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Global sea urchin diversity patterns reveal shifts between shallow-water and deep-water benthic assemblages

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Understanding how biodiversity patterns vary with depth is essential for interpreting global marine diversity. Here, we integrate occurrence records and model-based predictions to examine sea urchin diversity patterns, biogeographic structure, and their drivers across bathymetric zones. Sea urchins exhibit a conserved bimodal latitudinal diversity pattern with subtropical peaks across depths. However, the environmental mechanisms underlying this pattern shift from temperature-dominated controls in shallow waters to multi-factor, depth-constrained drivers in deep waters. Deep-water assemblages further display greater biogeographic fragmentation, characterized by broader latitudinal but narrower longitudinal ranges, possibly mediated through integrations among environment, seafloor topography, and life-history characteristics. In the North Atlantic, shallow-water assemblages affiliate with Indo-Pacific realms, whereas deep-water assemblages align with American realms, reflecting depth-dependent evolutionary histories. These findings demonstrate that depth mediates shifts in the mechanisms, composition, and spatial organization of benthic biodiversity, highlighting the importance of incorporating bathymetric processes into global marine biodiversity assessments and conservation planning.

Amidst accelerating global climate warming and the looming sixth mass extinction¹, biodiversity erosion has emerged as an inevitable consequence². This crisis necessitates systematic quantification of extant biodiversity and diagnostic assessment of its spatial architecture, wherein investigating the drivers governing biodiversity pattern constitutes a critical baseline for conservation and sustainable management. Despite constituting 71% of Earth's total surface area, marine ecosystems have received comparatively limited attention in biodiversity research due to the late onset of marine research and methodological challenges in marine sampling³. Compounding this knowledge gap, current marine biodiversity studies exhibit pronounced taxonomic bias, emphasizing motile pelagic species over benthic animals, such as echinoderms and crustaceans⁴. As an integral component of marine ecosystems, benthic fauna performs critical ecological functions and plays an irreplaceable role in shaping benthic environments⁵. Insufficient understanding of benthic organisms may compromise the accuracy of assessments of climate change impact on marine biota, consequently impeding the conservation of marine biodiversity.

Global diversity patterns, including the latitudinal diversity gradient (LDG) and biogeographic regionalization, remain incompletely understood in marine systems, particularly within deep-water ecosystems. The LDG describes the changes of biodiversity distribution from the equator to the poles⁶, while biogeographic regionalization reflects the spatial organization of faunal assemblages shaped by environmental, evolutionary, and geological processes^{7–10}. Terrestrial communities typically exhibit a unimodal LDG with equatorial diversity peaks, whereas many marine taxa display bimodal LDGs, with species richness peaks centering in distinct latitudinal bands across various taxa^{2,11}. Despite growing recognition of these differences, it remains unclear whether such bimodal LDG patterns are conserved across bathymetric zones. Previous studies on marine benthic regionalization, including starfish¹² and deep-water brittle stars¹³, have shown that faunal divisions differ between shallow and deep waters, yet whether similar depth-dependent differences occur within the same taxonomic group at a global scale remains unresolved. The prevailing hypotheses emphasize the importance of several dominant factors, including the primacy of temperature and productivity¹⁴, evolutionary history¹³, tectonic events¹⁵ and the

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direction of biological dispersal¹⁶. Notably, while marine systems exhibit stabilized environmental temperatures with increasing bathymetric gradients¹⁷, bathymetric gradients may exert multifaceted influences on benthic biogeographic regionalization through depth-stratified thermal regimes, habitat heterogeneity and dispersal bottleneck^{18,19}. Whether similar or distinct mechanisms structure in shallow- and deep-water benthic communities, therefore, remains an open question, underscoring the need for explicitly incorporating bathymetric structure into marine biodiversity assessments.

Progress in addressing the above knowledge gaps has been constrained by uneven sampling effort and inadequate knowledge of species distributions and taxonomy in many regions, a phenomenon commonly referred to as the “Wallacean shortfall”²⁰. Species distribution models (SDMs) offer a feasible solution to address the Wallacean shortfall²¹ by fitting existing distribution records with environmental data. A fundamental constraint in modeling studies resides in the substantial requirement for nonoverlapping georeferenced occurrence records to ensure reliability of model training²². This limitation becomes particularly true for stenotopic species, where spatially explicit occurrence data remain critically deficient. Ensembles of small models (ESMs) can establish a model group to integrate the results of multiple models to maximize the preservation of species and maintain statistical validity²³. Together, these approaches enable robust estimation of both observed and potential diversity across depth gradients, providing a basis for testing whether biodiversity patterns differ between shallow and deep benthic systems.

Sea urchins (Echinoidea) constitute an ideal model for investigating depth-dependent biodiversity patterns in marine benthic systems. This globally distributed benthic group comprises over 1000 extant species²⁴, and spans a wide range of bathymetric zones, life-history strategies and feeding modes. The most notable characteristic of sea urchins is their rigid shell composed of calcium carbonate plates and movable spines. Additionally, a proportion of them are omnivores possessing an Aristotle’s lantern, whereas others are detritivores that exhibit specialized atelostomate spines and a labrum²⁵. As significant consumers in many ecosystems, sea urchins are considered to play a crucial role in shaping community structures, often inducing shifts towards low-diversity and stable configurations in their habitats²⁶. Their feeding and burrowing activities, as well as the carbon sequestration resulting from the deposition of their skeletal plates after death, have substantial impacts on the composition of marine sediments and the structure of benthic substrates²⁷. From an evolutionary perspective, Echinoidea is a taxon that survived the global acidification and warming during the second and third mass extinctions with only a few lineages. These surviving lineages subsequently re-diversified during the Triassic period²⁸ and underwent repeated shifts between shallow and deep waters from the Cretaceous through the Late Miocene^{24,28–30}. Thus, the characteristics of sea urchin diversity can provide critical insights into biodiversity assessment and prediction under climate change, while also providing a natural framework for elucidating how trait evolution, life-history strategies, and extinction

events influence biodiversity patterns along depth gradients. However, current studies on sea urchins primarily focus on regional scales or on species-specific responses to climate change^{31,32}, leaving global patterns of diversity and depth-mediated biogeographic organization insufficiently explored.

Given the environmental contrasts across depths and the complex evolutionary history of repeated shifts between bathymetric zones in sea urchins, we hypothesized that global diversity patterns, biogeographic structures and driving mechanisms would differ between shallow- and deep-water assemblages, possibly reflecting depth-mediated ecological and evolutionary processes. To test this hypothesis, we first assembled a global database encompassing distribution records for the vast majority of known sea urchin species. We then examined both observed and model-predicted diversity to identify global centers of sea urchin richness, and assessed biogeographic regionalization for assemblages living above and below the thermocline. We further categorized sea urchins into epifaunal (living on the sea floor surface) and infaunal (buried within the substrate) groups to evaluate the role of life habits in shaping diversity patterns. Finally, we explored the factors contributing to the formation of the observed diversity pattern and regionalization across depths. By integrating empirical data with predictive modeling and biogeographic analyses, this study provides a framework for understanding how bathymetry structures global benthic biodiversity patterns and informs marine conservation planning under ongoing climate change.

Results

Global patterns of sea urchin richness

The completeness test shows that our data was acceptable in both shallow and deep waters, reaching 80% sample coverage (SC). Specifically, the areas lacking sampling are mainly located in the Indian Ocean, the Coral Triangle, and the Southern Atlantic (Fig. 1). In contrast, data coverage in the trench only reached 67%, with large areas remaining unsampled (Table 1 and Fig. S1). In species composition, the difference between shallow- and deep-water communities was firstly observed at the family level. We identified four families only present in shallow waters (Psychocidaridae, Glyptocidaridae, Taiwanasteridae, and Scutellidae) and five families exclusively inhabiting deep waters (Carnarechinidae, Calymnidae, Corystusidae, Aeropsidae, and Macropneustidae) (Fig. S2).

Based on Shannon index, overall alpha-diversity of sea urchins exhibits pronounced spatial heterogeneity, with particularly high species richness concentrated on the continental shelves of the southern Florida Peninsula, encompassing the Florida Keys coral reef, and the northeastern side of the West Indies in the Atlantic Ocean (Fig. 2a). Additional biodiversity hotspots include: (i) the northern coast of Madagascar; (ii) the Seto Inland Sea; (iii) the southern shelf of Luzon Island; (iv) the Hawaiian Islands; (v) the shelves of northern Australia, including the Ningaloo Coast and the Great Barrier Reef; and (vi) the eastern coast of New Zealand. When considering alpha-diversity across different depths, distinct biodiversity hotspots were observed between shallow- and deep-water assemblages. For shallow-water

Fig. 1 | A global map of sample completeness (SC) for sea urchins at a resolution of $1^\circ \times 1^\circ$. The warmer color indicates the higher sample completeness, and the colder color indicates the lower sample completeness.

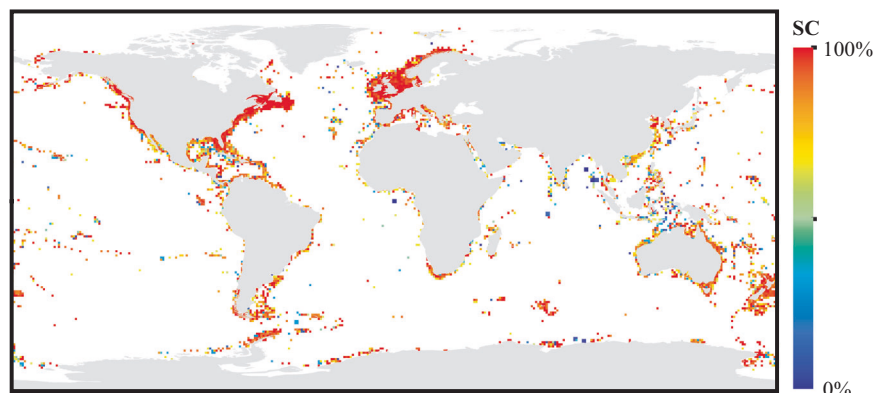


Table 1 | The completeness estimators at $q = 0$, $q = 1$, and $q = 2$

	$Q = 0$	$Q = 1$	$Q = 2$
Shallow water	0.826	0.992	0.999
Deep water	0.820	0.991	0.999
Trench	0.672	0.927	0.995

The completeness estimators range from 0 to 1, the higher the completeness estimator, indicates a higher the sample coverage.

taxa (211,042 occurrence records; 694 species), regions of high species richness concentrate on the shelves of the southern Florida Peninsula and the Great Barrier Reef. Additional richness hotspots include: (i) the northwest Mediterranean; (ii) the northern coast of Madagascar, and (iii) the South China Sea (Fig. 2b), exhibiting the peak of species diversity near 20°N/S latitudes. For deep-water assemblages (34,441 occurrence records; 694 species), primary richness was found concentrated on the shelf of the southern Florida Peninsula, and secondary hotspots of biodiversity are located in the northeastern coast of New Zealand and the South Shetland Islands (Fig. 2c).

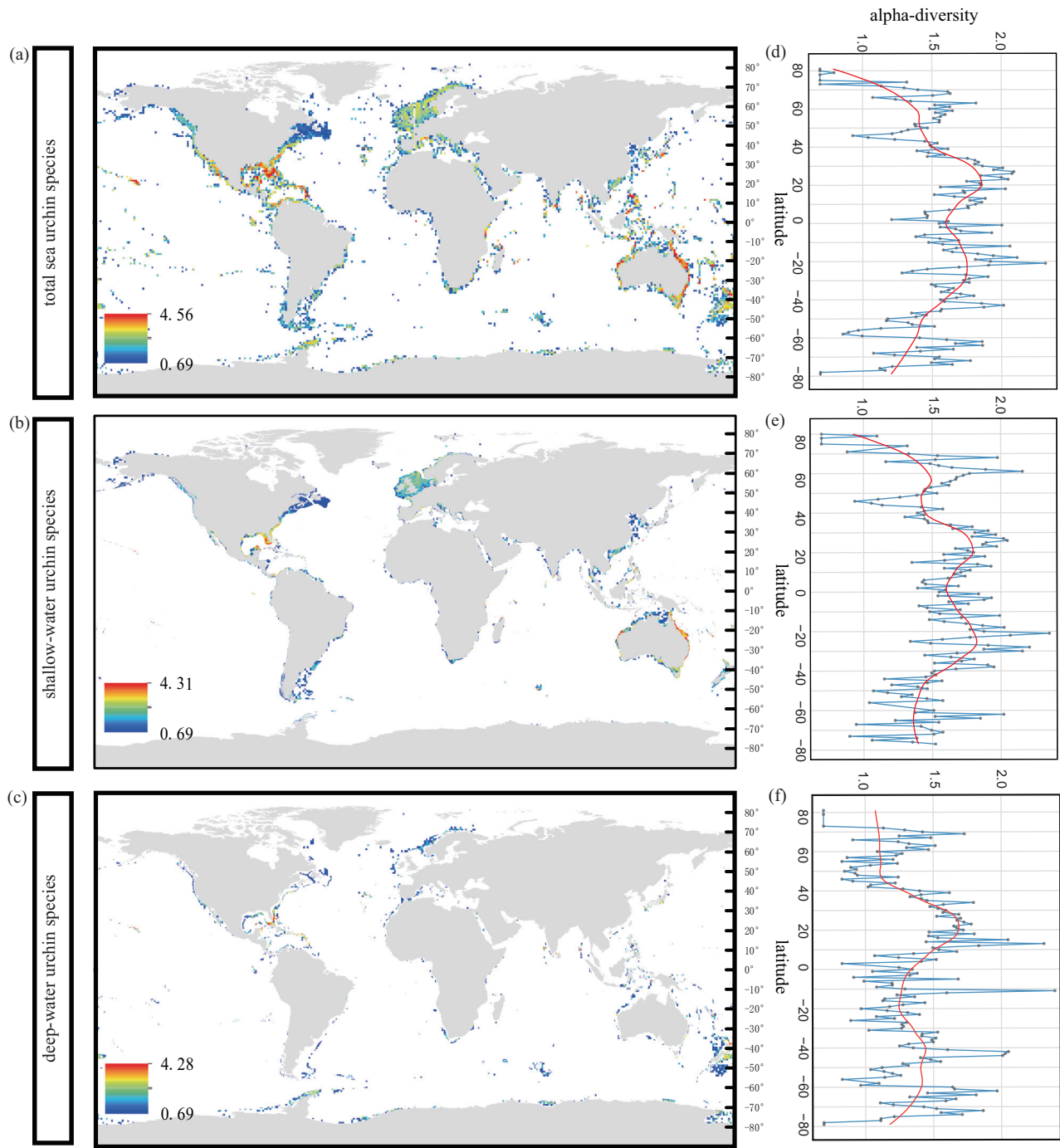


Fig. 2 | Global biogeography and diversity patterns of sea urchins. a–c Alpha-diversity of total, shallow-water (0–200 m) and deep-water (200–2000 m) sea urchins. **d–f** Latitudinal patterns of total, shallow-water (0–200 m) and deep-water (200–2000 m) sea urchins. The warmer color indicates the higher alpha-diversity (Shannon index), and the colder color indicates the lower alpha-diversity.

Table 2 | Generalized additive model results for the alpha-diversity of shallow- and deep-water sea urchins against environmental variable

	Environmental variable	EDF	p-value	R ²
Shallow water	DO	5.344	***	0.176
	pH	5.598	***	
	PP	6.04	***	
	SBT	7.864	***	
	SBS	6.983	***	
Deep water	DO	4.446	*	0.122
	pH	4.367	***	
	SBT	7.32	***	
	SBS	7.722	***	
	Rough	5.132	***	
	Depth	1.001	**	

Elevated effective degrees of freedom (EDF) in smoothing terms signify increasingly complex nonlinear relationships between alpha-diversity and environmental gradients.

SBT sea bottom temperature, CV current velocity, SBS sea bottom salinity, DO dissolved oxygen, PP primary productivity, Rough terrain ruggedness index, the higher the index indicates the seabed is steeper.

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Curve-fitting analyses of median alpha-diversity against latitude revealed a consistent bimodal pattern with diversity peaks in the subtropics. This pattern was most prominent in the Northern Hemisphere across all sea urchin assemblages, shallow-water taxa, and deep-water taxa (Fig. 2d–f). Analyses of species richness weighted by sampling effort (Fig. S3), species richness and gamma-diversity also confirmed this bimodal latitudinal pattern (Fig. S4). However, it was found that sea urchins have secondary alpha-diversity peaks around 50°–60° in latitude. We then mapped the global distribution of sea urchins using the second-order polynomial regression and GAM. The results consistently indicated a highly complex nonlinear relationship between latitude and alpha-diversity of all sea urchins, shallow-water taxa and deep-water taxa (second-order polynomial regression: $R^2 = 0.02$ – 0.04 , Fig. S5; GAM: $R^2 = 0.06$ – 0.07 , $p < 0.001$). In addition, different patterns of alpha diversity were observed across different types of life habits. For epifaunal sea urchins, their diversity exhibits a bimodal pattern, with centers of diversity located near 20° latitude in both the Northern and Southern Hemispheres, particularly in regions such as Australia and the Caribbean (Fig. S6a). In contrast, we did not find a typical bimodal pattern in infaunal sea urchins. Specifically, the center of diversity for infaunal sea urchins in the Northern Hemisphere is located along the coast of Florida, while the diversity center in the Southern Hemisphere is less pronounced (Fig. S6c).

As expected, sea urchin diversity was significantly influenced by environmental variables, exhibiting pronounced nonlinear relationships with most variables (Table 2). These variables accounted for 17.6% of the total variance in shallow-water assemblages and 12.2% in deep-water assemblages. For shallow-water assemblages, gradients in alpha-diversity demonstrated significant correlations with temperature, dissolved oxygen, pH, primary productivity and salinity, among which salinity and temperature were primary determinants (Fig. S7a–e). Partial dependence plots demonstrated a nonlinear relationship between temperature and shallow-water alpha-diversity: values arose across the suboptimal thermal range (8–24 °C), peaked near 24 °C, and exhibited a sharp decline beyond this critical threshold (Fig. S7a). With increasing depth, the environmental regulation of LDGs shifted substantially. Roughness and depth replaced dissolved oxygen and primary productivity as the dominant drivers significantly shaping LDG patterns. Notably, depth exhibited a strictly linear negative relationship with diversity (Table 2). Correspondingly, sea urchin diversity in deep-water habitats declined monotonically with increasing

depth (Fig. S7j). Using a reduced set of environmental factors (four variables), we detected a strong correlation between species richness and temperature in shallow waters of the Northern Hemisphere (Table S1). In contrast, species richness in deep-water regions was more strongly associated with salinity gradients. In the Southern Hemisphere, significant environmental effects on deep-water assemblages were detected only in the South Pacific (Table S2).

Potential species diversity of sea urchins

The potential diversity was characterized by the habitat suitability of the studied sea urchins. Among shallow-water species, we identified 281 common species and 184 rare species, with potential species diversity ranging from 0.8 to 130. For deep-water species, we identified 180 common species and 259 rare species, with a diversity range of 8.9–153 (Fig. 3a, b). The potential shallow-water species diversity patterns largely exhibit similar trends to those of actual species diversity, indicating that our dataset is representative of the broad patterns of shallow-water sea urchin species diversity (Fig. 3a). The primary discrepancy was observed at the Great Barrier Reef, which exhibited the highest potential species diversity, suggesting that its suitability for sea urchins may be higher than expected. For deep-water species, new potential species richness hotspots were detected around the northeastern coast of the Atlantic Ocean, the southeastern shelf of China and the Ryukyu Islands (Fig. 3b).

Latitudinal analysis also revealed bimodal distributions of potential species diversity for both shallow- and deep-water species, with peaks occurring around 20°N/S latitude. Notably, the latitudinal position of the peaks in deep-water sea urchins is slightly higher compared to those in shallow-water settings (Fig. 3d). Unlike the actual species diversity pattern, the secondary biodiversity peaks were not found in potential species diversity distributions.

Sea urchin bioregion partitioning across depth

Hierarchical clustering analysis based on Jaccard dissimilarity index revealed significant faunistic differences between shallow- and deep-water sea urchin assemblages. The shallow-water species assemblage is divided into two marine super realms aligning with the tectonic boundaries of continental plates. Specifically, the super realm American plate (red hues) consists of 4 realms: the Antarctic Ocean (group 3), the mid-Atlantic Ocean (group 5), the Arctic Ocean (group 6) and the Gulf of California (group 7). On the other hand, the super realm Pan-Indo-Pacific (blue hues) encompasses realms of Indo-Pacific mid-latitudes (group 1), Indo-Pacific low-latitudes (group 2), Northwestern Atlantic (group 4) and Sunda Strait (group 8) (Fig. 4a).

By contrast, deep-water species assemblage exhibits more fragmented biogeographic regionalization compared with shallow-water counterparts, forming 3 super realms containing 12 realms: (a) super- realm the Antarctic Ocean: shelf of Antarctica (group 4), southern shelf of South America (group 5) and Kerguelen (group 10); (b) super realm Indo-Pacific: Northern Indian Ocean and subtropical Japan (group 2), South China Sea, Coral Triangle, and Australia (group 1), Sumatra Island and South Africa (group 3) and North Pacific (group 12); (c) super realm North Atlantic: the Norwegian Sea (group 6), Mediterranean Sea (group 7), Davis Strait (group 11), and Caribbean Sea (group 8) (Fig. 4b).

Consistent with species-level patterns observed in our potential diversity analysis, there are differences in environmental factors driving the formation of realms across different depths. In shallow waters, all environmental variables except for primary productivity are significantly associated with the formation of certain realms ($r > 0.2$, $p < 0.05$), among which temperature demonstrated the strongest influence across most realms. The exceptions are the mid-Atlantic Ocean and the Gulf of California, where no environmental factors showed significant correlations with diversity patterns (Fig. 5a). In deep waters, temperature showed significant associations with only three realms (groups 2, 4, and 11), whereas dissolved oxygen exhibited the strongest statistical association with biogeographic partitioning (Fig. 5b).

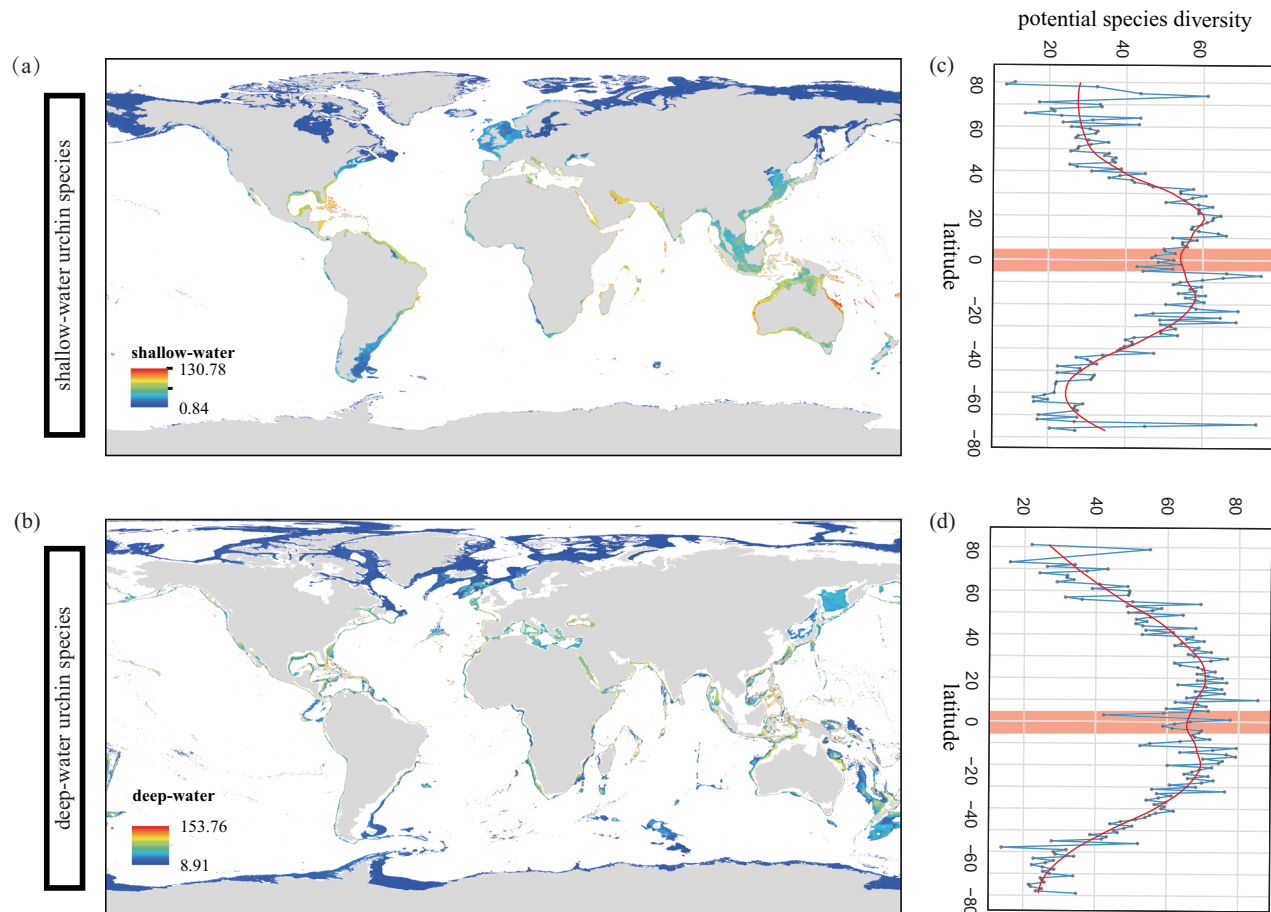


Fig. 3 | Global potential species diversity of sea urchins. Global potential species diversity pattern of **a** shallow-water sea urchins and **b** deep-water sea urchins and their potential latitudinal patterns (**c**, **d**). The warmer color indicates the higher

potential species diversity, and the colder color indicates the lower potential species diversity. The red bands indicate the equator area (5°S to 5°N).

Discussion

Depth-dependent shifts in diversity-environment relationships

The bimodal LDG in marine taxa, previously documented in fish and zoobenthos^{4,11,12,33,34}, is now confirmed in our study of sea urchins. Both empirical data and modeling prediction consistently identify subtropical zones as shallow-water diversity hotspots for this group. Despite a less pronounced subtropical biodiversity peak for deep-water sea urchins in the Southern Hemisphere revealed by the Shannon index, our model-based prediction, species richness and gamma-diversity analyses consistently revealed a remarkable diversity peak for these species in the Southern Hemisphere subtropics. Unlike the typical marine LDG, field biodiversity metrics reveal a secondary richness peak near 50°–60°N latitude, a pattern that persists consistently across shallow- and deep-water sea urchin assemblages. This feature remains absent in both potential diversity and gamma-diversity estimates, suggesting that its formation may be attributable to non-environmental mechanisms. We speculate that this may reflect systematic sampling biases, considering the disproportionately extensive marine survey records in the Northern Hemisphere's mid-high latitudes relative to other regions, which likely stems from the history of early oceanographic exploration in these resource-abundant areas³⁵. Additionally, we propose that the attenuated deep-water alpha-diversity peak in the Southern Hemisphere relative to the Northern Hemisphere may likewise reflect sampling biases. Quantitative analysis of alpha-diversity revealed substantially greater sampling heterogeneity in the Southern Hemisphere, where nearly one-third of records are located near New Zealand waters, potentially causing the shift of the diversity peak. Critically, the peak-richness cell in the Southern Hemisphere (17°S, 76 species) matches the Northern Hemisphere's maximum diversity (Fig. 2b), conforming to model

projections. However, the absence of sampling in adjacent cells in the Southern Hemisphere suggests the observed pattern likely underestimates true diversity. We therefore infer that deep-water sea urchin LDGs more closely resemble our model projections with diversity peaks in the subtropics of both hemispheres. When stratifying sea urchins by their life modes into infaunal and epifaunal categories, our analysis revealed that epifaunal species exhibited diversity patterns consistent with the overall assemblage. However, infaunal species demonstrated an absence of the classic LDG, maintaining unexpectedly high biodiversity in certain high-latitude regions. This spatial distribution pattern parallels those observed in soil organisms and earthworm communities, in which sedimentary environments may function as ecological buffers against climatic fluctuations³⁶.

The bimodal paradigm of the latitudinal distribution of species richness has been considered to be correlated with phylogenetics, physical barriers³⁷ and environmental factors¹¹. However, previous research on the influence of environmental factors has mainly focused on shallow-water regions, particularly along the American coast³⁸. Whether such shaping effects apply globally and whether they extend to the relatively stable deep waters remain undetermined. In this study, the successful reconstruction of the bimodal LDG in both shallow- and deep- waters using SDM indicated that the influence of environmental factors also exists in the deep water. Crucially, SDM analysis revealed that deep-water sea urchins exhibit a parallel equatorial diversity dip to shallow-water conspecifics, suggesting that this reduced equatorial diversity arises not from thermal constraint but from synergistic interactions among multiple environmental drivers. Moreover, our GAM results demonstrate a temperature limitation in shallow-water sea urchins, manifested as declining species diversity above a temperature of 24 °C (Fig. S7). This thermal constraint persisted only in the

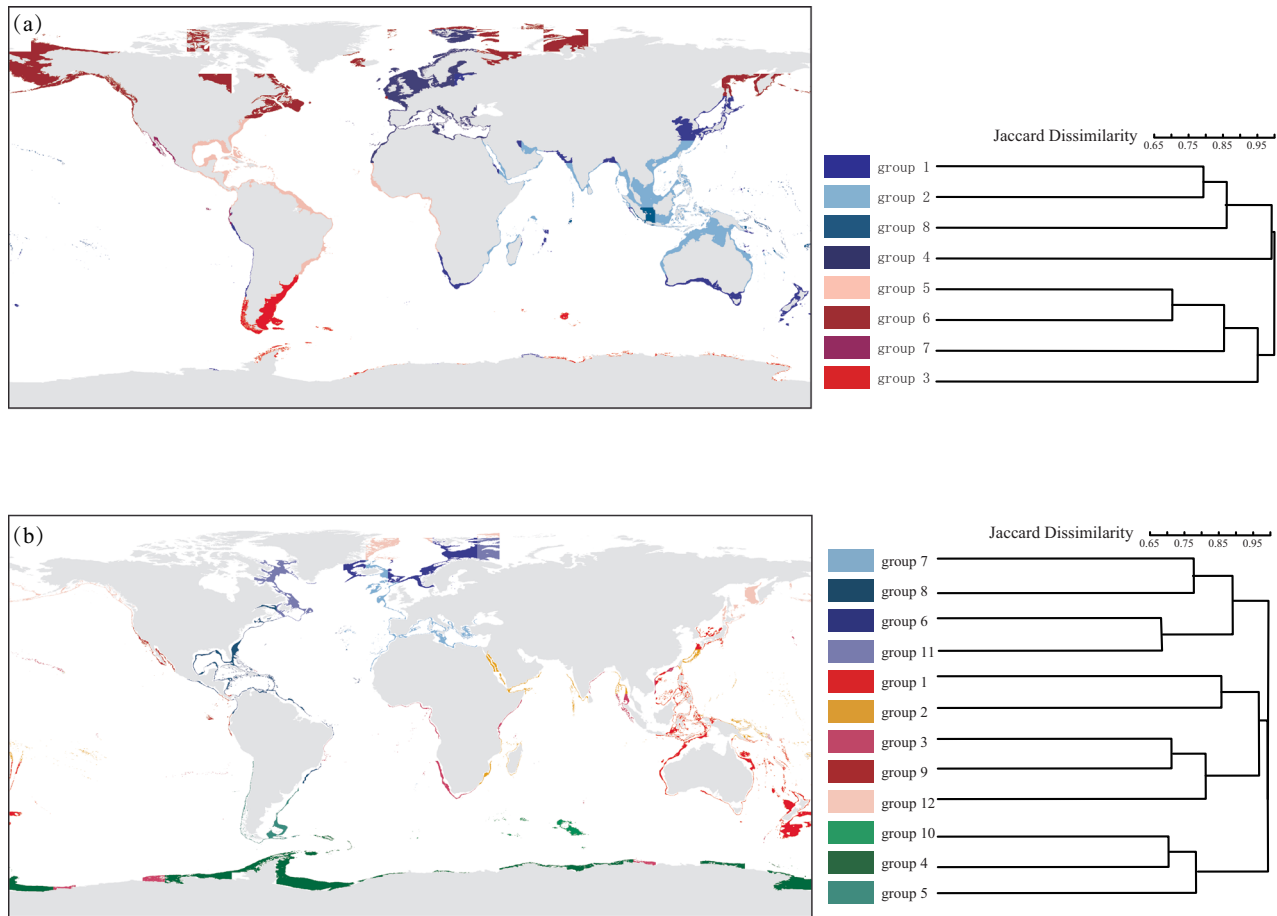


Fig. 4 | Global regionalization of sea urchins. a Fauna of shallow-water echinoids; the series of blue areas represent the Eurasian region, and the series of red areas represent the American regions (left). The zoogeographic clustering dendrogram for shallow-water echinoids, constructed using Jaccard dissimilarity. **b** Fauna of deep-

water echinoids; the series of blue areas represent the North Atlantic, the series of green areas represent the Arctic, and the series of red areas represent the Indo-Pacific (left). The zoogeographic clustering dendrogram for deep-water echinoids, constructed using Jaccard dissimilarity.

deep-water North Atlantic at approximately 15 °C, and was superseded by salinity as the dominant correlate in the North Pacific and Arctic Oceans. Such divergent diversity-environment relationships suggest potential differences in the way in which shallow- and deep-water species might respond to environmental change. For instance, the linear negative correlation between diversity and depth in deep waters impedes the vertical displacement of diversity hotspots to greater depths, making their persistence even more challenging under climate change.

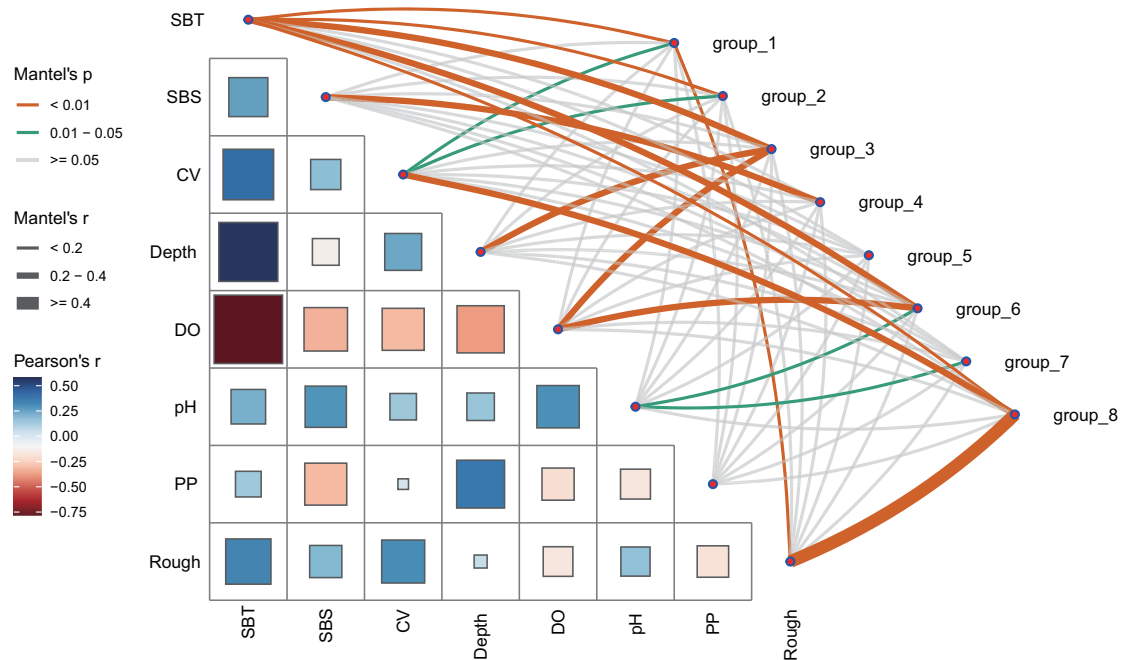
Our analyses revealed that the high diversity of shallow-water sea urchins is not uniformly distributed across subtropical regions, but is instead primarily concentrated in areas with abundant coral reefs (e.g., the Great Barrier Reef and Florida), a pattern consistently observed across both hemispheres. This can be attributed to the role of coral reefs in supporting high biodiversity. However, this dependence also renders these diversity hotspots particularly vulnerable to destruction under global warming due to coral degradation³⁹. Current marine protected areas (MPAs) have therefore been predominantly established in such well-recognized, high-biodiversity coral reef regions. However, our findings advocate for a proactive conservation strategy that also incorporates areas of high potential biodiversity. These candidate regions, frequently less impacted by anthropogenic activities, may reduce future costs associated with ecological restoration⁴⁰. This is empirically supported in the South China Sea, where sampling data has corroborated model-predicted high-diversity regions with newly documented sea urchin species exceeding 30 taxa. Despite these additions, sampling completeness in this region remains relatively low, implying substantial undiscovered diversity. We therefore recommend that MPA planning should incorporate potential species diversity estimates, rather

than relying solely on documented richness, to enhance long-term conservation efficacy.

Depth-dependent shifts in biogeographic realm affiliation

Our biogeographic framework for shallow-water sea urchin aligns with the coastal benthic bioregions proposed by Kocsis et al.⁴¹. Crucially, we established a novel 12-realm bioregion partitioning for deep-water sea urchins, different from the regionalization proposed for deep-water brittle stars¹³. Furthermore, our biogeographic analyses revealed a pronounced depth-dependent regional affiliation of sea urchin assemblages in the North Atlantic. Shallow-water assemblages cluster within the Indo-Pacific super realm, whereas deep-water assemblages are affiliated with the American super realm. This divergence, coupled with phylogeny-structured distribution patterns and fossil evidence, points to a complex evolutionary history as the key driver of this depth-dependent biogeographic structure. The echinoid phylogeny, although incomplete at the species level, is robust at higher taxonomic ranks (e.g., family or order level) to provide evolutionary inference. Following the morphological and molecular phylogenetic frameworks of Kroh⁴² and Nicolas²⁴, all deep-water specific families belonging to Atelostomata are placed on the relatively young clade of Echinoidea, while shallow-water specific families that are mainly distributed in the western Pacific, such as Psychocidaridae and Glyptocidaridae, consistently occur near the relatively basal positions of the echinoid tree. This pattern contrasts with ophiuroids, in which tropical shallow waters are considered centers of origination^{13,43}. Instead, our results in combination with previous findings^{44,45} concur in suggesting temperate shallow waters of the northwestern Pacific, particularly the continental shelves of China and

(a)



(b)

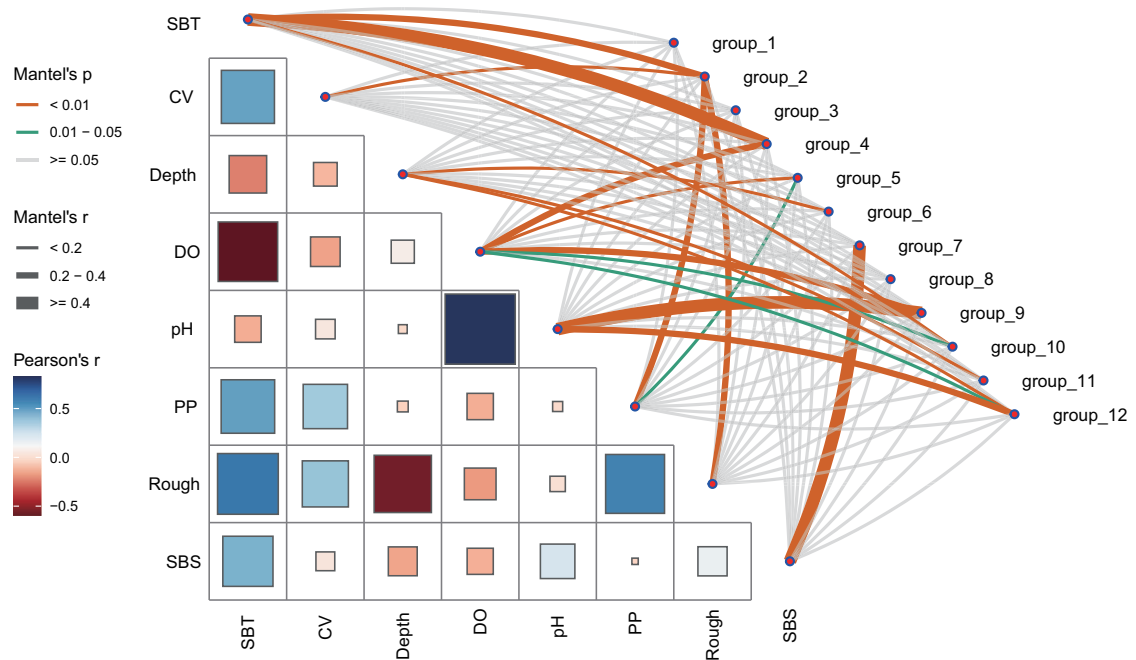


Fig. 5 | Environmental factors driving the division of biota. a Shallow-water assemblages **b** deep-water assemblages. The abbreviations are listed as follows: SBT sea bottom temperature, CV current velocity, SBS sea bottom salinity, DO dissolved oxygen, PP primary productivity, rough, terrain ruggedness index, the higher index indicates the seabed is steeper. The color of the rectangles represents the correlation

between environmental factors, the color of the connecting lines signifies the reliability of the Mantel test, and the thickness of the lines indicates the magnitude of the association between environmental factors and biotic zoning. Thicker lines denote a stronger correlation.

Japan, as an important origin for echinoid diversification, hosting several shallow-water ancestral families (Fig. S3a).

A pivotal evolutionary transition underlying deep-sea diversification in echinoids occurred within Spatangoida (heart urchins), the most species-rich order (268/1015) of sea urchins. This lineage is characterized by specialized spines and the complete transformation of the mouthpart from Aristotle's lantern to labrum, the major trait innovations that enabled a shift to an infaunal lifestyle⁴⁶. This ecological transition facilitated the exploitation of a broad range of sedimentary habitats and might have generated substantial ecological opportunity, particularly following the Late Cretaceous⁴⁷. Notably, the most basal spatangoid family, Aeropsidae, occurs exclusively in deep waters and is concentrated in the North Atlantic, whereas younger families exhibit broader bathymetric ranges spanning both deep and shallow environments (Fig. S3b). This pattern is consistent with an evolutionary scenario in which an ancestral shallow-water lineage invaded deep-water habitats across different ocean basins, underwent ecological specialization and radiation, and subsequently reinvaded shallow waters after successful niche establishment.

The asymmetric distribution of shallow- and deep-water families also reflects contrasting responses to major extinction events. Multiple echinoid lineages likely originated and diversified in shallow-water environments⁴², before expanding into the deep sea during the Late Cretaceous and the Middle Miocene⁴⁶. These expansion events coincide with periods of pronounced environmental instability in shallow waters, particularly in temperate regions, during which many lineages experienced severe declines, leaving only a limited number of surviving members. In contrast, the deep sea, with its stable environment, provides a shelter for a greater number of species⁴³. This may explain why the deep-water sea urchin assemblages, despite being sampled at only 16% of that in shallow waters, contain a greater number of families (Fig. S8). In such scenarios, surviving shallow-water echinoid lineages in the northwestern Pacific dispersed into the North Atlantic via the Tethys Ocean, resulting in shallow-water fauna in the North Atlantic that retains strong Indo-Pacific affinities. Following the closure of the Tethys Seaway, deep-sea lineages, particularly heart urchins, continued to diversify within the Atlantic, subsequently expanding into the South Atlantic and later dispersing into the Pacific via the Panama Seaway⁴⁸. Together, these processes provide an evolutionary framework for understanding why shallow and deep waters of the North Atlantic belong to different biogeographic realms. Our findings also highlight how trait innovation, extinction dynamics, and plate tectonics have jointly shaped a depth-dependent biogeographic structure in sea urchins, underscoring the importance of evolutionary history in structuring modern marine biodiversity.

Depth-dependent shifts in the spatial organization of biogeographic structure

We demonstrate that deep-water sea urchins, in contrast to their shallow-water counterparts, exhibit a more fragmented biogeographic structure characterized by a larger number of biogeographical realms. Furthermore, these deep-water realms span wider latitudinal ranges but are longitudinally narrower. We attribute the disparities between deep- and shallow-water assemblages to a combination of environmental factors, complex bottom topography and inherent traits of echinoids. Previous deep-sea biodiversity studies suggest that temperature significantly influences biodiversity only at high and low extremes, with minor impact within intermediate ranges¹⁷. Our findings corroborate this, identifying temperature as a primary driver for shallow-water realm formation, with significant influence only on equatorial and polar realms in deep waters (Fig. 5). The trans-equatorial biogeographic province identified in Indo-Pacific deep waters, which extends into high-latitude temperate zones of both hemispheres, likely originates from persistent thermal stability. This environmental consistency facilitates species dispersal by reducing physiological adaptation barriers.

The greater biogeographic fragmentation among deep-water sea urchins is also linked to species reproductive behaviors, larval development traits, and bottom topographic complexity. Sea urchins exhibit three

reproductive strategies with descending dispersal potential: planktotrophy, lecithotrophy, and brooding⁴⁹. The brooding reproductive mode is more prevalent among deep-water sea urchin species⁵⁰. This mode, coupled with the complex topography of the seafloor, may intensify the dispersal limit of larvae with low dispersal capabilities, making exchange between deep-water sea urchins more challenging and further enhancing species diversity differences among deep-water assemblages. Furthermore, some deep-water species exhibit prolonged or halted larval development as depth decreases⁵¹, preventing their rapid, long-distance dispersal via the surface ocean currents.

In conclusion, our global analysis of sea urchin diversity demonstrates that shallow- and deep-water assemblages of sea urchins are structured by pronounced depth-dependent shifts. Although both assemblages exhibit a similar bimodal LDG with subtropical peaks, the environmental mechanisms shaping this conserved pattern shift from temperature-dominated controls in shallow waters to multi-factor and depth-constrained drivers in deep waters. Beyond diversity-environment relationships, a depth-dependent biogeographic affiliation shift is evident in the North Atlantic, where shallow-water assemblages cluster with the Indo-Pacific realm, whereas its deep-water assemblages align with the Americas. This disparity likely reflects divergent evolutionary pathways mediated by trait innovation, extinction dynamics, and tectonic events. In addition, the spatial organization of biogeographic structure shifts with depth, as deep-water assemblages exhibit greater biogeographic fragmentation, likely driven by the combined effects of environmental factors, complex seafloor topography, and intrinsic life-history constraints on dispersal. Collectively, these depth-mediated shifts underscore the deep sea as an important component of global marine biodiversity, where depth-dependent ecological and evolutionary processes shape diversity pattern and biogeographic structure, with important implications for biodiversity assessment, projection and conservation in a changing ocean. Although biodiversity patterns below the thermocline remain constrained by uneven sampling, particularly at greater depths, our results provide a biologically grounded framework for understanding depth-dependent assemblage structure and for generating testable hypotheses on deep-sea biodiversification with increasing sampling resolution.

Materials and methods

Data source and filtration

Global occurrence records of sea urchins were compiled from three sources: benthic biological surveys between 2022 and 2024 organized by the Institute of Oceanology, Chinese Academy of Sciences; specimens deposited in the Marine Biological Museum of Chinese Academy of Sciences (Qingdao, China); and online databases including the Ocean Biodiversity Information System (OBIS, 2024) and the Global Biodiversity Information Facility (GBIF, 2024). The datasets were merged and cleaned in R version 4.1.2 (R Core Team, 2021). Following the World Register of Marine Species (WoRMS, <https://www.marinespecies.org/>) and advice from taxonomists, all records containing misspellings or synonyms were replaced with their corresponding scientific names.

We removed duplicates, records without coordinates, and those not identified down to the species level. All records that were found to be fossils or located on land were also removed. Then, records with equal scientific names and geographical coordinates were only retained once. Considering all sea urchins are zoobenthos and most of the occurrence records lack depth information, we assigned a sampling depth to each record by extracting bathymetric values from Bio-ORACLE v3.0 based on their geographic coordinates. Finally, the data were mapped with ArcGIS v.10.8. After filtration, the resulting dataset contained 248,486 occurrence records of 895 sea urchin species, belonging to 235 genera, 60 families, 15 orders. Compared with the global species list compiled from WoRMS, our dataset covers approximately 88% of all described sea urchin species thus far. A list of datasets from biological surveys and the museum can be found in the Supplementary Data file.

We evaluated the completeness of our database across several depth bands (shallow: 0–200 m, deep: 200–2000 m, trench: 2000–8000 m) using the R package “iNEXT4”⁵² with a raster of 1° grid cell. Considering that our study aims to prove the difference in bathymetric bands in species richness and regionalization, completeness profiles at orders $q = 0, 1$, and 2 were calculated to inspect the data reliability. An uncertainty map based on SC was also drawn for each band to ensure the areas lacking for sampling.

Alpha and gamma diversity analysis

The dataset was categorized into distinct groups according to sampling depth (0–200 m for shallow waters, 200–2000 m for deep waters) and species lifestyle (epifaunal and infaunal). There were insufficient records in deeper zones for subsequent analyses. The LDG of sea urchins was assessed based on two components of alpha diversity: the species richness (number of species) and the Shannon index. To analyze the number of species, the study area was divided into 1° latitude-longitude grid cells, and the species count was recorded for each cell. We measured taxonomic gamma-diversity as the total number of each 5° latitudinal band. The relationship between species richness and latitude was evaluated by calculating the mean species richness (with standard deviation envelopes) across latitudes and applying second-order polynomial curve fitting to each dataset. Meanwhile, to account for spatial variation in sampling effort, we quantified sample completeness for each grid cell using SC⁵³. Additionally, species diversity was weighted according to SC for each grid cell, and LDG curves were generated using the weighted diversity estimates.

To assess alpha diversity, an occurrence-absence matrix was constructed using the collected and cleaned species distribution data. Each 1° × 1° latitude-longitude grid cell was assigned a unique identifier, and the matrix was generated by linking these identifiers to the scientific names of the species. For each identifier, species counts were performed, with the corresponding matrix position assigned a value of 1 if the species was present in the area and 0 if absent. Using this matrix, alpha diversity was calculated for grid cells across different depths globally. Generalized additive models (GAM) were used to assess the relationship between alpha diversity and environmental variables in the same 1° × 1° latitude-longitude grid cell. GAM is flexible regarding the assumptions concerning the underlying statistical distribution of the data. Since alpha diversity (quantified using the Shannon index) exhibited characteristics suitable for Tweedie distribution modeling, a GAM employing a Tweedie family with a log link function was utilized. The model sets were as follows: minimized generalized cross-validation scores, maximized deviance explained and maximized adjusted r^2 . Akaike information criterion and Bayesian information criterion were used to assess distributional and smoothing assumptions. To better assess the influence of environmental factors on biodiversity, GAM was also conducted in ten marine regions separately, using only four key environmental variables: temperature, salinity, depth, and dissolved oxygen. The relationships of alpha diversity to each environmental variable were plotted. All calculations were conducted in R v.4.1.2 using the “vegan” and “mgcv”⁵⁴ packages. The results at different depths were visualized in ArcGIS v.10.8 using global bathymetric environmental data obtained from Bio-ORACLE v.3.0 (<https://bio-oracle.org/>)⁵⁵.

Potential species diversity analysis

Through analysis of the potential species diversity, we assessed the effect of multiple environmental factors on the LDG in shallow- and deep-water sea urchins, respectively. The potential species diversity was indicated by the probability of species distribution calculated by SDMs, using the maximum entropy model MaxEnt v 3.3.1⁵⁶ and ESMs (ensembles of small models) via the R package “biomod2”⁵⁷. The model produced by MaxEnt for a given species is a continuous sequence of values between 0 and 1 the higher value indicates the higher suitability. The resultant distribution probability generated by SDMs was mapped and statistically analyzed via ArcGIS v.10.8.

To reduce the impact of sampling bias on model fitting, we keep only one distribution record per 0.05° grid cell based on the resolution of environmental predictors. We retrieved 18 environmental predictors at a

spatial resolution of 3 arcmin from Bio-ORACLE v3.0. We checked collinearity between environmental predictors using pairwise Pearson’s correlation coefficients (r) and retained only one of the highly correlated predictors with a collinearity threshold of $|r| > 0.7$. Eight predictors were retained for subsequent analysis: depth, annual mean sea bottom salinity (SBS), annual mean sea bottom temperature (SBT), dissolved molecular oxygen (DO), primary productivity (PP), pH, terrain ruggedness index (rough), sea water velocity (CV), based on the biological importance⁵⁸ and their contributions in the pre-modeling for our SDM analysis.

In addition to species presence data, we randomly generated 10,000 background points within the study area as pseudo-absences. For species with more than 25 records, we considered them as “common species” and used software MaxEnt v. 3.3.1. For species with less than 25 records, we considered them as “rare species” and build ESMs by R package “biomod2” with models of GLM, RF, GBM and MaxEnt⁵⁹. The model accuracy was assessed by the area under the curve (AUC) of the receiver operating characteristic curve (ROC)⁶⁰. The AUC value ranges from 0 to 1, and a higher AUC indicates better model performance.

Delineating biogeographical regions and the Mantel test

We built an occurrence/absence matrix with geographic unit (GU) (10° × 10° latitude and longitude grid cell per unit with a unique identifier) and species⁵⁸. Jaccard dissimilarity index was used to evaluate the dissimilarity between species assemblages GUs⁵⁹. GUs with the highest similarity were first grouped together, and then the most similar groups were grouped into cluster until all GUs were grouped into a single cluster with the “hclust” function in the R package “stats” in R v.4.1.2. The delineation of realms was jointly determined by the average silhouette width and ecological realms proposed in previous research⁶⁰. We ensured that each realm possessed a degree of spatial contiguity. Subsequently, we reconstructed an occurrence/absence matrix based on the delineated realms and partitioned them into super-realms using a Jaccard dissimilarity index threshold of 0.99 (indicating complete dissimilarity). To validate the influence of environmental factors on biogeographical realm delineation, we first built a dissimilarity matrix containing pairwise Jaccard indices between GUs, and then grouped the matrix by realms. We further performed the Mantel test to statistically evaluate the correlation between environmental variables and GU dissimilarity patterns using the R package “LinkET” (<https://github.com/Hy4m/linkET>). Environmental factors for each GU were determined by the average values of all the pixels of the environmental predictors within that GU. GUs containing no data for specific environmental variables were omitted from subsequent analyses.

Data availability

The datasets and R code that support the findings of this study are openly available in Figshare at <https://doi.org/10.6084/m9.figshare.29827574> and Supplementary material.

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Author contributions

Z.S., J.C., and L.H. conceived and designed the research. J.C., L.H. carried out the modeling experiments, performed the analyses, and wrote the first draft of the manuscript. N.X. identified the collected specimens. Z.S., J.C., L.H., and M.H. discussed and interpreted the results and contributed to revising the manuscript. All authors approved the final version of the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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