

## RESEARCH ARTICLE OPEN ACCESS

# Marked Variability in Distance-Decay Patterns Suggests Contrasting Dispersal Ability in Abyssal Taxa

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## ABSTRACT

**Aim:** We assess the role of spatial distance and depth difference in shaping beta diversity patterns across abyssal seascape regions. We measured the decrease of faunistic similarity across the northeast Pacific seafloor, to test whether species turnover rates differ between deep and shallow-abyssal biogeographical provinces and whether these patterns vary across functionally or taxonomically different biotic groups.

**Location:** Abyssal NE Pacific Ocean.

**Time Period:** Present.

**Major Taxa Studied:** Benthic Invertebrates (13 Phyla).

**Methods:** We examined the relationship between compositional similarity ( $\beta_{sim}$ ) and spatial distance, distance-decay, in benthic megafauna communities (animals > 10 mm) based on seabed imagery data (> 36,000 specimens in 402 species) collected across 28 abyssal seascape locations spanning a total of 4000 km. By comparing the statistical parameters (intercept and slope) of decay curves, we investigated whether distance-decay patterns differ (i) between communities above and below the carbonate compensation depth (~4400 m at N Pacific), (ii) among taxa with contrasting life-habits and (iii) across dominant phyla.

**Results:** We found steeper species turnover rates in communities below 4400 m and variations in distance-decay patterns across biotic groups. Turnover was higher for taxa facultatively growing on hard-substratum patches (polymetallic nodules) than for

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sediment-dwelling or swimming organisms. Cnidaria and Porifera, respectively, depicted the most and least evident spatial decays in community similarity.

**Main Conclusions:** We demonstrate the utility of combining seabed imaging with distance-decay modelling to capture macroecological patterns in poorly explored deep-sea ecosystems. Our results suggest that chemical boundaries associated with depth are a very relevant niche-sorting mechanism driving large-scale beta-diversity patterns and an association between species life-habits and dispersal limitation in abyssal seabed communities. These findings have important implications for biodiversity conservation plans in the deep ocean, amid the need to protect vast abyssal seascape ecosystems from globally rising human threats.

## 1 | Introduction

The negative relationship between community similarity and spatial distance (i.e., distance-decay; Nekola and White 1999) is an ubiquitous macroecological pattern in terrestrial ecosystems (Condit et al. 2002; Soininen, McDonald, and Hillebrand 2007; Morlon et al. 2008) but has been rarely assessed in the deep ocean (Richer de Forges, Koslow, and Poore 2000; McClain, Stegen, et al. 2012; Wagstaff et al. 2014). Decay in community similarity can result either from the decrease of environmental similarity with distance (niche-sorting), as closer locations usually sustain more similar habitats (and therefore communities; e.g., Baselga and Gómez-Rodríguez 2021), or from the intrinsic ability of organisms to reach a particular site (dispersal limitation), which declines with spatial distance from source populations (e.g., Gómez-Rodríguez and Baselga 2018; Martín-Devasa et al. 2024). The shape and strength of the distance-decay relationship can hence vary across organisms, geographic gradients and environments (Soininen, McDonald, and Hillebrand 2007; Nekola and McGill 2014).

Understanding what drives beta-diversity is becoming particularly urgent in deep ocean abyssal seascapes (i.e., depths 3000–6000 m; > 60% of Earth's surface). These species-rich ecosystems are thought to provide vital services for the ocean (Thurber et al. 2014), such as climate regulation (Dunne, Sarmiento, and Gnanadesikan 2007) or nutrient cycling (Middelburg 2018). In the Pacific and Indian Oceans, these mud-dominated environments can also harbour large but irregularly distributed patches of polymetallic nodules (Hein, Koschinsky, and Kuhn 2020), forming a unique mosaic-habitat, where the heterogeneity provided by this hard substratum source sustains some of the most biodiverse communities surveyed in the abyss (Amon et al. 2016; Simon-Lledó, Bett, Huvenne, Schoening, et al. 2019). However, critical gaps on abyssal species biogeographical ranges and connectivity barriers (e.g., McClain and Hardy 2010; Taylor and Roterman 2017) currently limit the effective preservation of these vast seascapes from growing human threats, such as climate change (Levin et al. 2020; Harris et al. 2023) and polymetallic nodule mining (Simon-Lledó et al. 2019).

Although abyssal plains extend across relatively modest environmental gradients compared to more structurally complex deep-sea habitats (like canyons, seamounts and vents, e.g., Ramirez-Llodra et al. 2010), water depth is possibly the most common explanatory variable for niche-sorting in abyssal regions, being closely associated with key habitat-structuring environmental drivers, like nutrient supply from surface waters (Smith et al. 2008) or the distribution of geochemical boundaries (Simon-Lledó et al. 2023c). Decreasing food availability

with depth in the abyss is thought to reduce faunal abundance (Simon-Lledó et al. 2020, 2023c), body size (Rex et al. 2006) and metabolic rates (McClain, Allen, et al. 2012). The carbon compensation depth (CCD) delineates an oceanic transition zone (lysocline) below which seabed sediments contain little or no calcium carbonate (Woosley 2016), which is an essential component for the development of many organisms, such as shelled molluscs (Feng et al. 2000), soft corals (Watabe and Kingsley 1992) or echinoderms (Lebrato et al. 2010). As such, the CCD (~4400 m in N Pacific) can act as a biogeographical boundary between deep and shallow-abyssal seabed communities (Simon-Lledó et al. 2023c). Ocean warming is expected to lead to a decrease in the food supply to the abyssal seafloor (Jones et al. 2014) and the shoaling of the CCD (a rising 'snow-line'; Harris et al. 2023). However, the type and magnitude of these impacts on abyssal ecosystems remains largely unclear because studies linking changes in these variables to current species distribution patterns are lacking.

Relatively non-motile as adults, most of the invertebrates that populate seafloor ecosystems exhibit complex life cycles providing significantly greater spatial dispersal potential during larval phases than adult movement or migration (Bradbury et al. 2008; Shanks 2009). Therefore, reproduction strategy and larval typology are thought to play a key role regulating dispersal limitation in the deep ocean (Young et al. 1997; Metaxas and Saunders 2009; Hilário et al. 2015). Traits like yolk size, swimming ability or feeding mode can affect larval duration or enable vertical migration to shallower waters, where faster currents can largely expand dispersal ranges (e.g., Young et al. 2018). However, very few abyssal species have ever been associated with a collected larva or reproductive mode (Hilário et al. 2015; Kersten, Smith, and Vetter 2017), which are traits that can in turn greatly vary among phylogenetically close taxa (Young 2004). Moreover, scarcity of molecular data at regional scales (Baco et al. 2016) constrains formulation of relevant hypothesis based on genetic connectivity evidence. Instead, studies in continental shelf communities have shown that dispersal can be inferred based on species life-habits (Mercier, Sewell, and Hamel 2013), as reflected by the functional species turnover resulting from variations in climate (Álvarez-Noriega et al. 2020) or habitat type (Grantham, Eckert, and Shanks 2003). As such, Young et al. (2018) suggest dispersal strategies in abyssal seascapes could be analogous to continental shelves, where, to reduce propagule loss, species that can only grow on scattered strips of hard substratum like rock patches tend to exhibit narrower dispersal than those living on the more widely available soft sediments (e.g., Grantham, Eckert, and Shanks 2003; Shanks 2009). Whether dispersal limitation is associated with life-habit traits could

be particularly relevant to address the resilience and recolonisation capacity of abyssal communities, for instance to the impacts of nodule mining. Mining operations are expected to cause most severe disturbances on the species depending on scattered nodule hard substratum for growth (Simon-Lledó, Simon-Lledó, Bett, Koser, et al. 2019), a life-habit that can represent up to 50% of the local species richness in abyssal benthic communities (Amon et al. 2016; Simon-Lledó, Bett, Huvette, Schoening, Benoist, Jeffreys, et al. 2019).

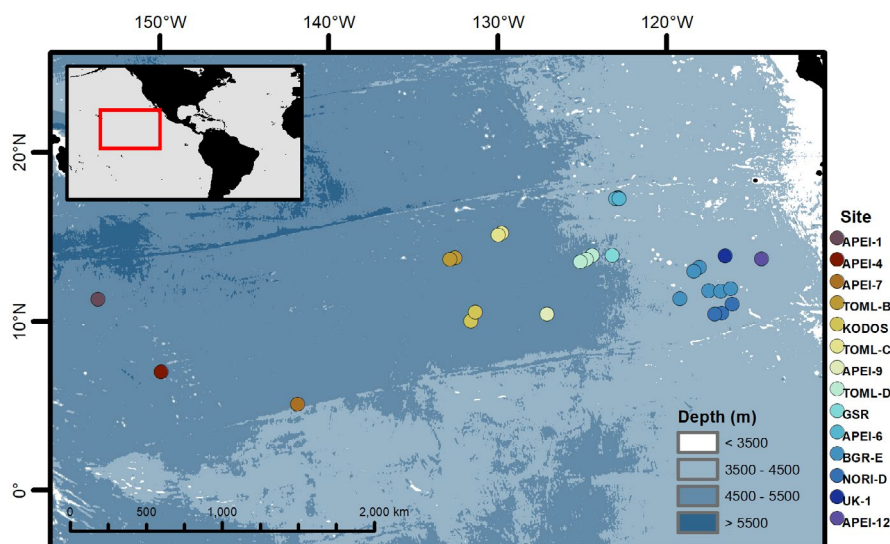
Here, we assess the role of spatial distance and depth difference in shaping beta-diversity patterns across abyssal plain regions. Specifically, we examine the decrease of similarity in benthic megafauna (animals > 10 mm) communities across the Clarion–Clipperton Zone (CCZ; northeast Pacific), an abyssal seascape spanning ~6 million km<sup>2</sup> of seabed between Kiribati and Mexico (Figure 1), and also the world's largest area currently in exploration phase for seabed mining (Hein, Koschinsky, and Kuhn 2020). Using seabed imagery data (i.e., > 36,000 specimen occurrences of 402 invertebrate taxa, spanning across 4000 km of seabed), we compared the statistical parameters (intercept and slope) of distance-decay curves capturing variations in biotic similarity across space and depth, for the whole megabenthic metacommunity (13 Phyla) and for different functional or taxonomic species groups. Our aim was to assess: (i) whether the relationship between compositional similarity and spatial distance differs above and below the CCD; and whether similarity decay patterns vary (ii) among taxa with different life-habits (i.e., Nodule-growing, Sediment-dwelling and Swimming) or (iii) across dominant phyla (i.e., Cnidaria, Porifera, Echinodermata and Arthropoda). This study expands our fundamental understanding of large-scale biological change in abyssal seascapes (Simon-Lledó et al. 2023c), by exploring the environmental and biotic mechanisms regulating community assembly in these poorly explored ecosystems, where most species remain undescribed (Rabone et al. 2023). Addressing these knowledge gaps in vast abyssal ecosystems is essential to determine the true resilience of global deep ocean biodiversity to the rapidly growing human impacts that threaten Earth's largest biome.

## 2 | Methods

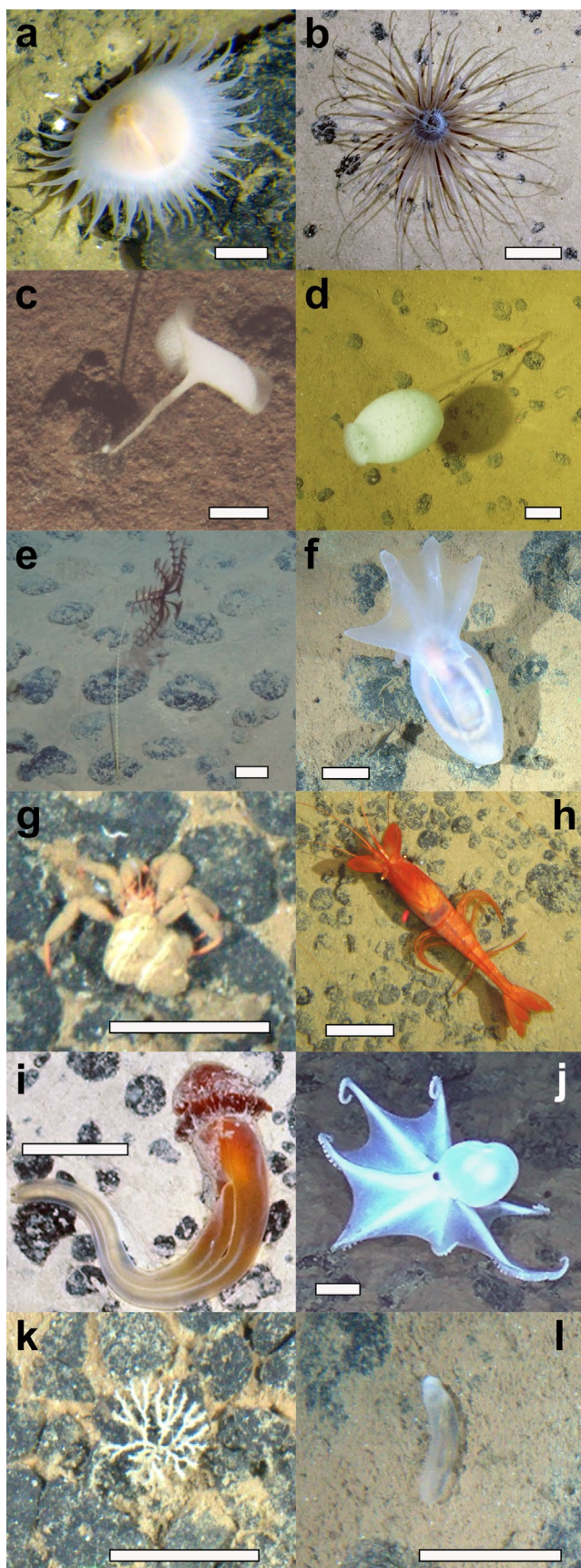
### 2.1 | Study Area and Data

We used distribution data of invertebrate benthic megafauna (animals > 10 mm) compiled in the Abyssal Pacific Seafloor Megafauna Dataset v.1 (AP SMA dataset; [www.zenodo.org/records/7982462](https://zenodo.org/records/7982462)), sampled across the northeast Pacific basin (CCZ, Figure 1). Important abiotic factors show little variation across the north Pacific abyss, exhibiting low currents, extremely low sedimentation rates (Volz et al. 2018) and near constant bottom-water salinity and temperatures (Heezen and Laughton 1963). In contrast, there is a gradual increase in water depth from east to west (3800–5500 m; Figure 1) and a gradient in nutrient flux reaching the seafloor, generally decreasing with depth but enhanced towards the southeast (Henson, Sanders, and Madsen 2012). These conditions are thought to promote the extremely slow formation of polymetallic nodules, potato-sized mineral concretions growing on the seabed, providing one of the largest known sources of hard substratum in the abyss, in irregularly distributed patches throughout the Pacific and Indian Ocean (Hein, Koschinsky, and Kuhn 2020).

The APSMA dataset collates over 50,000 specimen records across 13 metazoan phyla, classified in 402 taxonomically standardised morphotypes (e.g., Figure 2). In image-based numerical ecology, these are defined as the lowest taxonomic hierarchy (typically Genus or Family level in undescribed species) that specimens detected in photographs can be identified to (Horton et al. 2021). The dataset contains faunal occurrences imaged across space and depth in 28 study locations (Figure 1) delimited within 10×10 km sized quadrants (more details; Simon-Lledó et al. 2023c). Faunal occurrences were reanalysed from source seabed imagery data (Table S1) obtained with comparable methodology (i.e., standardised animal detectability) within each quadrant. Identifications were taxonomically aligned across surveys to match the APSMA catalogue v.1 (Simon-Lledó et al. 2023a), using the 'Label Review Grid Overview' tool in



**FIGURE 1** | Map of study locations (28) with invertebrate megafauna occurrence data collated from comparable seabed imagery surveys conducted across the abyssal northeast Pacific basin. *Source:* APSMA v.1 dataset (Simon-Lledó et al. 2023b).



**FIGURE 2** | Examples of invertebrate megafauna taxa with varying hard-substratum dependency across different Phyla within the northeast abyssal Pacific seafloor metacommunity. (a) Nodule-growing Cnidaria, Sicyonidae gen. indet. (ACT\_002). (b) Sediment-dwelling Cnidaria, Ceriantharia order. indet. (CER\_009). (c) Nodule-growing Porifera, *Sympagella clippertoniae* sp. inc. (HEX\_008). (d) Sediment-dwelling Porifera, *Hyalonema* sp. indet. (HEX\_003). (e) Nodule-growing Echinodermata, Hyocrinidae fam. inc. (CRI\_005). (f) Sediment-dwelling Echinodermata, *Amperima* sp. indet. (HOL\_023). (g) Sediment-dwelling Arthropoda, *Parapagurus microps* sp. inc. (DEC\_027). (h) Swimming Arthropoda, *Cerataspis monstrosus* (DEC\_001). (i) Sediment-dwelling Hemichordata, Torquaratoridae gen. indet. (HEM\_005). (j) Swimming Mollusca, Octopodidae gen. indet. (MOL\_009), informally named 'Casper octopus' (Purser et al. 2016). (k) Nodule-growing Bryozoa, *Smithsonianus* sp. indet. (BRY\_001). (l) Sediment-dwelling Nemertea, Pilidiophora order indet. (NEM\_006). Scale bars = 5 cm. Source: APSMA v.1 taxonomic atlas (Simon-Lledó et al. 2023a).

BIIGLE 2.0 software (Langenkämper et al. 2017) and following an iterative quality control protocol, repeated by the same experts across all surveys, to minimise observer bias (Durden et al. 2016).

## 2.2 | Sample Processing and Survey Design

We selected a subset of the APSMA dataset containing only specimen occurrences identified to morphotype level (36,432 specimens). All morphotypes were determined by taxonomic group experts as sufficiently different morphologically to be confidently considered separate taxa (see Simon-Lledó et al. 2023c). Based on observational knowledge, and by reference to existing literature, each of the 402 morphotypes was assigned to a specific life-habit relative to its hard-substratum dependency for development: Nodule-growing (can only grow on hard substratum), Sediment-dwelling (grow or crawl on sediment) or Swimming (can move fast and at will across the water column for prolonged periods). We randomly resampled faunal occurrences without replacement within each survey location to generate replicate samples containing exactly 200 specimens each; a sample unit size that ensures accurate characterisation of local benthic community features at the abyssal Pacific (Ardrón et al. 2019; Simon-Lledó, Bett, Huvenne, Schoening, Benoist, Jeffreys, et al. 2019). In study locations where surveys covered a depth range > 200 m, occurrences were further constrained to 200 m depth bins during sample generation. This standardised sample generation process reduces potential spatial autocorrelation biases (see e.g., Legendre 1993; Dormann 2007), for instance stemming from the patchy distributions that many benthic species show at local scales (Simon-Lledó, Bett, Huvenne, Schoening, Benoist, Jeffreys, et al. 2019; Simon-Lledó et al. 2020), and hence within the 10 × 10 km quadrants that delimit our study locations. In turn, this approach also minimises the bias in shared species estimation that could stem from comparing locations

with differing total fauna densities, e.g. in 1000 m<sup>2</sup> of seabed imaged, we typically find ~80 specimens in deeper, western communities and ~1300 in the shallower, eastern locations of the dataset (Simon-Lledó et al. 2023c). In addition, to balance sampling effort, a maximum number of five randomly selected replicate samples were used for each location or depth bin within it (e.g., at the more explored BGR-E, APEI-6, NORI-D or TOML-D sites). This process yielded a total of 140 samples standardised for community analyses across 28 geographical locations at varying depths. Distance (km) and depth difference (m) between pairs of samples were calculated using the ‘geosphere’ R package (Hijmans et al. 2022). All data processing and subsequently detailed analyses were conducted using R software (R Core Team 2017); codes and data are available in Zenodo (<https://zenodo.org/records/14479422>).

### 2.3 | Distance-Decay Models

We modelled the decay of faunistic similarity (i.e., abundance-based beta-diversity) with spatial distance and depth to capture the potential effect of niche-sorting and dispersal limitation mechanisms on community assembly patterns across the northeast abyssal Pacific basin. All distance-decay models were based on the Bray–Curtis similarity index ( $\beta_{sim}$ ), calculated between pairs of samples from locations within each target spatial scale, using the *beta.pair.abund()* and *decay.model()* functions in ‘betapart’ v.1.6 package (Baselga et al. 2023). However, since abyssal communities are typically composed by few prominent dominant species and a vast majority of rare taxa (Smith et al. 2008; McClain 2021), all samples were previously log ( $x+1$ ) transformed to mitigate the effects of uneven abundance distributions (Hardersen and La Porta 2023), while emphasising smaller differences between less common species (Májeková et al. 2016).

To capture the potential niche-sorting effect of the CCD with depth (4400 m at the N Pacific, Berger, Adelseck Jr., and Mayer 1976), models were computed at two spatial scales, for the entire study area (basin-scale; 1–4000 km) and for each of the two biogeographical regions (regional scale: 1–1100 km) found above and below the CCD in the abyssal Pacific (Simon-Lledó et al. 2023c). The most distant locations were removed to ensure spatial ranges were comparable in regional analyses (max distance: 1100 km). Given the bathymetric profile of the northeast Pacific basin, where depth generally increases from NE to SW (Figure 1), this split inherently divided our replicate sample sets into eastern (shallow-abyssal: 3800–4400 m, 65 samples) and western (deep-abyssal: 4400–5100 m, 71 samples). Additionally, a set of models were computed using depth difference between replicate sample locations instead of geographical distance to assess the relationship between similarity decay and depth difference. Two-factor models were hence computed to estimate the proportion of variance in community similarity solely explained by spatial distance, depth difference and their interaction at both basin and regional scales. To do so, we fitted a non-linear multiple matrix regression for each independent predictor as well as for both of them using the ‘minpack.lm’ package (Elzhov et al. 2016).

Distance-decay models were calculated at both scales for the whole invertebrate community (402 taxa) and separately for particular (functional and taxonomic) biotic groups. To explore Young’s abyssal dispersal hypothesis on variation of decay patterns relative to hard-substratum dependency, models were computed at both scales for the Nodule-growing (148 taxa), Sediment-dwelling (213 taxa) and Swimming (41 taxa) communities. In addition, models were computed for each of the four most numerically dominant phyla, to assess whether distance-decay patterns might rather reflect intrinsic abilities among phylogenetic groups. Specifically, models at both scales were built for: Cnidaria (mostly Actiniaria, Scleractyonacea and Antipatharia; 106 taxa); Porifera (Hexactinellida and Demospongiae; 84 taxa); Echinodermata (Ophiuroidea, Asteroidea, Holothuroidea, Echinoidea and Crinoidea; 126 taxa); and Arthropoda (mostly Decapoda and Peracarida: 27 taxa).

#### 2.3.1 | Model Function, Scale Dependency and Species Rarity

A set of preliminary distance-decay models were fitted using different functional forms and data subsets to determine what model function most effectively captured similarity variations in our data, explore scale-dependencies, and evaluate the effect of rare taxa in our analyses (Appendix S1). These were computed based on the whole community sample, using both negative exponential and power law functional forms, at both regional and basin scales, and with and without the inclusion of rare species (<10 occurrences: 214/402 taxa). The fit and significance of different model runs was assessed using the Akaike’s information criterion (AIC) and site-block significance tests that accounted for pairwise dependence in non-linear models of distance-decay (pseudo- $r^2$ , Martínez-Santalla et al. 2022). Results of this preliminary assessment (Figures S1–S3 and Tables S2–S5) indicated an almost negligible effect of the inclusion of rare taxa, and a relatively higher performance of power law functions in most models computed at the smaller regional scale. However, exponential forms clearly outperformed power law at basin scales, while yielding lower though relatively close AIC and pseudo- $r^2$  scores at regional scales to those obtained using power law functions (Table S2). Consequently, and to facilitate comparisons, we report only results of distance-decay models computed including rare taxa and fitted with negative exponential forms.

#### 2.3.2 | Statistical Comparisons

Differences between distance-decay models computed at the same scale, that is, between deep and shallow-abyssal regions or across biotic groups, were examined with pairwise comparisons of the intercept and slopes of similarity decay curves, using the  $z_{dep}$  function in the ‘betapart’ package (Martín-Devasa et al. 2022). While the intercept can be interpreted as the expected community similarity at short distances (‘initial similarity’), the slope is the rate at which communities change with spatial distance (Soininen, McDonald, and Hillebrand 2007), reflecting turnover or abundance gradients in species occurrences.

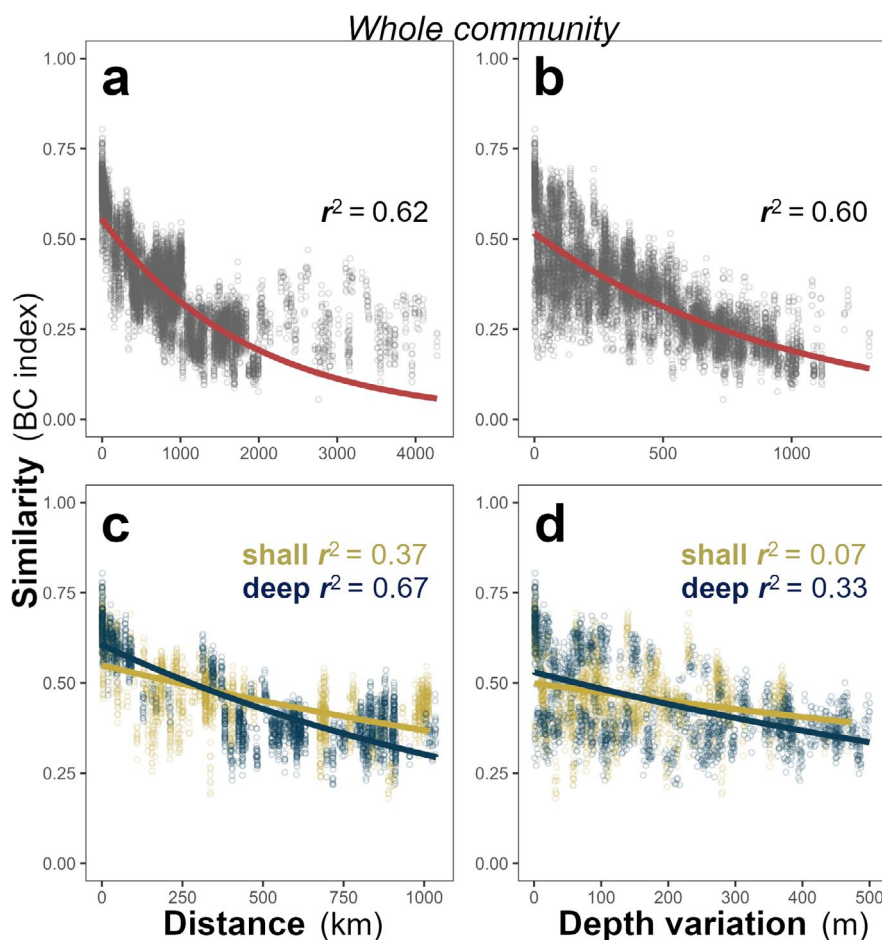
As such, quantifying variations in intercept and slope across decay curves (Martín-Devasa et al. 2022) has proven effective to measure the role of dispersal limitation and niche-sorting mechanisms among populations that cohabit in a similar geographical context (Gómez-Rodríguez and Baselga 2018; Martín-Devasa et al. 2024). Last, to control the false discovery rate under various dependency conditions among test statistics, we applied a Benjamini–Yekutieli multiple testing procedure (Benjamini and Yekutieli 2001).

### 3 | Results

#### 3.1 | Distance-Decay Patterns: Metacommunity

In basin-scale models (range: 1–4000 km), computed for the whole invertebrate community across all 28 abyssal Pacific locations, both spatial distance (pseudo- $r^2=0.62$ ; Figure 3a) and depth difference (pseudo- $r^2=0.60$ ; Figure 3b) explained a similarly large fraction of the variance in decay of community similarity. Interestingly, while decay was relatively uniform with increasing depth difference between samples (Figure 3b), the relationship of community similarity

with spatial distance showed a tipping point at intermediate distances, suggesting an increase in similarity between communities at similar depths at spatial distances between 1000 and 3000 km (Figure 3a). In contrast, in regional-scale models (range: 1–1100 km), computed across locations either above or below 4400 m, spatial distance (Figure 3c) explained a larger proportion of the variance (pseudo- $r^2$ : deep-abyssal=0.67; shallow-abyssal=0.37) than did depth difference (deep-abyssal=0.33; shallow-abyssal=0.07) across each separate region (Figure 3d). Comparison of model parameters (intercept and slope; Table 1) revealed statistically significant differences (i.e.,  $z_{\text{dep}}$  statistic; Table S6) between the distance-decay curves of shallow- and deep-abyssal regions (Figure 3c). For deep communities, ‘initial similarity’ was significantly higher at closer locations (intercept,  $z_{\text{dep}}=-6.4$ ,  $p<0.001$ ) and turnover rates significantly steeper (80%, slope;  $z_{\text{dep}}=10.0$ ,  $p<0.001$ ) than in the shallow-abyssal region. Despite exhibiting proportionally lower intercept and slope (Table 1), decay curves computed upon depth difference across each region (Figure 3d, Table 1) also depicted significantly larger slopes ( $z_{\text{dep}}=6.2$ ,  $p<0.001$ ) and initial similarity ( $z_{\text{dep}}=-3.2$ ,  $p<0.002$ ) across the communities of the deep region (Table S6).



**FIGURE 3** | Patterns of decay in community similarity with spatial distance (a, c) and depth difference (b, d) for the whole invertebrate megafauna metacommunity (402 taxa) across the abyssal northeast Pacific seafloor. Decay models fitted with negative exponential functions were calculated at: Basin-scale (a, b), for the entire study area (samples: 140), and regional scale (c, d), for areas above and below 4400 m depth (samples: 71 at deep and 65 at shallow-abyssal region). All decay models were statistically significant ( $p<0.03$ ; see Table 1-top).

**TABLE 1** | Statistical parameters of distance-decay models computed for different invertebrate groups at different scales across the abyssal northeast Pacific seafloor (see distance-decay curves: Figures 3–5). *p*-values were adjusted by Benjamini–Yekutieli correction.

Factor	Group/Region	Intercept	Slope	<i>p</i> -value	Display
Depth	Whole community	0.52	$-10.1 \times 10^{-4}$	0.024	Figure 3b
Depth	Whole community/shallow	0.50	$-5.2 \times 10^{-4}$	0.024	Figure 3d
Depth	Whole community/deep	0.53	$-9.1 \times 10^{-4}$	0.024	Figure 3d
Distance	Whole community	0.55	$-5.3 \times 10^{-4}$	0.024	Figure 3a
Distance	Whole community/shallow	0.55	$-3.9 \times 10^{-4}$	0.024	Figure 3c
Distance	Whole community/deep	0.61	$-7.1 \times 10^{-4}$	0.024	Figure 3c
Distance	Nodule-growing	0.64	$-5.9 \times 10^{-4}$	0.031	Figure 4a
Distance	Nodule-growing/shallow	0.62	$-2.1 \times 10^{-4}$	0.031	Figure 4d
Distance	Nodule-growing/deep	0.68	$-6.8 \times 10^{-4}$	0.031	Figure 4d
Distance	Sediment-dwelling	0.48	$-4.5 \times 10^{-4}$	0.031	Figure 4b
Distance	Sediment-dwelling/shallow	0.48	$-6.8 \times 10^{-4}$	0.031	Figure 4e
Distance	Sediment-dwelling/deep	0.56	$-7.1 \times 10^{-4}$	0.031	Figure 4e
Distance	Swimming	0.24	$-2.0 \times 10^{-4}$	0.031	Figure 4c
Distance	Swimming/shallow	0.22	$-5.1 \times 10^{-4}$	0.085	Figure 4f
Distance	Swimming/deep	0.30	$-4.5 \times 10^{-4}$	0.031	Figure 4f
Distance	Cnidaria	0.66	$-6.4 \times 10^{-4}$	0.031	Figure 5a
Distance	Cnidaria/shallow	0.63	$-3.2 \times 10^{-4}$	0.031	Figure 5e
Distance	Cnidaria/deep	0.65	$-4.8 \times 10^{-4}$	0.031	Figure 5e
Distance	Echinodermata	0.50	$-4.1 \times 10^{-4}$	0.031	Figure 5b
Distance	Echinodermata/shallow	0.53	$-7.7 \times 10^{-4}$	0.031	Figure 5f
Distance	Echinodermata/deep	0.59	$-7.1 \times 10^{-4}$	0.031	Figure 5f
Distance	Porifera	0.50	$-1.6 \times 10^{-4}$	0.031	Figure 5c
Distance	Porifera/shallow	0.50	$-1.1 \times 10^{-4}$	0.031	Figure 5g
Distance	Porifera/deep	0.50	$-1.6 \times 10^{-4}$	0.031	Figure 5g
Distance	Arthropoda	0.45	$-2.1 \times 10^{-4}$	0.031	Figure 5d
Distance	Arthropoda/shallow	0.50	$-4.8 \times 10^{-4}$	0.031	Figure 5h
Distance	Arthropoda/deep	0.49	$-2.4 \times 10^{-4}$	0.031	Figure 5h

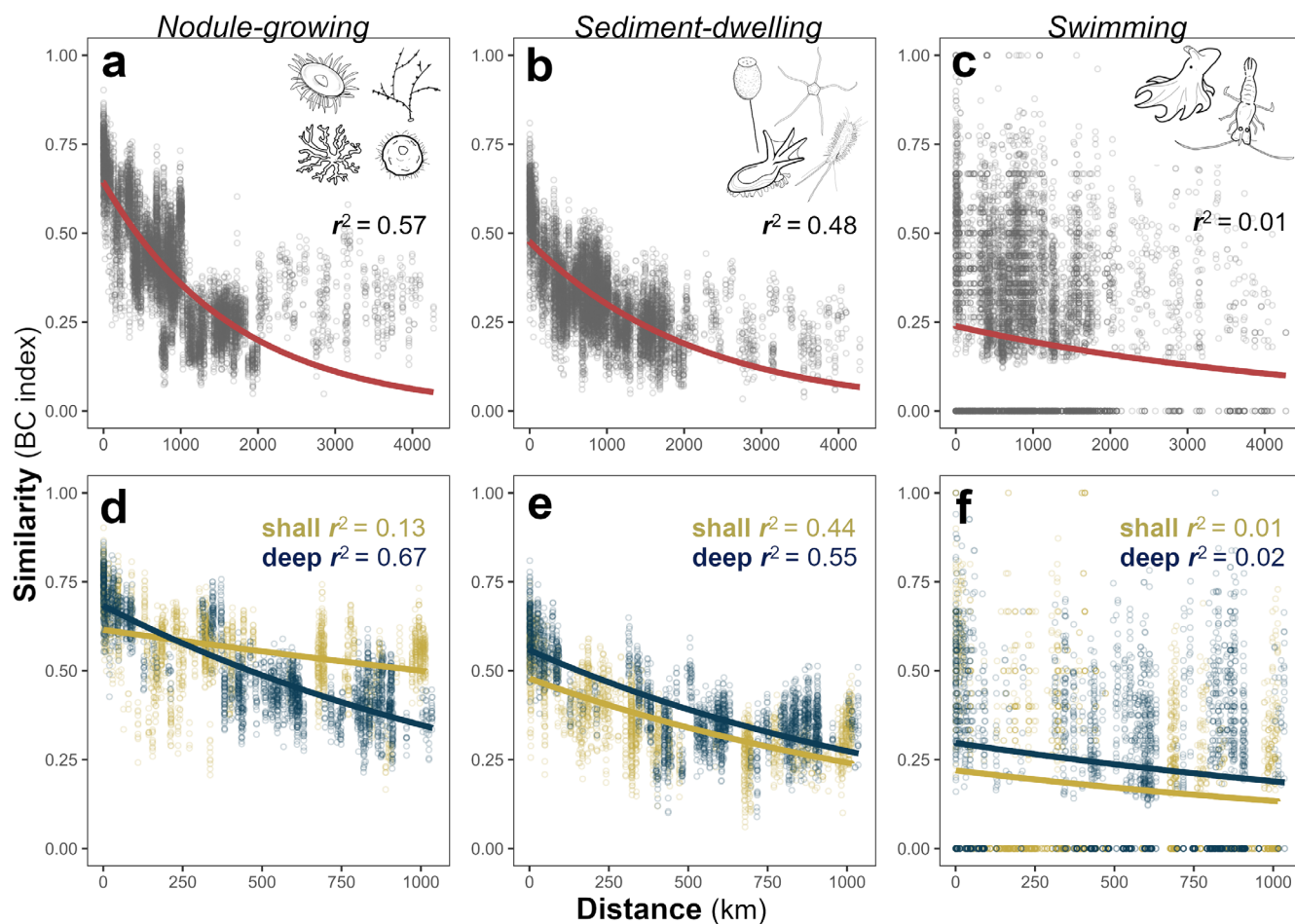
### 3.1.1 | Disentangling the Effect of Spatial Distance and Depth Difference

At basin-scale, when including depth difference and spatial distance in 2-factor models based on the whole community sample, the proportion of explained variance increased to pseudo- $r^2=0.70$ , and most of this variation was jointly explained by both predictors (0.51). This likely resulted from the high collinearity between spatial distance and depth difference across the northeast Pacific basin (e.g., Mantel test, Spearman  $r=0.76$ ,  $p<0.01$ ). A much lower proportion of this variation was either uniquely explained by spatial distance (0.11) or depth difference (0.08) at this scale. In contrast, at smaller scales, when including depth difference and spatial distance, the proportion of explained variance increased to pseudo- $r^2=0.40$  in the shallow-abyssal region, most uniquely

explained by spatial distance (0.33), with a much smaller fraction solely explained by depth difference (0.03), or by the joint effect of both factors (0.04). In the deep region, the proportion of variance explained by the 2-factor model was pseudo- $r^2=0.67$ , with 0.33 jointly explained by both predictors, 0.34 by spatial distance alone and the effect of depth difference being negligible ( $<0.01$ ). Consequently, for the comparisons between particular faunal groups, we report only results computed for spatial distance.

### 3.2 | Distance-Decay Patterns: Functional Groups

In basin-scale models, spatial distance explained a large fraction of the variance in similarity decay of Nodule-growing (pseudo- $r^2=0.56$ ; Figure 4a) and Sediment-dwelling communities



**FIGURE 4** | Distance-decay patterns for invertebrate megafauna groups with different life-habit relative to hard-substratum dependency (a, d: Nodule-growing; b, e: Sediment-dwelling and c, f: Swimming) across the abyssal northeast Pacific seafloor. Decay models fitted with negative exponential functions were calculated at: Basin-scale (a–c), for the entire study area (samples: 140), and; regional scale (d–f), for areas above and below 4400 m depth (samples: 71 at deep and 65 at shallow-abyssal region). All decay models except f (Shallow region Swimming taxa), were statistically significant ( $p < 0.032$ ; see Table 1-middle).

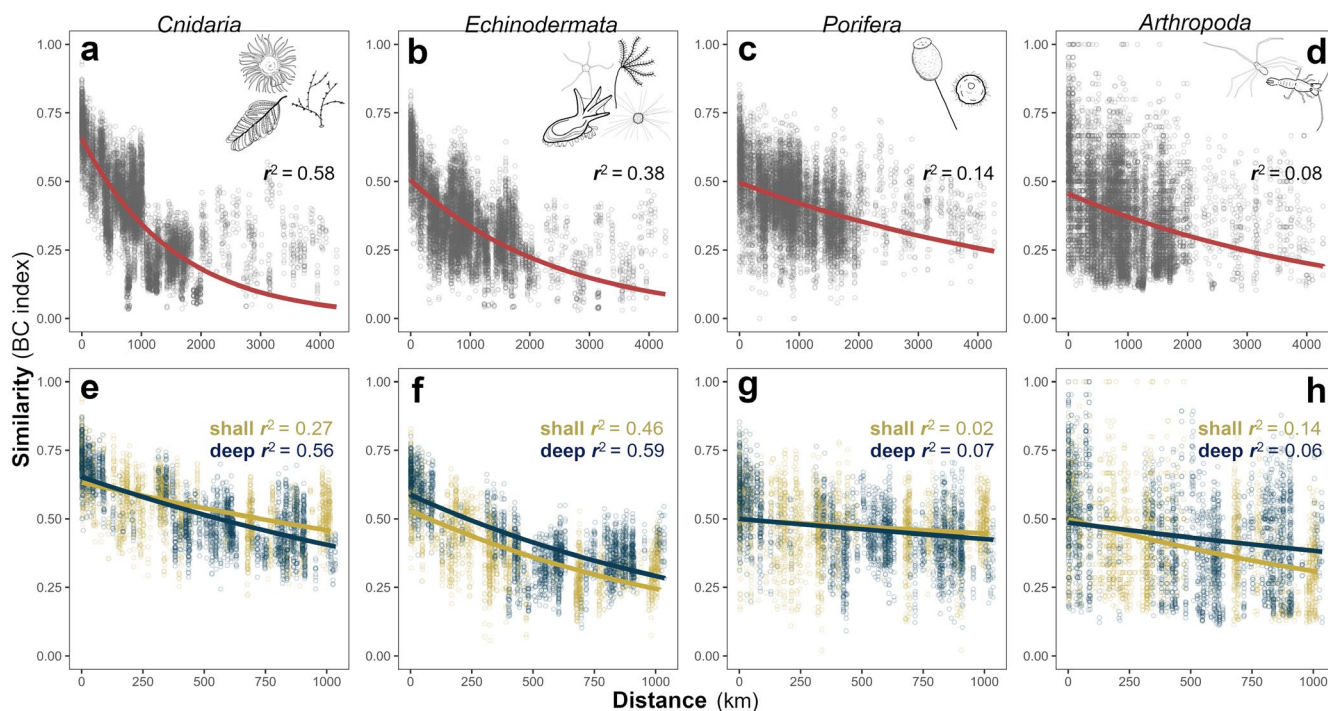
(pseudo- $r^2 = 0.48$ ; Figure 4b), but showed a poor fit for Swimming fauna (pseudo- $r^2 = 0.01$ ; Figure 4c). Nodule-growing communities exhibited the most pronounced distance-decay, with similarity decreasing by ~25% at 500 km distances and 50% at 1000 km (range  $\beta_{\text{sim}}$ : 0.64–0.05; Figure 4a), while for Sediment-dwelling fauna, similarity decreased by ~15% at 500 km distances and ~35% at 1000 km (range  $\beta_{\text{sim}}$ : 0.48–0.08; Figure 4b). Curves significantly differed between these two functional groups (in both intercept and slope; Table S6), as the similarity decay in the Nodule-growing community was 31% steeper (and initial similarity 33% higher) than that depicted by the Sediment-dwelling (Table 1).

In regional-scale models, initial similarity was significantly higher in the deep compared to the shallow-abyssal region (Table 1, Table S6), for both Nodule-growing ( $z_{\text{dep}} = -6.1$ ,  $p < 0.001$ ; Figure 4d) and Sediment-dwelling communities ( $z_{\text{dep}} = -8.1$ ,  $p < 0.001$ ; Figure 4e). However, while the decay in similarity of Nodule-growing communities was significantly steeper (slope over two times higher) in the deep-abyssal region ( $z_{\text{dep}} = 17.8$ ,  $p < 0.001$ ; Figure 4d), distance-decay slopes of Sediment-dwelling fauna were almost identical between deep and shallow-abyssal communities ( $z_{\text{dep}} = 0.6$ ,  $p = 0.58$ ; Figure 4e). As observed at basin-scale,

the variance explained by models computed for Swimming communities at regional scales were extremely low (Figure 4f).

### 3.3 | Distance-Decay Patterns: Taxonomic Groups

In basin-scale models, spatial distance explained a large fraction of the variance in distance-decay for Cnidaria (pseudo- $r^2 = 0.58$ ; Figure 5a) and Echinodermata (pseudo- $r^2 = 0.38$ ; Figure 5b), but only a small fraction for Porifera (pseudo- $r^2 = 0.14$ ; Figure 5c) and Arthropoda communities (pseudo- $r^2 = 0.08$ , Figure 5d). Cnidaria exhibited the most pronounced decay, with mean similarity decreasing by ~30% at 500-km distances and ~50% at 1000 km (range  $\beta_{\text{sim}}$ : 0.66–0.05; Figure 5a), followed by Echinodermata, which decreased in mean similarity by 18% at 500 km and 36% at 1000 km ( $\beta_{\text{sim}}$ : 0.50–0.06; Figure 5b). Distance-decay models significantly differed between these two phyla (in both intercept and slope; Table S2), as the decay in Cnidaria had a 57% steeper slope and a 30% higher initial similarity than in Echinodermata taxa (Table 1). In contrast, curves depicted flatter and similar slopes in Porifera (range  $\beta_{\text{sim}}$ : 0.50–0.24; Figure 5c) and Arthropoda (range  $\beta_{\text{sim}}$ : 0.45–0.22; Figure 5d).



**FIGURE 5** | Distance-decay patterns for the four most dominant invertebrate megafauna Phyla (a, e: Cnidaria; b, f: Echinodermata; c, g: Porifera; d, h: Arthropoda) across the abyssal northeast Pacific seafloor. Decay models fitted with negative exponential functions were calculated at: Basin-scale (a–c), for the entire study area (samples: 140), and regional scale (d–f), for areas above and below 4400 m depth (samples: 71 at deep and 65 at shallow-abysal region). All decay models were statistically significant ( $p < 0.032$ ; see Table 1-bottom).

In regional-scale models, initial similarity (but not slope; Table S6) of Echinoderm communities was significantly higher in the deep region ( $z_{\text{dep}} = -4.6$ ,  $p < 0.001$ ; Figure 5f, Table 1), while the slope (but not the intercept, Table S6) of similarity decay in Cnidarian communities was significantly steeper (48%) in the deep compared to the shallow-abysal region ( $z_{\text{dep}} = 3.9$ ,  $p < 0.001$ ; Figure 5e, Table 1). In turn, neither of these parameters differed significantly (Table S6) between deep and shallow-abysal Porifera decay curves (Figure 5g, Table 1). However, as observed at the basin-scale, the proportions of variance explained by models computed for Porifera and Arthropoda at regional scales were extremely low (range pseudo- $r^2$ : 0.02–0.14; Figure 5g,h).

#### 4 | Discussion

Based on one of the largest biodiversity datasets ever compiled in the abyss (402 taxa), this study provides some of the first evidences of contrasting beta-diversity patterns at a metacommunity level across an abyssal seascape basin spanning over 4000 km. Similarity of the whole invertebrate community decreased with both spatial distance and depth difference across the northeast Pacific basin, but decay patterns significantly varied between deep and shallow-abysal regions, that is, above and below the CCD cline at 4400 m (Harris et al. 2023). Despite extending along much less prominent environmental gradients, abyssal plain species turnover was comparably steeper than commonly observed across a similar spatial domain (i.e., 4000 km) in hydrothermal vents, but flatter than that in seamount communities (Richer de Forges, Koslow, and Poore 2000). In turn, Nodule-growing fauna exhibited significantly higher species

turnover rates across space than the Sediment-dwelling, particularly in deep-abysal communities. From these, cnidarians exhibited the steepest and sponge communities the flattest species turnover rates across space. Combined, these results provide further evidence of the structuring effect of the CCD on benthic communities at large scales at abyssal seascapes (Simon-Lledó et al. 2023c). This structure is likely underpinned by an evolutionary adaptation to environmental variation within depth bands in the deep ocean (Wagstaff et al. 2014), and indicates an association between adult life-habits and dispersal distance in abyssal megafauna communities, similar to previously suggested for Isopoda macrofauna (Brix et al. 2020).

Overall, when considering the whole community, beta-diversity patterns differed above and below the CCD, with higher initial similarities and turnover rates in the deep than the shallow-abysal region. Moreover, while both spatial distance and depth did similarly explain decay patterns at the basin-scale, the explanatory power of depth difference was diminished in models computed above and below the CCD. This pattern further supports the niche-sorting role of this boundary at the larger, whole-basin scale. However, the fit and shape of similarity decay curves largely differed across biotic groups.

Phylogenetically, Cnidaria and Echinodermata exhibited more evident geographic structuring and contrasting similarity decay patterns above and below the CCD than Porifera and Arthropoda communities, suggesting that either the former have more limited dispersal capacity (particularly Cnidaria) or the latter are less sensitive to environmental variations across abyssal seascapes—or combinations of both factors. In the abyssal Pacific, high abundances of a few dominant soft-corals (Cnidaria) and

brittle star species (Echinodermata) are replaced below the CCD by a larger number of taxa, respectively anemones and holothurians, with more even occurrences (Simon-Lledó et al. 2023c). This variation likely results from the oversaturation of calcite carbonate above 4400m, promoting higher densities of taxa most dependant on this resource, (essential for the development of a range of body structures among deep ocean fauna, such as sclerites in soft-corals (Watabe and Kingsley 1992) or the exoskeleton of equinoderms like sea and brittle stars (Lebrato et al. 2010). As such, variations in calcite availability are known to regulate the distribution of stony coral species in shallower deep-sea habitats (Guinotte et al. 2006). In contrast, distance decay models for Arthropoda did not have a good geographic fit, similar to previously reported for amphipod communities assessed at a similar domain across the Pacific abyss (Bribiesca-Contreras et al. 2021), likely owing to the characteristically high dispersal capacity of this group (e.g., Havermans et al. 2013). This result was expected because most taxa in our dataset are fast swimming crustaceans capable of vertical migrations (to higher calcite saturation), often showing near cosmopolitan distributions, like the prawns *Cerataspis monstrosus* (Figure 2h) and *Hymenopenaeus nereus* (Swan et al. 2021). In turn, weak geographic structuring of Porifera similarity likely suggests a wide environmental tolerance of this group in the abyss, which could result from the highly adaptable metabolisms and skeleton typologies among deep-sea sponges (Tabachnick 1991; Falcucci et al. 2021), and the lack of calcareous sponge species in our dataset. These results add to the growing evidence of high regional connectivity of sponges in the deep ocean (Brown, Davis, and Leys 2017; Taboada et al. 2018, 2023). Yet the similarity in decay patterns for Porifera, and all sessile taxa, and Arthropoda, suggest that adult mobility is not a reliable predictor of beta-diversity patterns across abyssal phyla. Instead, life-habit appeared to be more relevant for variations in similarity decay patterns across the abyssal Pacific.

Our analyses revealed significantly higher species turnover rates (31% steeper) in hard-substratum facultative fauna (Nodule-growing), particularly Cnidarians, compared to the Sediment-dwelling or Swimming communities of the abyssal northeast Pacific basin. This finding suggesting an analogy between abyssal seascapes and continental shelves, where many clades of sessile animals growing on scattered strips of rock-hard substratum develop more restricted dispersal strategies to minimise propagule loss, while fauna living on more ubiquitous sediment resource tend to have wider dispersal strategies (e.g., Grantham, Eckert, and Shanks 2003; Shanks 2009). Although reproductive strategy is still only known for a few deep-sea invertebrates (Hilário et al. 2015; Young et al. 2018), examples of a relation between life-habit and larval dispersal behaviour exist for hard bottom Cnidaria species, such as the anemone *Urticina* sp., which produce planulae larvae that remain within 1 m from the parents during development (Mercier et al. 2017), or the bathyal soft-coral *Drifa glomerata*, which has demersal larvae (Sun, Hamel, and Mercier 2010). In line with these results, constrained dispersal and larval retention within the benthic boundary layer are thought to maintain higher epibenthic diversity in larger or more closely located bathyal drop-stones (Meyer et al. 2016) and within local abyssal nodule field communities (Kersten, Smith, and Vetter 2017). Beyond cnidaria, life

habit in abyssal isopods (swimming or burrowing adapted), has also shown to be a relatively good proxy of dispersal capacity within this clade (Brix et al. 2020). In combination, these results underscore the importance of considering functional traits to explore beta-diversity in the abyss, as is commonplace in terrestrial landscape research (Graco-Roza et al. 2022). However, our results also stress an urgent need to further characterise abyssal larvae, species traits and reproduction strategies to obtain a comprehensive view of the dispersal limitation mechanisms operating in these vast ecosystems.

#### 4.1 | Conclusions

This study demonstrates the value of combining image-based benthic community analysis with distance-decay modelling to investigate beta diversity patterns in poorly explored deep ocean ecosystems like abyssal seascapes. Amid the scarce available knowledge on dispersal strategies (Hilário et al. 2015) and the true scales of population connectivity (Baco et al. 2016), our findings provide a robust stepping stone to further disentangle the role of dispersal limitation and niche-sorting mechanisms in regulating abyssal community assembly and biodiversity patterns. Our results suggest that chemical boundaries have an important niche-sorting effect, driving higher species turnover rates in seascape communities below the CCD, and that an association between species life-habit and dispersal limitation likely exists in abyssal fauna. These findings have important implications for the preservation of deep ocean biodiversity, given the growing need to protect vast abyssal regions from globally rising threats. For example, our results point to major shifts in abyssal benthic community structure as a result of the global rise of the CCD, predicted to gradually push >20% of the northeast Pacific seafloor (millions of km<sup>2</sup>) currently supporting oversaturated calcium carbonate-adapted communities under the CCD by 2100 (Harris et al. 2023). In turn, the more restricted dispersal ability of hard-substratum-dependent species, such as nodule-growing Cnidaria, could yield a lower recolonisation potential to the fragmentation of habitat associated to the reduction of nodule 'dispersal stepping-stones' by seabed mining (Simon-Lledó, Simon-Lledó, Bett, Koser, et al. 2019). Moreover, as opposed to current practice in marine conservation policy (e.g., Wedding et al. 2013; Lodge et al. 2014), our analyses also evidence that shallow and deep-abyssal regions are best not treated as ecological surrogates, but rather studied and managed separately (e.g., deeper reserve networks must either be larger or more numerous and closely spaced). However, while our study shows that image-based distance-decay approaches can provide novel means to infer and formulate new macroecological hypothesis, it also highlights the need for further characterising species, life-history traits and genetic connectivity to fully address the complex mechanisms that regulate biodiversity in one of Earth's last wilderness.

#### Author Contributions

Erik Simon-Lledó, Andrés Baselga and Carola Gómez-Rodríguez designed the study. Erik Simon-Lledó collated, processed and analysed the data, aid by Andrés Baselga, Carola Gómez-Rodríguez and G. Bribiesca-Contreras. Erik Simon-Lledó wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

## Conflicts of Interest

The authors declare no conflicts of interest.

## Data Availability Statement

All data and code are deposited in Zenodo (<https://zenodo.org/records/1447942>).

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## Supporting Information

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