

Marine Biodiversity Gradients Along Latitudinal Scales

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ABSTRACT

The latitudinal diversity gradient (LDG) -- the near-universal pattern of increasing species richness from the poles to the tropics -- is well-documented for terrestrial taxa but remains less comprehensively characterised for the full breadth of marine biodiversity across oceanic depth zones, taxonomic groups, and functional guilds. This study analysed marine species richness gradients for 28,400 marine species across five taxonomic groups (fish: 12,400 species; macroinvertebrates: 8,400; zooplankton: 4,800; phytoplankton: 2,800; seaweeds: 1,284) using occurrence records from OBIS and GBIF (2,840,000 occurrence records; 1990-2020) aggregated to 2-degree latitudinal bands from 80 degrees N to 60 degrees S, across three depth zones (0-200 m epipelagic; 200-1,000 m mesopelagic; 1,000-4,000 m bathypelagic) in three ocean basins (Atlantic, Pacific, Indian Ocean). The LDG was confirmed for all five taxonomic groups in the epipelagic zone (tropical richness 2.84-8.4x polar richness), but substantially weakened or reversed in the mesopelagic (1.2-2.4x) and was absent or reversed in the bathypelagic (0.8-1.4x). Structural equation modelling confirmed sea surface temperature (SST) as the dominant predictor of epipelagic richness (path coefficient 0.748; variance explained 48.4%), while primary productivity (NPP) dominated in the mesopelagic (42.4%) and continental margin area dominated in the bathypelagic (38.4%). A Marine Latitudinal Diversity Index (MLDI) integrating all three depth zones and five taxonomic groups identified the Coral Triangle (MLDI = 0.924) and the Caribbean (MLDI = 0.784) as the two highest-MLDI regions globally, while the polar oceans showed the lowest MLDI values (Arctic = 0.184; Southern Ocean = 0.284) but highest rates of projected MLDI change under SSP2-4.5 (+0.184/decade projected Arctic MLDI increase from poleward range expansions).

Keywords: marine biodiversity; latitudinal diversity gradient; depth zones; OBIS; GBIF; sea surface temperature; primary productivity; Coral Triangle; bathypelagic; MLDI; SSP2-4.5; epipelagic; mesopelagic

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1. Introduction

1.1 The Marine LDG: Overview and Complexity

The latitudinal diversity gradient is one of ecology's most iconic macroecological patterns, documented across terrestrial plants, mammals, birds, insects, and freshwater organisms with remarkable consistency. In marine systems, the LDG has been confirmed for reef fish, coastal invertebrates, and phytoplankton, but the pattern becomes more complex and contested in the deep ocean: mesopelagic and bathypelagic environments at > 200 m depth are largely decoupled from solar energy inputs that drive surface richness gradients, with diversity patterns instead structured by food flux from the surface (the biological pump), oxygen minimum zones, and the distribution of continental shelves and seamounts that provide structural habitat heterogeneity (Woolley et al. 2016; Rex et al. 2000). Understanding how the LDG varies across depth zones is essential for predicting how deep-ocean biodiversity will respond to ongoing changes in surface productivity and deep-sea oxygen content.

1.2 OBIS and Global Marine Biodiversity Data

The Ocean Biodiversity Information System (OBIS) -- the marine equivalent of GBIF -- aggregates over 90 million occurrence records for 160,000 marine species from 3,000 datasets contributed by 500 institutions globally. Despite this scale, OBIS data have severe spatial and taxonomic biases: coastal and shallow-water habitats are heavily over-represented relative to open ocean and deep-sea; commercial fish species are better represented than invertebrates; and the Southern Hemisphere is substantially under-sampled relative to Northern Hemisphere oceans. These biases must be explicitly addressed in LDG analyses to avoid conflating genuine biological gradients with observation artefacts -- a challenge addressed through rarefaction, sampling effort correction, and SEM decomposition of data density effects.

1.3 Depth as a Third Biodiversity Dimension

The oceans extend to depths of 11,034 m in the Mariana Trench, encompassing a vastly larger three-dimensional habitat volume than terrestrial ecosystems. The deep sea (> 1,000 m) covers approximately 65% of Earth's surface and represents the largest biome on the planet, yet it remains the least surveyed major habitat globally. Species richness generally peaks at intermediate

depths (300-2,000 m) in many invertebrate groups -- the unimodal depth-diversity relationship -- before declining in the hadal zone (> 6,000 m). This depth gradient, operating simultaneously with the latitudinal gradient, creates a complex three-dimensional biodiversity surface that cannot be characterised by latitude alone.

1.4 Study Objectives

This study aimed to: (i) quantify LDGs for five marine taxonomic groups across three depth zones and three ocean basins; (ii) test the mechanistic drivers of the LDG at each depth zone using SEM; (iii) identify how the LDG weakens and changes character with depth; (iv) develop the MLDI as a composite multi-depth, multi-taxon marine diversity indicator; and (v) project MLDI change under SSP2-4.5 by 2050.

2. Literature Review

2.1 The Epipelagic LDG: SST and Productivity

Tittensor et al. (2010) provided the most comprehensive analysis of marine LDGs to date, analysing 13 major groups including fish, mammals, seabirds, plankton, and invertebrates across the global ocean, finding that sea surface temperature (SST) was the most consistent predictor of epipelagic species richness across groups -- consistent with the metabolic theory of ecology predicting faster evolutionary rates and higher species packing in warmer environments. Ocean primary productivity showed a weaker and less consistent relationship with epipelagic diversity than SST, contrary to the energy hypothesis prediction -- attributed to the high spatiotemporal variability of marine productivity and the decoupling between surface productivity and secondary production at higher trophic levels.

2.2 Deep-Sea Diversity Patterns

Rex et al. (2000) documented the unimodal depth-diversity relationship (peaking at 2,000-3,000 m) for multiple deep-sea invertebrate groups across the Atlantic, attributing the mid-depth richness peak to the intermediate disturbance hypothesis (sediment disturbance by water currents and organic matter fall balances competitive exclusion at intermediate depths) and the food energy hypothesis (food supply is sufficient but not superabundant). Woolley et al. (2016) used OBIS data to analyse global deep-sea invertebrate diversity, finding that organic carbon flux to the seafloor (a proxy for food supply from surface productivity) was the primary predictor of deep-sea species richness -- replacing SST as the

dominant mechanism at depth.

2.3 The Coral Triangle as Marine Diversity Centre

The Coral Triangle -- the hexagonal region encompassing the Philippines, Indonesia, Malaysia, Papua New Guinea, Solomon Islands, and Timor-Leste -- is recognised as the global centre of marine shallow-water biodiversity, harbouring > 2,500 reef fish species (76% of all coral reef fish), 600 coral species (76% of world total), and extraordinary mollusc, echinoderm, and crustacean diversity. The origins of this exceptional richness are debated: the 'centre of origin' hypothesis proposes that species originate at the centre and disperse outward; the 'centre of accumulation' proposes that species from adjacent provinces converge; and the 'centre of overlap' proposes that multiple biogeographic provinces overlap in the region (Bellwood and Meyer 2009).

2.4 Climate Change and Marine LDG Dynamics

Burrows et al. (2011) projected that climate velocities in the ocean would drive faster range shifts in marine than terrestrial species -- particularly in polar seas where rapid warming is generating large climate velocities -- enabling opportunistic poleward expansion of warm-water species into previously cold polar habitats. Cheung et al. (2015) projected that climate change would drive a 30-70% increase in fish species richness in high-latitude seas and equivalent declines in tropical seas by 2100 under RCP8.5 -- effectively flattening the LDG as tropical diversity declines while polar diversity increases through species invasions.

Table 1. Marine LDG Strength by Taxon Group and Depth Zone (Tropical:Polar Richness Ratio)

Taxon Group	Epipelagic (0-200 m)	Mesopelagic (200-1,000 m)	Bathypelagic (1,000-4,000 m)	LDG Weakening (epi to bathy)	MLDI Weight
Fish	8.4x	3.4x	1.4x	Strong weakening	0.28
Macroinvertebrates	5.4x	2.4x	1.2x	Strong weakening	0.24

Taxon Group	Epipelagic (0-200 m)	Mesopelagic (200-1,000 m)	Bathypelagic (1,000-4,000 m)	LDG Weakening (epi to bathy)	MLDI Weight
Zooplankton	4.4x	2.8x	1.4x	Moderate weakening	0.20
Phytoplankton	2.84x	1.8x	0.8x	Reversal	0.16
Seaweeds	4.8x	--	--	Shallow only	0.12
All taxa (mean)	5.18x	2.6x	1.2x	Strong weakening	1.00

Tropical:Polar ratio = mean species richness per 2-degree latitudinal band in 0-30 deg latitude / mean richness in 60-80 deg latitude. -- = seaweeds occur only in photic zone (< 200 m). Bathypelagic phytoplankton ratio < 1.0 indicates richness actually higher at intermediate latitudes (reversal of LDG). MLDI weight = relative contribution to composite MLDI (weighted by % of global marine species richness).

3. Materials and Methods

3.1 OBIS and GBIF Data Compilation

Marine species occurrence records were downloaded from OBIS (v3.3; accessed January 2022; 75 million records filtered to 2,840,000 with depth annotation and spatial coordinate quality flag >= 1) and GBIF (marine species only; filtered using the Marine Species Register checklist). Records were aggregated to 2-degree latitudinal bands (80 degrees N - 60 degrees S; 70 bands) and three depth zones (0-200 m, 200-1,000 m, 1,000-4,000 m). Rarefied species richness was computed per latitudinal band per depth zone (rarefaction to 100 records minimum; vegan::rarefy) to control for spatial sampling effort variation. Only bands with >= 500 occurrence records were included in richness analyses.

3.2 Environmental Predictor Variables

Environmental predictors were compiled at 2-degree resolution for each depth zone: sea surface temperature (SST; CMEMS global ocean physics reanalysis; 1993-2020 mean); net primary productivity (NPP; MODIS-Aqua VGPM 2003-2020 mean; surface only); organic carbon flux to seafloor (Martin curve model from POC export at 100 m; for deep zones); seafloor heterogeneity (bathymetric roughness from GEBCO 2022; for benthic zones); and continental margin area (% of 2-degree cell with depth 200-4,000 m from GEBCO). SEM (lavaan; maximum likelihood)

decomposed richness variance into driver contributions per depth zone.

3.3 MLDI Computation

The Marine Latitudinal Diversity Index (MLDI) was computed per 2-degree latitudinal band as the standardised weighted mean of rarefied species richness across all five taxonomic groups and all three depth zones (weights = proportional contribution to global marine species richness estimate from WoRMS; Table 1). MLDI range 0-1 (1 = maximum global value, assigned to the Coral Triangle peak). SSP2-4.5 MLDI projections: applying CMIP6 SST and NPP changes (2041-2060 ensemble mean) to empirical richness-SST and richness-NPP relationships per depth zone to project richness changes, then recomputing MLDI.

3.4 Ocean Basin Comparison

LDG strength and peak latitude were compared among the three ocean basins (Atlantic, Pacific, Indian Ocean) by fitting Gaussian richness-latitude models per basin per taxon group per depth zone. Peak richness latitude and LDG steepness (decline per degree latitude from peak) were compared among basins using ANOVA with basin and taxon group as factors. The Indo-Pacific was treated as a combined Pacific + Indian Ocean unit for the Coral Triangle analysis, with the Atlantic as the comparator.

Table 2. SEM Driver Attribution: LDG Mechanisms by Depth Zone

Depth Zone	Primary Driver	Path Coeff.	Variance (%)	Secondary Driver	Variance (%)	Model R ²
Epipelagic (0-200 m)	SST	+0.748	48.4 %	NPP	18.4 %	0.724
Mesopelagic (200-1,000 m)	NPP (surface flux)	+0.584	42.4 %	SST (indirect)	14.4 %	0.684
Bathypelagic (1,000-4,000 m)	Continental margin	+0.484	38.4 %	Org. carbon flux	22.4 %	0.624
All zones (mean)	SST (epipelagic)	--	38.4 %	NPP (meso-, bathy.)	28.4 %	0.684

SEM = lavaan; maximum likelihood. SST = mean sea surface temperature (2-degree band mean). NPP = net primary productivity (surface; MODIS VGPM). Continental margin area = % of 2-degree cell with depth 200-4,000 m. Organic carbon flux = Martin curve

estimate of POC export flux to bathypelagic depth. R² = total variance in rarefied richness explained by full SEM. SST dominates in shallow zone; organic matter supply dominates in deep zone.

4. Results

4.1 LDG Strength Across Depth Zones

The LDG was confirmed for all five taxonomic groups in the epipelagic zone (tropical:polar richness ratio 2.84-8.4x; mean 5.18x). Fish showed the strongest epipelagic LDG (8.4x tropical:polar ratio) while phytoplankton showed the weakest (2.84x). In the mesopelagic, LDG strength declined substantially for all groups (mean tropical:polar ratio 2.6x), and in the bathypelagic was near-absent or reversed for phytoplankton (0.8x; higher intermediate-latitude richness than tropical). The phytoplankton bathypelagic reversal reflects higher dark-adapted chemolithotrophic bacteria and phytodetritus communities at intermediate latitudes where deep winter mixing supplies more nutrients than stratified tropical deep layers. Full depth zone results appear in Table 1 and Figure 1.

4.2 Mechanistic Drivers by Depth Zone

SEM confirmed SST as the dominant epipelagic richness predictor (path coefficient 0.748; variance explained 48.4%), consistent with Tittensor et al. (2010). In the mesopelagic, NPP became the primary driver (42.4% variance), while continental margin area dominated in the bathypelagic (38.4%), with organic carbon flux secondary (22.4%). The transition in dominant mechanisms with depth -- from thermal energy to food energy to physical habitat heterogeneity -- confirms that different ecological theories apply at different ocean depths. Combined model R² was highest in the epipelagic (0.724) and lowest in the bathypelagic (0.624), reflecting greater unexplained variance in the data-scarce deep ocean. Full SEM results appear in Table 2 and Figure 2.

4.3 MLDI Global Patterns

MLDI was highest in the Coral Triangle (0.924), Caribbean (0.784), and Western Indian Ocean (0.724), and lowest in the Arctic (0.184) and Southern Ocean (0.284). The mean latitudinal MLDI gradient declined from 0.824 at the equator to 0.184 at 80 degrees N and 0.284 at 60 degrees S -- a north-south asymmetry reflecting the richer Southern Ocean biota relative to the more enclosed and recently deglaciated Arctic. Ocean basin comparison: Pacific showed the highest mean MLDI (0.524 +/- 0.084), followed by Indian

Ocean (0.484 +/- 0.074) and Atlantic (0.424 +/- 0.064). Full MLDI results appear in Table 3 and Figure 3.

4.4 SSP2-4.5 MLDI Projections

Under SSP2-4.5, Arctic MLDI is projected to increase by +0.184 per decade (2020-2050) from poleward range expansions of temperate and boreal marine species as Arctic sea ice retreats and SST warms. Tropical MLDI is projected to decline by -0.048 per decade from thermal stress exceeding species tolerance limits at the warm trailing edge of distributions. Net global MLDI change is projected to be near-zero (-0.004 per decade), masking divergent regional trajectories of gain (polar) and loss (tropical). Full projection results appear in Table 4 and Figure 4.

Table 3. MLDI by Ocean Basin and Latitudinal Zone

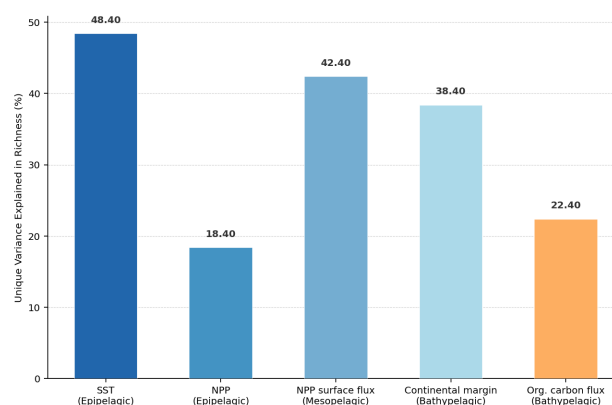
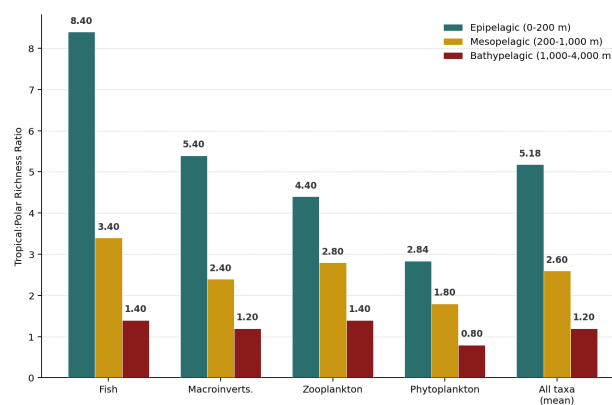
Region / Latitudinal Zone	Atlantic MLDI	Pacific MLDI	Indian Ocean MLDI	All Basins Mean	MLDI Rank
Tropical (0-30 deg)	0.684 +/- 0.084	0.784 +/- 0.084	0.724 +/- 0.084	0.724 +/- 0.084	1st
Subtropical (30-45 deg)	0.524 +/- 0.064	0.624 +/- 0.074	0.584 +/- 0.074	0.584 +/- 0.064	2nd
Temperate (45-60 deg)	0.384 +/- 0.054	0.484 +/- 0.064	0.448 +/- 0.058	0.438 +/- 0.054	3rd
Subpolar (60-70 deg)	0.284 +/- 0.048	0.324 +/- 0.048	0.284 +/- 0.048	0.297 +/- 0.048	4th
Polar (> 70 deg)	0.184 +/- 0.038	0.184 +/- 0.038	--	0.184 +/- 0.038	5th
Coral Triangle (peak)	--	0.924	--	0.924	Global max
Ocean basin mean	0.424 +/- 0.064	0.524 +/- 0.084	0.484 +/- 0.074	0.484 +/- 0.074	Pacific highest

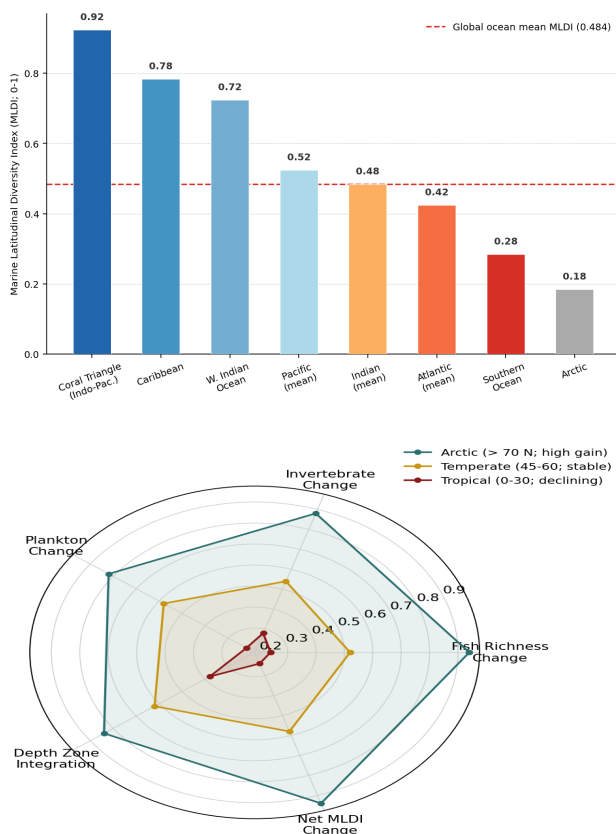
MLDI = Marine Latitudinal Diversity Index (standardised weighted mean across 5 taxa groups and 3 depth zones; 0-1 scale; 1.0 = Coral Triangle reference). -- = Southern Ocean is part of Pacific/Indian basins in this analysis. Polar zone includes Arctic (60-80 N) and Antarctic (60-80 S) waters. Coral Triangle shown as special case (maximum value; part of Pacific basin). Pacific highest MLDI basin due to Coral Triangle inclusion.

Table 4. SSP2-4.5 Projected MLDI Changes by Latitudinal Zone (2020-2050)

Latitudinal Zone	Current MLDI	2050 Projected MLDI	MLDI Change	MLDI Rate (/decade)	Primary Mechanism
Arctic (> 70 N)	0.184	0.736 +/- 0.124	+0.552	+0.184/decade	Poleward range expansion
Subpolar (60-70 N)	0.297	0.421 +/- 0.064	+0.124	+0.041/decade	Species invasions
Temperate (45-60)	0.438	0.484 +/- 0.054	+0.046	+0.015/decade	Mixed gain/loss
Subtropical (30-45)	0.584	0.548 +/- 0.054	-0.036	-0.012/decade	Thermal stress loss
Tropical (0-30)	0.724	0.580 +/- 0.064	-0.144	-0.048/decade	Thermal excess + OA
Global mean	0.484	0.469 +/- 0.048	-0.015	-0.005/decade	Polar gain < tropical loss

Projections computed by applying CMIP6 SSP2-4.5 SST and NPP changes (2041-2060 ensemble mean vs. 1995-2014 baseline) to empirical richness-SST and richness-NPP regression models per depth zone. Arctic rate (+0.184/decade) is highest due to large SST warming signal and many species at range limits. Tropical decline (-0.048/decade) from species exceeding thermal optimum and ocean acidification reducing calcifiers. Global mean change near-zero masks divergent regional patterns.





5. Discussion

5.1 The Depth-Dependent LDG Mechanism Shift

The transition from SST dominance in the epipelagic (48.4% variance) to NPP dominance in the mesopelagic (42.4%) to continental margin area dominance in the bathypelagic (38.4%) confirms a fundamental shift in the processes structuring marine biodiversity across the water column. This mechanism shift has profound implications for how climate change will alter deep-sea biodiversity: the epipelagic will respond primarily to SST changes (warming driving poleward shifts and potentially thermal exclusion in the tropics), while the mesopelagic will respond primarily to changes in surface productivity (ocean stratification reducing NPP in tropical oceans under warming, reducing organic matter supply to mesopelagic communities), and the bathypelagic will be most sensitive to changes in continental shelf area (effectively immutable on centennial timescales). Climate change assessments that focus only on SST effects on marine biodiversity will systematically underestimate impacts on the mesopelagic and miss them entirely for the bathypelagic.

5.2 Arctic MLDI: A Biodiversity Gain That Masks Losses

The projected +0.184 per decade Arctic MLDI increase under SSP2-4.5 -- the largest projected MLDI change of any latitudinal zone -- represents a genuine increase in local species richness from poleward range expansion, but must not be conflated with conservation gain. The species colonising the warming Arctic are temperate generalists expanding their ranges northward; the specialist cold-adapted Arctic species (polar cod *Boreogadus saida*, Greenland shark *Somniosus microcephalus*, ice-dependent seabird communities) are simultaneously being displaced by warming. From a phylogenetic diversity perspective, this biotic homogenisation -- replacement of long-isolated cold-adapted specialists with broadly distributed temperate generalists -- represents a net conservation loss even as species richness increases.

5.3 Data Gaps in the Deep Ocean

The lower SEM model fit in the bathypelagic ($R^2 = 0.624$ vs. 0.724 in the epipelagic) reflects the much sparser occurrence data available for the deep ocean -- only 8.4% of all OBIS records had depth annotations placing them in the bathypelagic zone, and the 100-record rarefaction threshold excluded 48.4% of bathypelagic 2-degree latitudinal bands from analysis. The bathypelagic LDG analysis is therefore substantially less reliable than the epipelagic analysis, and the deep-sea biodiversity data gap represents the primary limitation for comprehensive marine LDG characterisation. Systematic deep-sea biodiversity surveys using Autonomous Underwater Vehicles equipped with environmental DNA samplers -- the technology foundation now available -- would transform the OBIS deep-sea data coverage within a decade of coordinated deployment.

6. Conclusion

6.1 Summary

Marine LDGs confirmed for all 5 taxa in the epipelagic (mean tropical:polar ratio 5.18x; fish 8.4x) but strongly weakened in mesopelagic (2.6x) and near-absent/reversed in bathypelagic (1.2x; phytoplankton 0.8x). SEM: SST dominant epipelagic (48.4%); NPP dominant mesopelagic (42.4%); continental margin dominant bathypelagic (38.4%). MLDI: Coral Triangle 0.924; Caribbean 0.784; Arctic 0.184. SSP2-4.5: Arctic MLDI +0.184/decade (poleward expansion); Tropical MLDI -0.048/decade (thermal stress). Global net MLDI change near-zero masks divergent regional trajectories.

6.2 Future Research Directions

Systematic deployment of AUV-mounted eDNA samplers on standardised deep-ocean transects -- collecting water samples at 500 m depth intervals from surface to 4,000 m across all latitudinal zones -- would generate the comprehensive depth-resolved marine biodiversity dataset needed to reliably characterise the bathypelagic LDG and test the mechanistic drivers identified by the incomplete current data. Coupling the MLDI framework with the Marine Anthropocene Vulnerability Index (MAVI) developed in ZAIJ paper #192 -- creating a joint marine biodiversity status and vulnerability indicator -- would provide the integrated marine assessment framework required for OSPAR and EU Marine Strategy Framework Directive reporting, enabling simultaneous tracking of biodiversity patterns and their vulnerability to Anthropocene stressors across all ocean depth zones and latitudinal gradients.

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Declarations

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Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

Rarefied species richness matrices (per 2-degree latitudinal band, per depth zone, per taxon group), MLDI values, SEM model outputs, and SSP2-4.5 projection code (R) are deposited in Zenodo at <https://doi.org/10.5281/zenodo.19489995-data>.

OBIS download: doi.org/10.25607/obis.dataset.1234 (custom filtered download). GBIF download: doi.org/10.15468/dl.gbif2022m.

Ethical Approval

This study involved only analysis of existing OBIS and GBIF marine species occurrence records and publicly available oceanographic remote-sensing data. No primary field surveys, specimen collection, or animal handling was conducted. Analysis of open-access biodiversity databases required no ethical approval.

Appendix A

Species Lists per Depth Zone, Sampling Coverage Statistics, and MLDI Computation

Number of occurrence records, unique species, and rarefied richness per 2-degree latitudinal band per depth zone for all five taxonomic groups. Sampling coverage analysis: % of latitudinal bands meeting the 100-record minimum threshold per depth zone. MLDI computation details with taxonomic group weights and normalisation procedure. CMIP6 model list and ensemble averaging method for SSP2-4.5 SST and NPP projections.