D_\gamma$, Hill 1 gamma; ${}^2D_\alpha$, Hill 2 alpha; ${}^2D_\beta$, Hill 2 beta; ${}^2D_\gamma$, Hill 2 gamma; N, abundance; N_{cv}, abundance cv; N_{tot}, abundance total; for further details, see Table 2). Confidence plots for each model are shown in Appendix S1: Figure S5.

appropriate metrics for regression and classification. Variable importance and partial dependence plots were used to explore the influence of key environmental predictors on biodiversity patterns. Environmental predictors describing seabed substrate, topography, hydrodynamics, and biogeochemical conditions were compiled from multiple sources. To support interpretation and decision-making, we also considered spatially explicit confidence assessment approaches applicable to both categorical and numeric outputs (Mitchell et al., 2018). Full details of predictor selection, model fitting, and evaluation are provided in Appendix S1: *Environmental predictors* and *Random forest modeling*.

Explaining patterns

We analyzed relationships between biodiversity metrics and environmental predictors using random forest variable importance and partial dependence plots. For biodiversity clusters, multivariate analyses (*best* and *adonis* functions in R) were used to identify key environmental drivers. Full methodological details are provided in Appendix S1: *Explaining patterns*.

RESULTS

Biodiversity metrics

Spatial models for each metric (Figure 2) provide different perspectives on biodiversity based on Hill numbers (row 1 = Hill 0, row 2 = Hill 1, row 3 = Hill 2), abundance (row 4) and the Whittaker (1960, 1972) framework of alpha-, beta-, and gamma-diversity (columns 1–3). Model performance was variable, with R^2 values ranging from 0.32 to 0.69 (Table 3). The highest values were obtained for gamma-diversity models (${}^0D_\gamma$, ${}^1D_\gamma$, and ${}^2D_\gamma$), which consistently showed strong performance ($R^2 = 0.69$). In contrast, alpha-diversity, beta-diversity and counts models exhibited low to moderate performance ($R^2 = 0.32–0.51$), reflecting the higher natural variability and stochasticity inherent in these finer scale metrics. Associated model confidence maps are provided in Appendix S1: Figure S3.

Building on model performance, we examined the predicted spatial patterns for each diversity metric across the region. Areas of moderate to high alpha-diversity occur widely, with hotspots found in the English Channel and Southwest Approaches, in the mid Celtic Sea and up through the Irish Sea, and around Swallow Hole (see

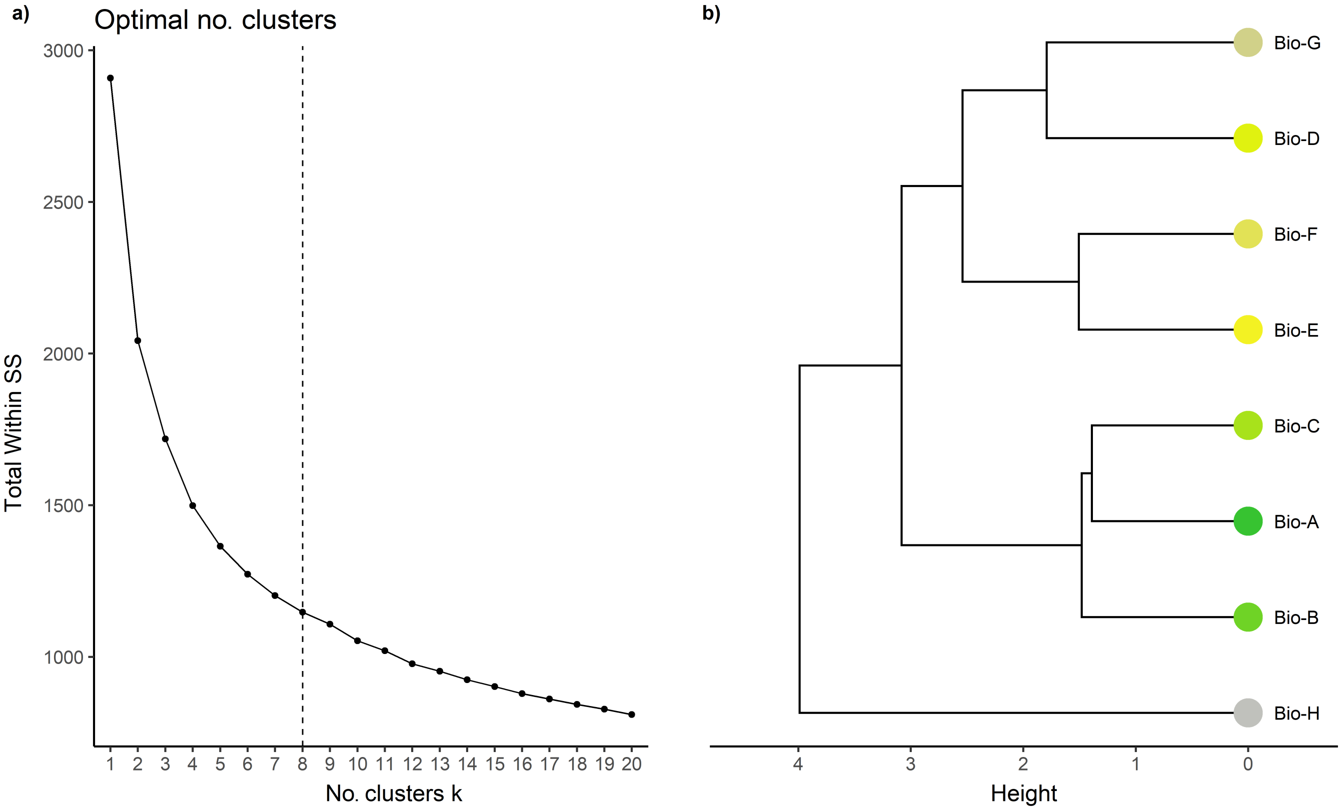

FIGURE 3 (a) Elbow plot, and (b) dendrogram associated with the k-means clustering of selected biodiversity metrics: Hill 0 alpha (${}^0D_\alpha$), Hill 0 beta (${}^0D_\beta$), Hill 2 beta (${}^2D_\beta$), Hill 0 gamma (${}^0D_\gamma$), abundance (N), abundance cv (N_{cv}), and abundance total (N_{tot}).

Figure 1 for place names). In contrast, alpha-diversity is low across much of the southern North Sea, and in many inshore areas along the west coast of the United Kingdom. In large part, beta-diversity patterns are the inverse of alpha, with generally higher values present in the southern North Sea and along coastal margins. Notable hotspots for beta-diversity, indicating adjacent communities that are very different from one another, are found in the Inner Silver Pit, outer Thames Estuary, English Channel, Irish Sea, at Jutland Bank/off west coast of Denmark, and in the Norwegian Trench. Gamma-diversity is high in the English Channel, mid Irish Sea, and Inner Silver Pit. The northern North Sea, Celtic Sea, parts of the Sea of Hebrides, and the Southwest Approaches are characterized by moderately high gamma-diversity, whilst the south-eastern North Sea, Fladen Ground (a small area of the northern North Sea), and more offshore areas of the Hebrides have relatively lower levels of gamma-diversity. Abundance plots show higher values in the south-eastern part of the North Sea (Oyster Ground and German Bight), and in patches across the Irish Sea, English Channel, and Inner Silver Pit. Key differences between metrics also reveal how biodiversity hotspots can be generated, for example, although alpha-diversity is relatively low at Inner Silver Pit, large changes in species composition between samples (beta-diversity) produce the highest gamma-diversity across all Hill numbers in the North Sea. In the Irish Sea and English Channel, both alpha- and beta-diversity were relatively high, producing two spatially extensive areas of high gamma-diversity.

Biodiversity clusters

The elbow plot relating to the biodiversity data did not suggest an obvious number of groups for k-means clustering (Figure 3a). We chose a solution based on eight groups, as this number coincided with a slight leveling out of the plot and explained >80% of the inherent variability. Whilst cluster groups are categorical in nature, they can be ordered in terms of relative biodiversity, with coloring used to create a simple heat map based on the

TABLE 4 Biodiversity cluster group centers for the metrics used in clustering.

	Cluster							
Metric	**Bio-A**	**Bio-B**	**Bio-C**	**Bio-D**	**Bio-E**	**Bio-F**	**Bio-G**	**Bio-H**
${}^{0}D_{\alpha}$	0.47	0.58	0.48	0.21	0.29	0.43	0.17	0.23
${}^{0}D_{\beta}$	0.60	0.48	0.55	0.61	0.46	0.35	0.49	0.31
${}^{2}D_{\beta}$	0.81	0.46	0.53	0.77	0.58	0.34	0.41	0.21
${}^{0}D_{\gamma}$	0.70	0.71	0.66	0.58	0.49	0.48	0.44	0.31
N	0.79	0.80	0.56	0.41	0.75	0.60	0.35	0.40
N_{cv}	0.68	0.56	0.76	0.76	0.61	0.52	0.73	0.54
N_{tot}	0.78	0.75	0.74	0.72	0.67	0.57	0.55	0.39
Total	**4.83**	**4.34**	**4.27**	**4.06**	**3.85**	**3.28**	**3.14**	**2.39**

Note: Values represent the group mean for each metric, with column totals provided in the bottom row. These totals were used to assign colors to cluster groups in Figure 4, following the BiodiversityStripes palette (https://biodiversitystripes.info/global), where the highest values correspond to dark green and the lowest to gray. Abbreviations: ${}^{0}D_{\alpha}$, Hill 0 alpha; ${}^{0}D_{\beta}$, Hill 0 beta; ${}^{0}D_{\gamma}$, Hill 0 gamma; ${}^{1}D_{\alpha}$, Hill 2 alpha; ${}^{2}D_{\beta}$, Hill 2 beta; ${}^{2}D_{\gamma}$, Hill 2 gamma; N, abundance; Ncv, abundance cv; N_{tot}, abundance total.

TABLE 5 Mean and SD of model validation statistics for cluster groups 1–8 and overall based on 10 random split sample runs.

Cluster	***n***	**Sensitivity**	**Specificity**	**Balanced accuracy**
Bio-A	481	0.53 ± 0.02	0.90 ± 0.01	0.72 ± 0.01
Bio-B	416	0.55 ± 0.02	0.93 ± 0.00	0.74 ± 0.01
Bio-C	335	0.25 ± 0.02	0.95 ± 0.00	0.60 ± 0.01
Bio-D	319	0.33 ± 0.02	0.94 ± 0.00	0.63 ± 0.01
Bio-E	518	0.52 ± 0.02	0.90 ± 0.01	0.71 ± 0.01
Bio-F	619	0.62 ± 0.01	0.90 ± 0.01	0.76 ± 0.01
Bio-G	359	0.42 ± 0.03	0.93 ± 0.01	0.68 ± 0.01
Bio-H	298	0.49 ± 0.03	0.95 ± 0.00	0.72 ± 0.01
Overall	13,106	0.49 ± 0.01	0.93 ± 0.00	0.71 ± 0.00

color palette used by the BiodiversityStripes initiative (see https://biodiversitystripes.info/global). Accordingly, cluster centers were summed across all the metrics used in clustering, with highest values colored dark green and lowest in gray (see Table 4). The dendrogram (Figure 3b) reveals the similarity/dissimilarity between groups in terms of patterns in the range of metrics considered. It is these patterns, rather than the overall level of biodiversity that determines each group's position in the plot.

Performance statistics for the biodiversity cluster model show high values of Specificity, indicating the model correctly identifies negative instances in the majority of cases (Table 5). Values for sensitivity, indicating correct group prediction, are predictably lower, but still average ~0.5. The lowest values of sensitivity are shown for groups Bio-C and Bio-D, although the confusion matrix (Appendix S1: Figure S4) indicates that incorrect predictions for these groups are typically of a similar

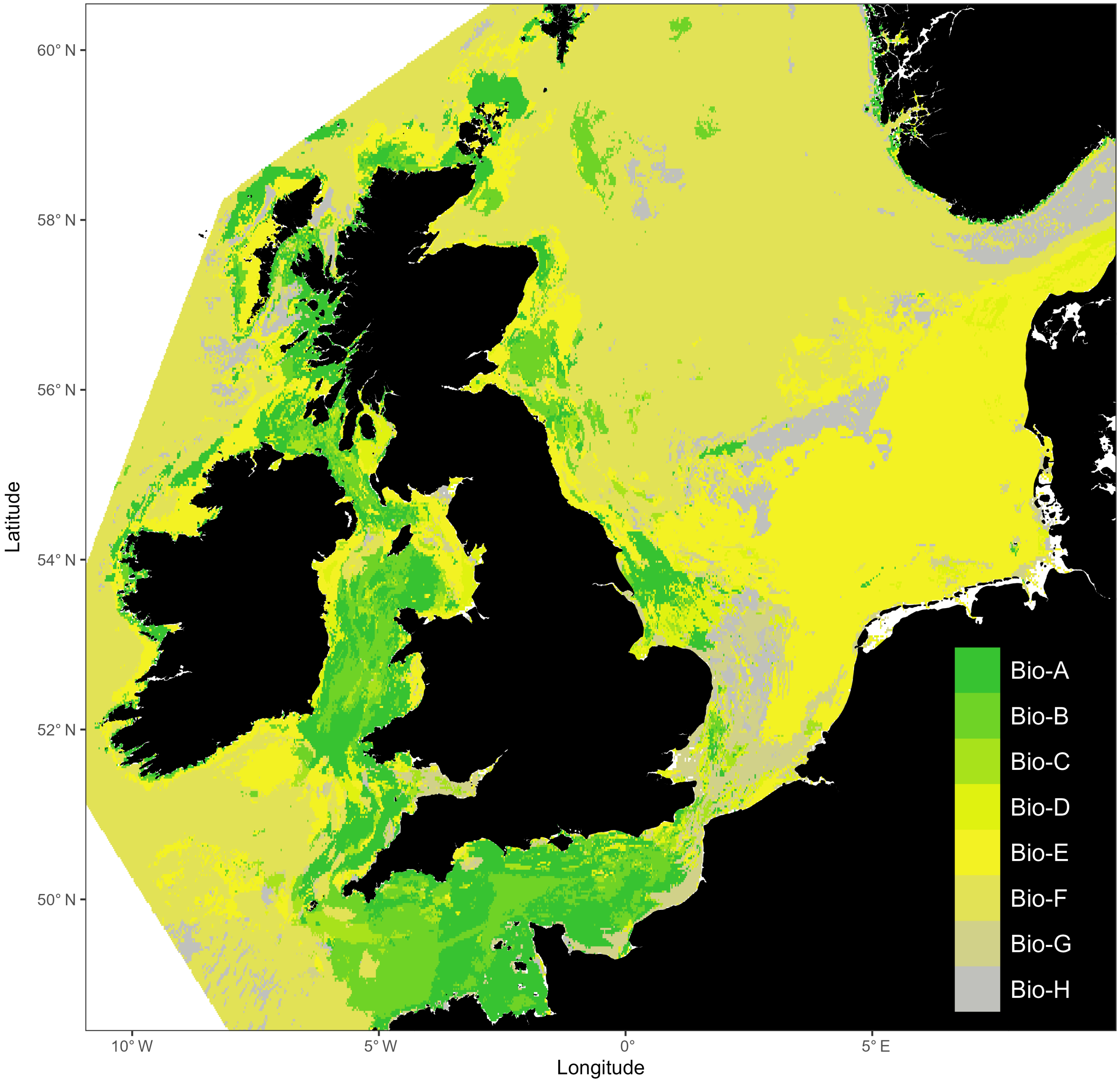

FIGURE 4 (a) Modeled biodiversity groups Bio-A to Bio-H based on a k-means clustering of individual metrics: Hill 0 alpha (${}^{0}D_{\alpha}$), Hill 0 beta (${}^{0}D_{\beta}$), Hill 2 beta (${}^{2}D_{\beta}$), Hill 0 gamma (${}^{0}D_{\gamma}$), abundance (N), abundance cv (N_{cv}), and abundance total (N_{tot}). Whilst categorical in nature, cluster groups are colored using a "heat map" scale in which the most diverse group (Bio-A) is dark green and the least diverse group (Bio-H) is gray (see https://biodiversitystripes.info/global). The level of biodiversity, and hence color, is based on a summing of the cluster group centers across the different metrics.

higher biodiversity group. The spatial distribution of biodiversity cluster groups is shown in Figure 4, with group characteristics outlined in Table 4. An associated model confidence map is provided in Appendix S1: Figure S5.

The highest biodiversity groups (Bio-A, Bio-B, and Bio-C) are found throughout large parts of the Inner Silver Pit, English Channel, Irish Sea, Celtic Sea, Sea of Hebrides, north of Scotland (including parts of Orkney), and to the east of the Firth of Forth (Figure 4). These groups show high values across all metrics but differ in the relative contribution of each. For instance, Bio-A shows high species turnover and abundance, indicating a dynamic community. Bio-B has the highest local richness and abundance but lower turnover, suggesting more homogeneous communities, whereas Bio-C presents a more balanced profile (Table 4). Intermediate levels of biodiversity are associated with groups Bio-D, Bio-E, and Bio-F. Bio-D, characterized by particularly high beta-diversity but low alpha-diversity and counts (N), is found at Inner Silver Pit, Jutland Bank and the north coast of Denmark, off The Netherlands, in the southern Hebrides, and in coastal areas of the United Kingdom and Ireland. Bio-E, characterized by moderate values across most metrics and representing a transitional assemblage with balanced yet reduced diversity, occurs in the southern North Sea, parts of the Celtic Sea, and around the northern coasts of the United Kingdom and Ireland. Bio-F has slightly higher alpha-diversity than Bio-D and Bio-E, but lower turnover and abundance (N_{tot}), indicating a more homogeneous and less diverse community. This group is found across much of the northern North Sea, Norwegian Trench, Southwest Approaches, outer Celtic Sea and shelf margins.

Bio-G and Bio-H represent the lowest biodiversity clusters, distinguished by low richness, abundance, and turnover. Bio-G shows slightly higher beta-diversity than Bio-H, suggesting sparse communities with some compositional variation. It occupies large areas of the Southern Bight and Bristol Channel, indicating broad but low-diversity coverage. In contrast, Bio-H exhibits consistently low values across all metrics, reflecting the most homogeneous and least diverse assemblage. It is found off the east coast of the United Kingdom, Dogger Bank, Fladen Ground, Skagerrak, and in deeper water in the Sea of Hebrides.

By comparing across Hill numbers, we can identify which areas of high biodiversity (Bio-A, Bio-B, Bio-C) are especially influenced by rare taxa and distinguish these from areas where biodiversity is driven by more common species (see Appendix S1: Figure S6).

Explaining patterns

Individual metrics

Variable importance varied among metrics, but broad similarities were evident within alpha-, beta-, gamma-diversity, and count groups (Table 6). Using Hill 1 and count CV as midpoints, the alpha-diversity model was most strongly influenced by current speed, gravel, and relative slope position, with values positively associated with current speed and gravel, and negatively with relative slope position (Figure 5a). Beta-diversity was most strongly influenced by phytoplankton, gravel, and dissolved iron, with values positively associated with phytoplankton and dissolved iron, and negatively with gravel (Figure 5b).

TABLE 6 Top three ranked predictor variables for each biodiversity metric model.

Metric	1	2	3
${}^{0}D_{\alpha}$	Current speed	Wave velocity	Gravel
${}^{1}D_{\alpha}$	Current speed	Gravel	Rel. slope pos.
${}^{2}D_{\alpha}$	Current speed	Gravel	Bottom temp.
${}^{0}D_{\beta}$	Gravel	pH	Salinity range
${}^{1}D_{\beta}$	Phytoplankton	Gravel	Diss. iron
${}^{2}D_{\beta}$	Phytoplankton	Mean Suspended Particulate Matter	Salinity range
${}^{0}D_{\gamma}$	Salinity range	Phytoplankton	Bottom temp. range
${}^{1}D_{\gamma}$	Salinity mean	Salinity range	Mud
${}^{2}D_{\gamma}$	Salinity range	Salinity mean	Wave velocity
N	Gravel	Bottom temp. range	Chlorophyll
N_{cv}	Phosphate	Gravel	Valley depth
N_{tot}	Phytoplankton	Gravel	Silicate

Note: Ranks identified from Variable Importance plots (not shown).

Abbreviations: ${}^{0}D_{\alpha}$, Hill 0 alpha; ${}^{0}D_{\beta}$, Hill 0 beta; ${}^{0}D_{\gamma}$, Hill 0 gamma; ${}^{1}D_{\alpha}$, Hill 1 alpha; ${}^{1}D_{\beta}$, Hill 1 beta; ${}^{1}D_{\gamma}$, Hill 1 gamma; ${}^{2}D_{\alpha}$, Hill 2 alpha; ${}^{2}D_{\beta}$, Hill 2 beta; ${}^{2}D_{\gamma}$, Hill 2 gamma; N, abundance; Ncv, abundance cv; N_{tot}, abundance total.

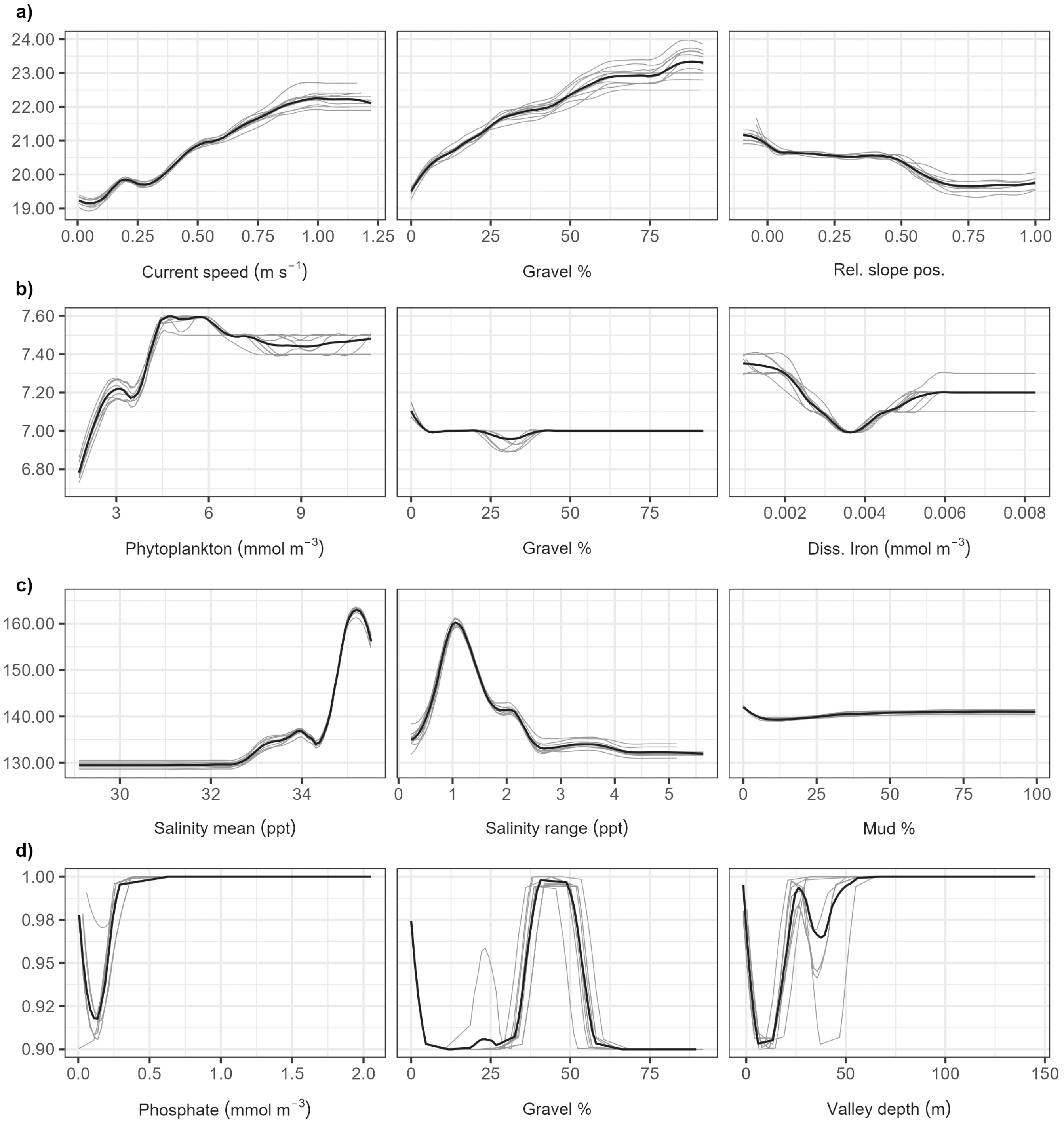

FIGURE 5 Partial dependence plots for the three most important environmental predictor variables across biodiversity metrics: (a) Hill 1 alpha ($1D_\alpha$), (b) Hill 1 beta ($1D_\beta$), (c) Hill 1 gamma ($1D_\gamma$) and (d) abundance cv (N_{cv}).

Gamma-diversity was driven by mean salinity, salinity range, and mud, with values positively associated with mean salinity above 32.5 ppt and negatively with mud. It also showed a nonlinear relationship with salinity range, peaking around values of 1 ppt (Figure 5c).

Counts were influenced by phosphate, gravel, and valley depth (Figure 5d). For phosphate, values declined slightly at low concentrations before increasing sharply and plateauing at higher levels. Counts peaked at intermediate gravel cover (~30%–60%) and at valley depths greater than ~25 m.

Biodiversity clusters

The *best* analysis identified a six-variable model (phytoplankton, current speed, channel network distance, LS-factor, gravel, and mud) as providing the highest

TABLE 7 Results of a *best* analysis identifying the subset of environmental variables that are most correlated with the biodiversity data. LS-factor refers to the slope length and steepness factor derived from SAGA-GIS.

Size	Variables	Correlation (ρ)
1	Current speed	0.1250
2	Current speed, gravel	0.1542
3	Current speed, LS-factor, gravel	0.1649
4	Current speed, LS-factor, gravel, mud	0.1656
5	Current speed, Ch. network distance, LS-factor, gravel, mud	0.1662
6	**Phytoplankton, current speed, Ch. network distance, LS-factor, gravel, mud**	**0.1665**

Note: Bold indicates the best output.

correlation with patterns in the biodiversity data ($\rho = 0.17$; Table 7). Although the correlation between biological and environmental resemblance matrices was moderate, results from the *adonis* test indicated that these predictors accounted for a total of 20.8% of the total variability. The strongest contributors were gravel (8.0%, $p < 0.001$) and phytoplankton (6.7%, $p < 0.001$), followed by mud (3.1%, $p = 0.001$), current speed (2.2%, $p = 0.001$), LS-factor (0.6%, $p = 0.001$), and channel network distance (0.2%, $p = 0.01$). Importantly, gravel and current speed were consistently retained in all of the higher performing *best* models, suggesting they represent the most robust predictors, while phytoplankton, mud, LS-factor, and channel network distance provided smaller, context-dependent contributions.

When considered alongside the dbRDA ordination (Figure 6) and heat maps of the most consistent predictors, gravel and current speed (Appendix S1: Figure S7), these results provide ecological insight into the spatial distribution of biodiversity cluster groups (Figure 4). High-biodiversity clusters (Bio-A, Bio-2, Bio-C) were associated with elevated gravel and higher current speeds, while other variables such as phytoplankton and mud appeared to exert weaker, context-dependent influences on community structure.

DISCUSSION

This study presents the first integrated, high-resolution maps of benthic biodiversity across alpha-, beta-, and gamma-diversity scales, alongside a synthesis into a single holistic output. By combining Hill numbers (Hill, 1973), abundance, and the Whittaker framework (1960, 1972), we offer a novel approach to biodiversity mapping that simplifies complex, multidimensional data into actionable insights. While previous studies have compared biodiversity patterns across metrics (e.g., Santini et al., 2017), we are not aware of any that have merged these metrics into a single, usable entity. Our holistic map therefore represents a significant advancement in biodiversity assessment, offering a practical tool for marine spatial planning and environmental decision-making.

Understanding where biodiversity is high—and where protection may be most warranted—is essential for sustainable development. The biodiversity maps produced here provide new insights that can inform licensing decisions for activities including offshore wind, aggregate extraction, cable installation, and other developments that may affect the seabed. By identifying areas of high conservation value and integrating biodiversity considerations into management processes, we can help ensure that human activities are conducted in ways that minimize ecological impacts and promote biodiversity conservation. Importantly, our approach also highlights the role of rare taxa in supporting biodiversity in certain areas, underscoring the need for conservation strategies that account for both overall diversity and the protection of rare species. This approach is applicable not only in the United Kingdom, but also in other regions experiencing rapid offshore development.

Our findings are supported by earlier studies documenting benthic biodiversity patterns (e.g., Barrio Froján et al., 2012; Bolam et al., 2008; Kröncke et al., 2011; Reiss et al., 2010). However, those studies typically relied on limited sampling and did not interpolate between points, limiting their utility for planning decisions that require full-coverage, high-resolution maps (Baker & Harris, 2020; Brown et al., 2012).

To better understand the drivers of biodiversity, we applied a *best* analysis, which identified a six-variable model—phytoplankton, current speed, channel network distance, LS-factor, gravel, and mud—as most informative. Among these, gravel and current speed consistently emerged as the strongest predictors, reflecting the influence of hydrodynamic forces on sediment distribution. These forces help shape the availability of stable coarse habitats, which are known to promote higher biodiversity by providing persistent, heterogeneous substrates that support diverse benthic assemblages (Cooper & Barry, 2017; Gutow et al., 2022; Kaiser & Spencer, 1996). The smaller contributions of phytoplankton, mud, LS-factor, and channel network distance suggest additional, context-dependent influences, with phytoplankton reinforcing the importance of primary productivity as a driver of benthic biodiversity (Saeedi et al., 2022).

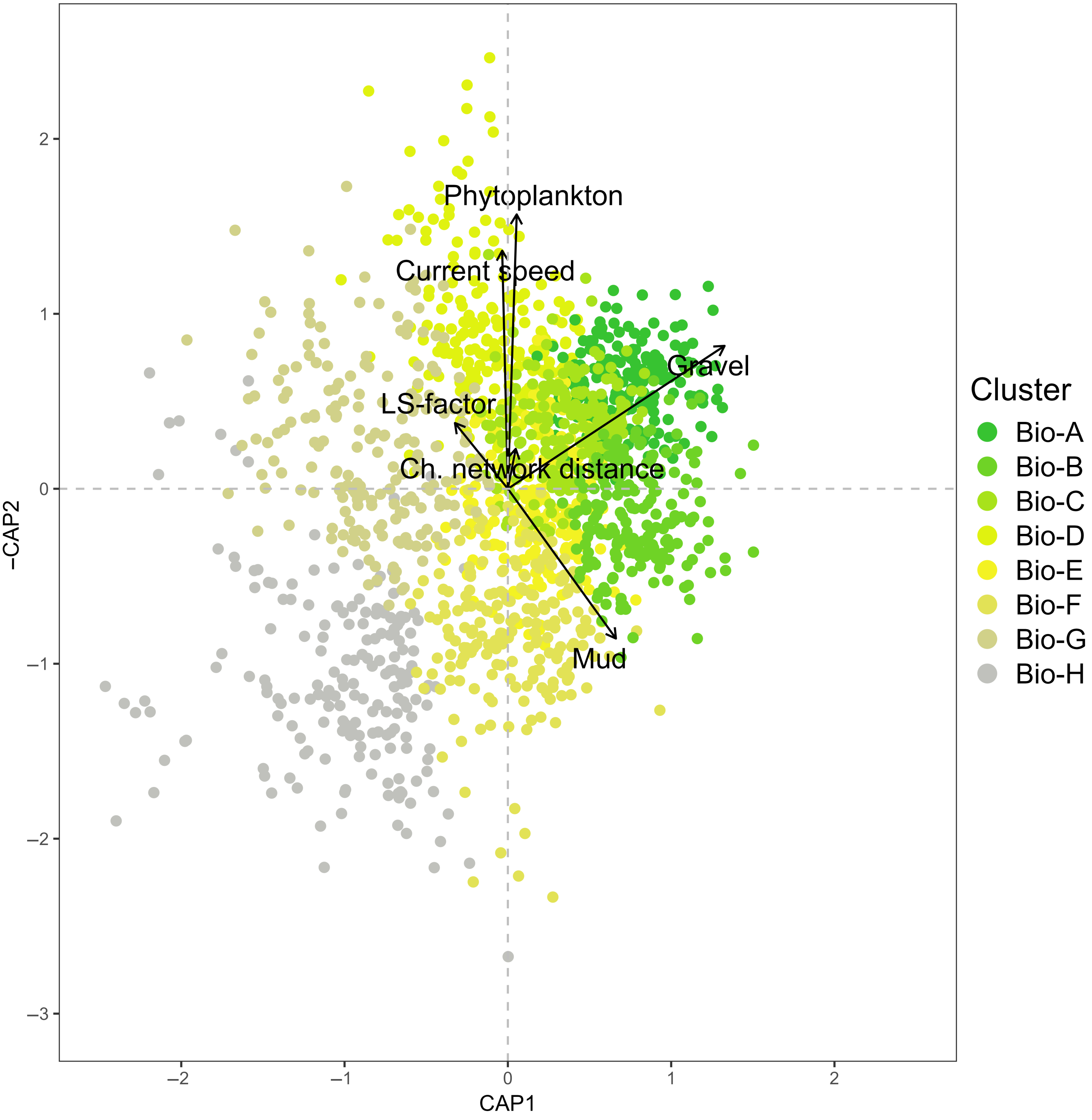

FIGURE 6 Distance-based redundancy analysis (dbRDA) ordination showing sampling sites (colored by biodiversity cluster group) and vectors for the main environmental predictor variables. Axes CAP1 and CAP2 represent the first and second canonical axes from the Canonical Analysis of Principal coordinates (CAP), summarizing variation in biodiversity constrained by the environmental variables.

Limitations and future directions

Several limitations should be acknowledged. Firstly, the dataset spans 39 years (1983–2023), though most samples (>90%) were collected post-2000. While biodiversity patterns may have shifted due to climate change or local pressures such as demersal fishing (Kröncke et al., 2011), this concern is more relevant to species distribution models than to the biodiversity metrics used here, which integrate across species within samples. Supporting this, Cooper & Barry (2017) found that assemblage distributions across the UK shelf remained broadly consistent between 1976 and 2016. Temporal shifts may slightly reduce the performance of our models, but are unlikely to bias spatial patterns.

Secondly, data density varies across the study area, contributing to differing levels of confidence in the mapped outputs. Thirdly, while we carefully selected biodiversity metrics (e.g., Magurran, 2021), we acknowledge that others could have been included. This study is intended as a proof of concept, and we encourage further exploration using alternative or additional metrics (e.g., Taxonomic Distinctness, Clarke & Warwick, 1998; Phylogenetic diversity, Cardillo, 2023; Biological Traits, Bremner et al., 2006; Rao's Quadratic Entropy, Botta-Dukat, 2005).

Although we applied a correlation threshold ($r > 0.7$) to exclude highly redundant metrics prior to clustering, moderate correlations remained among those retained. This led to uneven representation of Hill numbers across diversity components, potentially introducing bias in clustering and summary outputs (e.g., Table 4). However, our selection was guided by the principle of complementarity—prioritizing metrics that offer distinct ecological insights rather than overlapping information. By including descriptors that differ in sensitivity to abundance, richness, and turnover, we aimed to capture a broader picture of benthic biodiversity. Future studies might adopt a more focused a priori selection—for example, using only ${}^0D$ (species richness) across all diversity scales, combined with abundance (N)—to enhance consistency and interpretability, though this may come at the cost of ecological nuance.

Broader implications

This study, alongside others (Arvanitidis et al., 2009; Bolam et al., 2023; Cooper & Barry, 2017; Escaravage et al., 2009; Grémare et al., 2009; O'Brien et al., 2022; Renaud et al., 2009; Runting et al., 2020; Somerfield, Arvanitidis, Faulwetter, et al., 2009; Somerfield, Arvanitidis, Vanden Berghe, et al., 2009; Vanden Berghe et al., 2009; Webb et al., 2009), demonstrates how new insights can be generated from existing data. The expansion of big data approaches in ecology offers a pathway to understanding organism–environment interactions across scales (Farley et al., 2018). As new data become available, it should be possible to update existing models to ensure decisions are based on the best available evidence. In parallel, future work can begin to address the important issue of temporal change in biodiversity patterns. Increasing resolution in future iterations of the holistic layer could involve more cluster groups, offering a more nuanced view of biodiversity patterns. As highlighted by Canhos et al. (2015), this new way of working will require ongoing support for maintaining infrastructure, and continued ingestion of data.

We advocate the development of similar outputs for other benthic components, such as epifauna from trawl samples. In the United Kingdom, current tools (e.g., Marine Life Information Network, https://www.marlin.ac.uk/) reference biodiversity but typically focus on individual species or habitats. Our approach treats biodiversity as a comprehensive, quantitative entity, helping to avoid neglecting areas critical for ecosystem services and overall biodiversity maintenance.

Building on earlier work (Thompson et al., 2020), future research should also assess how biodiversity hotspots respond to pressures such as demersal fishing, offshore wind, aggregate dredging, dredge disposal, oil and gas, and cable installation. Not all high-biodiversity areas are equally vulnerable—some may host taxa that are resilient to disturbance, while others may be highly sensitive. Assemblage sensitivity can be assessed using biological traits responsive to specific pressures (Bolam et al., 2014, 2021; Certain et al., 2015; Kenny et al., 2018) and this perspective can be usefully brought into any assessment of risk to the benthos posed by offshore development (Bolam et al., 2025).

CONCLUSION

Improving the understanding of benthic biodiversity is critical for restoration and conservation, especially in the context of increasing seabed use and offshore wind expansion. This study shows how benthic big data can be used to generate biodiversity maps, and how multiple complementary metrics can be combined into a single decision-support output. Our findings underscore the importance of integrating biodiversity into marine spatial planning and licensing to ensure sustainable development. As new data emerge, models can be rerun to reflect the best available evidence—though this requires ongoing infrastructure support and data harvesting. Finally, work is needed to ensure these insights are incorporated into decision-making alongside existing measures, and to assess biodiversity sensitivity to anthropogenic pressures.

AUTHOR CONTRIBUTIONS

Keith M. Cooper developed the initial concept for this paper, with input from Stefan G. Bolam and Murray S. A. Thompson. The manuscript and R code were drafted by Keith M. Cooper, Murray S. A. Thompson (R script for calculating biodiversity metrics), Anna-Leena Downie (random forest modeling), and Connor M. Peach. All authors reviewed and contributed to the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Cooper et al., 2025) are available from the Cefas Data Hub (https://doi.org/10.14466/CefasDataHub.187). This record includes links to the primary datasets, associated R scripts, and an API for accessing the modeled biodiversity layers. A small number of third-party datasets used under data-sharing agreements are not publicly available; summary information for these datasets is provided in Appendix S1: Table S3. Qualified researchers may contact EDF Energy (hello@edfenergy.com) for permission to access the datasets and the corresponding author (keith.cooper@cefas.gov.uk) for the datasets.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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