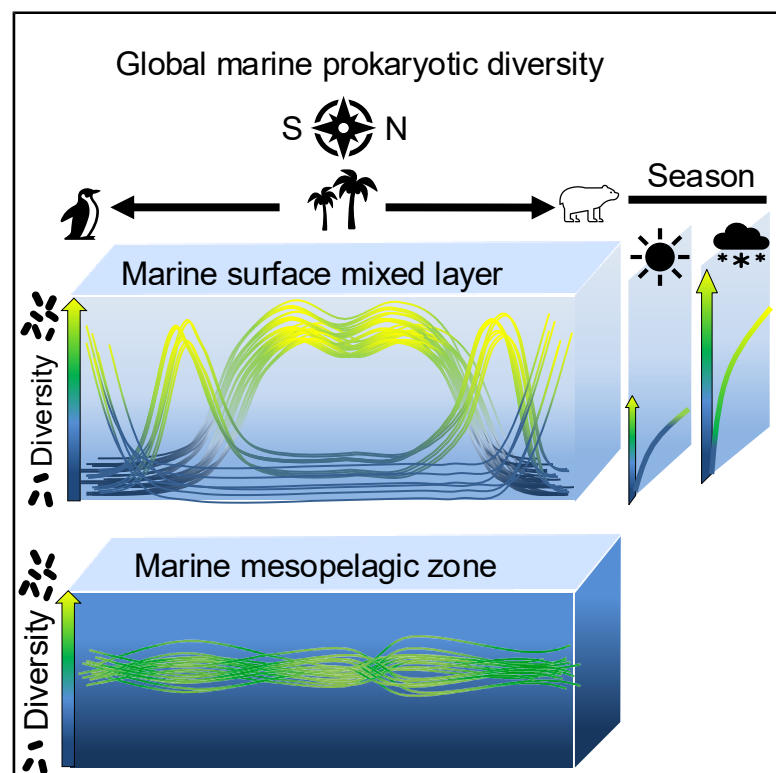


Cell Host & Microbe

Variations in the latitudinal diversity gradients of the ocean microbiome

Graphical abstract



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In brief

Eriksson et al. conduct a global marine microbiome diversity analysis and demonstrate how the surface ocean latitudinal diversity gradient is disproportionately shaped by a few species-rich taxa. Masked by dominant taxa, a variety of diversity patterns are uncovered, frequently reflecting taxon-specific metabolic traits and environmental adaptations.

Highlights

- The marine microbial latitudinal diversity gradient (LDG) is depth dependent
- Seasonality modulates prokaryotic diversity in the surface ocean
- The surface ocean LDG is disproportionately shaped by a few species-rich taxa
- Taxonomic resolution uncovers a masked variety of LDG patterns



Article

Variations in the latitudinal diversity gradients of the ocean microbiome

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SUMMARY

Latitudinal diversity gradients (LDGs), which typically decline from the equator to the poles, are a pervasive macroecological pattern. However, their generality and drivers in the ocean microbiome remain widely unresolved. We integrated global-scale metagenomic data with habitat modeling to study marine microbial LDGs across seasons and depths. Surface mixed-layer microbiomes exhibit diversity peaks at (sub)tropical latitudes and a poleward decline, whereas mesopelagic communities (200–1,000 m) show no latitudinal diversity structuring. Taxonomic resolution reveals that the mixed-layer LDG is underpinned by Alphaproteobacteria and Cyanobacteria, while other taxa exhibit distinct or contrasting LDGs. Diversity structuring also varies by seasons and regions and is governed by temperature and nutrient availability. Together, these findings highlight that, within the ocean microbiome, LDGs are not universal but reflect lineage-specific ecological strategies and responses to environmental gradients. Our study provides fundamental insights into the structuring of ocean microbiome diversity and lays the foundation for predicting responses to environmental change.

INTRODUCTION

Latitudinal diversity gradients (LDGs) have been recognized since the early 19th century, when Alexander von Humboldt documented a decline in diversity from the equator to the poles.¹ Since then, LDGs have been observed across a wide range of terrestrial and aquatic ecosystems and organismal groups,^{2–5} reflecting the combined influence of ecological and evolutionary processes across environmental gradients. Understanding how and why diversity is structured along latitudinal and environmental gradients is thus critical, as it provides insights into the mechanisms shaping diversity and informs predictions of how ecosystems may respond to global change.

In marine planktonic communities, LDGs have been observed for both eukaryotes and prokaryotes, but their generality and underlying drivers remain unresolved. Early molecular surveys of marine bacteria, based on 16S rRNA gene fingerprinting and clone library sequencing approaches, reported a decline in richness (the number of unique taxa observed in a sample) toward

higher latitudes, consistent with the traditional LDG concept.^{6,7} However, the expansion of global ocean sampling, together with advances in sequencing technologies, has challenged these findings and revealed a more complex and inconsistent picture. For instance, a study using high-throughput 16S rRNA gene amplicon sequencing in the South Pacific Ocean reported a bimodal LDG for prokaryotes, with peaks at mid-latitudes.⁸ Mid-latitudinal peaks were further supported by metagenomic sequencing of globally distributed samples,⁹ while proposed alternatives include a diversity plateau within tropical and subtropical regions,¹⁰ and even an absence of LDGs altogether.¹¹ Together, these contrasting observations highlight the uncertainty surrounding LDG patterns in marine prokaryotes, which likely reflects both methodological differences and variation in the spatial and temporal coverage of datasets.

Statistical models represent a powerful framework for overcoming some of the limitations of inferring general patterns based on observational datasets, which are often sparse and unevenly distributed across spatial and temporal scales.¹² Such



models provide a means to explore large-scale distributions of microbial plankton species. They assume that species are not dispersal limited in the open ocean, a trait consistent with the generally wide geographic ranges of prokaryotes,¹³ and that their global distributions are primarily controlled by rapid responses to abiotic environmental factors.¹⁴ Ladau et al.¹⁵ applied such an approach to ribosomal DNA to investigate the seasonal variation of near-surface ocean LDGs. They found that during winter months, global prokaryotic richness peaks at high latitudes, which would represent an inversion of the classical LDG pattern. Although this study provided strong indications of seasonal fluctuation in diversity, it was constrained by a relatively small dataset and methodological heterogeneity.

With the growing availability of databases containing uniformly processed metagenomic data (e.g., Ocean Microbiomics Database [OMDB]: <https://omdb.microbiomics.io>; searchable, planetary-scale microbiome resource [SPIRE]¹⁶), we can now strive to assemble datasets with extensive spatiotemporal coverage to yield global models with higher resolution. Metagenomic sequencing provides a broad genomic context, enabling consistent species-resolution taxonomic profiling from multiple marker genes (e.g., metagenomic operational taxonomic units [mOTUs]¹⁷), which is independent of primer-based amplification. This makes it particularly well suited for meta-analyses integrating data from multiple sources, as it minimizes the technical variability that hampers the integration of amplicon-based datasets generated with different primers, sequencing regions, or clustering thresholds.

Here, we combined a systematically processed metagenomic dataset with extensive spatial and temporal coverage with habitat models (comprehensive ensemble pipeline for habitat modeling across large-scale ocean pelagic observation datasets [CEPHALOPOD]¹²) to study LDGs of marine prokaryotes across depths, seasons, and taxonomic ranks. Our analyses revealed pronounced LDGs for both Bacteria and Archaea in the surface mixed layer (SML), which were absent in the mesopelagic zone (MZ). Furthermore, we observed a spatial decoupling of bacterial and archaeal richness in the SML of (sub)tropical regions, seasonal modulation of diversity without inversion of the general LDG pattern, and variation in LDGs across taxonomic ranks. By linking global diversity patterns to environmental drivers, we found that marine prokaryotic lineages occupy structured ecological niches. Furthermore, we developed a framework for characterizing diversity hotspots for different taxonomic groups.

RESULTS

Global dataset and study design

To characterize global patterns in oceanic prokaryotic diversity, we assembled a metagenomic dataset based on the OMDB: <https://omdb.microbiomics.io>. For our analyses, we considered samples obtained within the SML, the surface layer of the surface ocean that is well mixed, and samples from the MZ (200–1,000 m depth; [STAR Methods](#)). In total, 2,342 samples from the SML and 281 MZ samples matched our selection criteria ([data and code availability](#)). Spatially, the dataset provides comprehensive coverage across all major ocean basins ([Figure 1](#)). The majority of samples from the SML were collected from the Pacific Ocean (~49%), followed by the Atlantic Ocean

(~28%) and Indian Ocean (19%), with additional coverage extending into polar regions (~4%). Temporally, the dataset represents sampling efforts spanning all seasons and a latitudinal range from –65° to 85°.

From these data, we generated taxonomic profiles, resolving species-level mOTUs. To account for unequal sampling efforts, we standardized the taxonomic profiles to a fixed number of species observations. Using a rarefaction cutoff of 5,000 species observations, we retained 1,595 samples from the SML and 238 MZ samples. From the rarefied taxonomic profiles, we computed the species richness (number of unique species observed per sample), as well as the Shannon¹⁸ (which accounts for both richness and evenness) and Chao1¹⁹ (which estimates unobserved species) diversity indices. These indices were computed across all prokaryotes and at taxonomic ranks (from domain to genus) ([Figure 1](#); [STAR Methods](#)). We subsequently used the resulting species richness after rarefaction to 5,000 species observations as our primary metric for diversity. We first analyzed the diversity pattern emerging from the samples alone and then expanded our scope using a habitat-modeling approach ([STAR Methods](#)).

To assess the influence of uneven sampling across ocean basins on the modeling of prokaryotic richness in the SML, we conducted a basin-stratified subsampling ([STAR Methods](#)). Sampling bias mainly increased model uncertainty in estimates of prokaryotic richness in sparsely sampled polar regions, while global diversity patterns remained robust ([Figure S1A](#)). Model performance was most robust for open-ocean environments and lower in dynamic coastal regions ([Figure S1B](#)). This study therefore focused on the prokaryotic diversity of the open ocean.

LDGs are depth dependent

As a first step in assessing the global distribution of marine prokaryotic diversity, we used within-sample species richness to examine LDGs of Bacteria and Archaea in the SML and MZ.

In the SML, species richness followed a clear LDG, with an ~3-fold change (FC) increase in richness for both Bacteria and Archaea in (sub)tropical regions (0°–40° absolute latitude) compared with high latitudes (Bacteria: FC = 3.1; Archaea: FC = 2.8; both $p < 0.001$, Wilcoxon test; [Figure 2](#)). Chao1-estimated richness was likewise elevated at (sub)tropical latitudes compared with high latitudes (Bacteria: FC = 2.9, $p < 0.001$; Archaea: FC = 2.9, $p < 0.001$), and the Shannon diversity index followed the same trend, albeit with smaller FCs (Bacteria: FC = 1.4, $p < 0.001$; Archaea: FC = 1.6, $p < 0.001$). Prokaryotic richness in the SML was highly correlated with bacterial richness (Pearson's $r = 0.998$, $p < 0.001$; [Figure 2A](#)), consistent with the dominance of Bacteria in overall prokaryotic richness (97% of total richness; [Figure S2A](#)). Although archaeal richness showed FCs between low and high latitudes that were similar to those of Bacteria, it was only moderately correlated with prokaryotic richness ($r = 0.41$, $p < 0.001$; [Figure 2B](#)), suggesting domain-specific biogeographic structuring.

In contrast to the SML, species richness did not differ significantly between low and high latitudes in the MZ for either Bacteria or Archaea (Bacteria: FC = 1.0^{ns}; Archaea: FC = 1.0^{ns}; ns: $p > 0.05$, Wilcoxon test; [Figure 2](#)). This absence of a latitudinal gradient was consistent across Chao1 and Shannon indices (FC = 0.9–1.0^{ns} for both domains; [Figure 2](#)). To account for differences in sampling

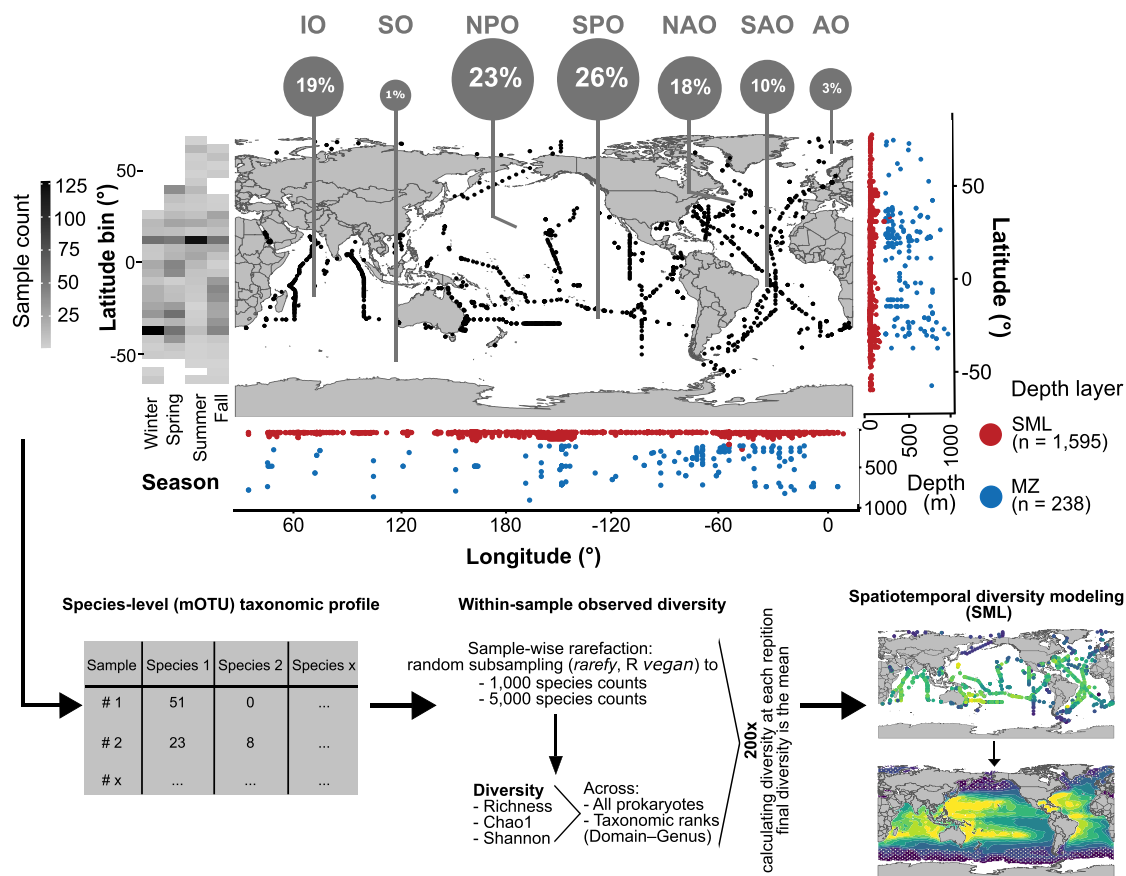


Figure 1. Global dataset of prokaryotic diversity and study design

Global map showing the distribution of metagenomic samples from the surface mixed layer (SML) and the mesopelagic zone (MZ; 200–1,000 m). Sample locations and percentage contributions are indicated for the Indian Ocean (IO), Southern Ocean (SO), North Pacific Ocean (NPO), South Pacific Ocean (SPO), North Atlantic Ocean (NAO), South Atlantic Ocean (SAO), and Arctic Ocean (AO). Marginal scatterplots illustrate sample depth distribution across the SML ($n = 1,595$) and MZ ($n = 238$). Sample counts are also shown across 5° latitude bins and seasons (left). Seasons were defined as follows: Northern Hemisphere: winter, December–February; spring, March–May; summer, June–August; autumn, September–November; Southern Hemisphere: reversed. Species-resolved taxonomic profiles were generated and used to calculate within-sample diversity (observed richness, Chao1, and Shannon index) across all prokaryotic species, as well as by taxonomic rank (from domain to genus). For each sample, 200 independent rarefactions were performed, and diversity metrics were calculated as the mean across repetitions. Within-sample diversity metrics were then extrapolated across the SML using habitat modeling.

effort, we randomly downsampled SML samples to match the number of MZ samples. The lower richness of Bacteria and Archaea at high versus low latitudes in the SML remained robust even after accounting for sampling differences (Figure S3). Thus, our results suggest that MZ diversity does not conform to an LDG characterized by declining richness toward the poles.

The SML and MZ exhibited distinct microbial diversity structures. For Archaea, species richness was higher in the MZ (46 ± 18 , mean $\pm$ SD) than in the SML (29 ± 19) (Figures S2A and S2B). Archaeal richness in the SML was largely dominated by members of the class Poseidoniiia (27 ± 17), whereas MZ richness was more evenly distributed across classes Nitrososphaeria (24 ± 10) and Poseidoniiia (19 ± 11). In contrast, bacterial species richness was higher in the SML (815 ± 250) than in the MZ (421 ± 155). In the SML, species richness was heavily skewed toward classes Alphaproteobacteria (444 ± 172 ; predominantly belonging to the genus *Pelagibacter*: 226 ± 102) and Cyanobacteriia (111 ± 69 ; predominantly belonging to the genus *Prochlor-*

ococcus_A: 101 ± 70). Together, these two classes accounted for 66% of the mean prokaryotic species richness in the SML (Alphaproteobacteria: 52% and Cyanobacteriia: 14%; Figure S4A).

Frequently used taxonomic definitions, such as 97% sequence-identity clustering of the 16S rRNA gene sequence, result in broader taxonomic granularities than species-level definitions.²⁰ To test the sensitivity of marine prokaryotic diversity structure to taxonomic granularity, we calculated genus richness in addition to species richness. Genus richness in the SML was less strongly dominated by Alphaproteobacteria and Cyanobacteriia, which contributed only 31% of the mean prokaryotic richness (Alphaproteobacteria: 29% and Cyanobacteriia: 2%; Figure S4B). In agreement with the dominance of *Pelagibacter* and *Prochlorococcus_A*, this confirmed that a limited number of genera contributed to the high species richness of Alphaproteobacteria and Cyanobacteriia in the SML. In contrast to species resolution, genus richness was higher in the MZ than in the SML (MZ: 229 ± 52 , SML: 179 ± 51 ; Figure S4B),

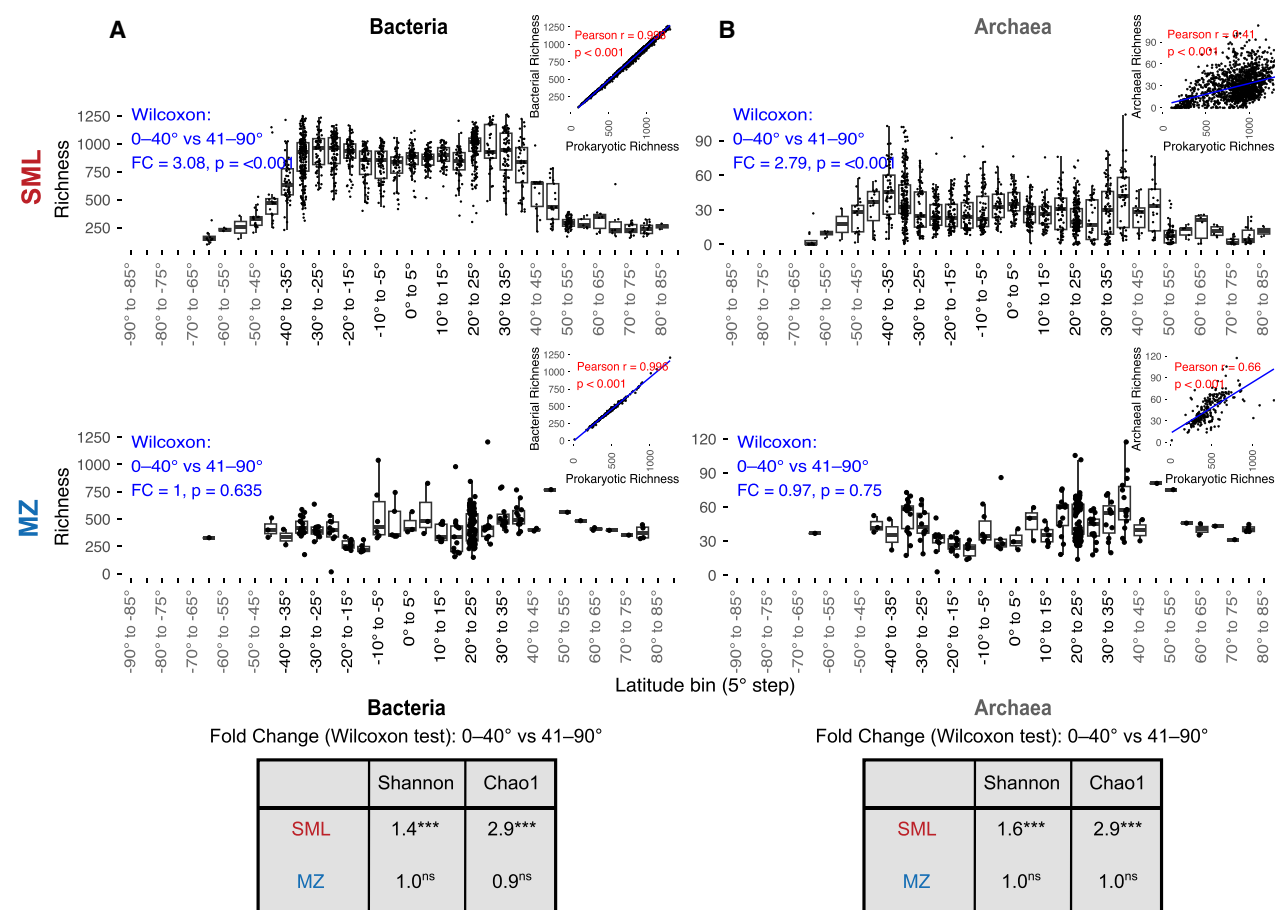


Figure 2. Latitudinal patterns of within-sample richness in Bacteria and Archaea across ocean depths

Observed within-sample richness for (A) Bacteria and (B) Archaea in the SML (top) and the MZ (bottom), shown across 5° latitude bins. Statistical comparisons (blue) indicate fold change (FC) and *p* values (Wilcoxon test) between (sub)tropical and high-latitude regions (0°–40° vs. 41°–90° absolute latitude). The top-right plots show correlations between prokaryotic richness and bacterial or archaeal richness. Tables summarize FCs between 0°–40° and 41°–90° absolute latitude for Shannon index and Chao1 diversity metrics in (A) Bacteria and (B) Archaea (Wilcoxon test; ns, *p* > 0.05 and ***, *p* < 0.001). See also Figures S2–S5.

consistent with previous reports utilizing taxonomic granularities broader than species units.^{9,21–23} Notably, genus richness also showed no significant difference in the MZ between low- and high-latitude regions (FC = 1.0^{ns}; Figure S4B). Although these results were not affected by incomplete taxonomic annotation (>99.99% of mean prokaryotic richness had GTDB annotations at least to the class rank; Figure S2), differences in baseline richness across depth layers may partly reflect the higher fraction of unassigned taxa in the MZ (median 28.3%–43.1%) compared with the SML (20.5%–27.3%; Figure S5A). Independent of taxonomic assignment, rarefaction analyses indicated that richness estimates were largely robust to sampling depth. Rarefaction curves rarefied to 5,000 species-resolved mOTUs approached saturation across ocean regimes, with median slope values ranging from 0.016 to 0.046 in the MZ and high-latitude SML, and slightly higher slopes in low- to mid-latitude SML samples (0.066–0.08; Figure S5B). Together, the comparison of species and genus richness underscores the importance of taxonomic granularity when interpreting microbial diversity patterns across ocean layers.

Spatial and temporal variations of ocean microbiome diversity in the SML

To extend our analyses and compare SML archaeal and bacterial LDGs across the global ocean and seasons, we applied a second, habitat-modeling-based approach. In this framework, observed diversity was extrapolated in space and time using an ensemble of models trained on environmental variables (Figure S6). These environmental variables are monthly averaged climatologies with a 1° by 1° spatial resolution, thus representing prevailing environmental conditions (STAR Methods). A comparison with *in situ* measurements from the Tara Ocean expedition²⁴ showed high agreement between *in situ* and gridded environmental data (Pearson's *r* > 0.7 for all variables except chlorophyll-*a*, *r* = 0.26; all *p* < 0.001; Figure S7). Global-scale modeled diversity patterns of Bacteria and Archaea were highly consistent across rarefaction cutoffs (Pearson's *r* ≥ 0.98, all *p* < 0.001; Figure S8), indicating that overall results were robust to this methodological choice.

At the domain level, the biogeography of bacterial and archaeal diversity was similar across diversity metrics

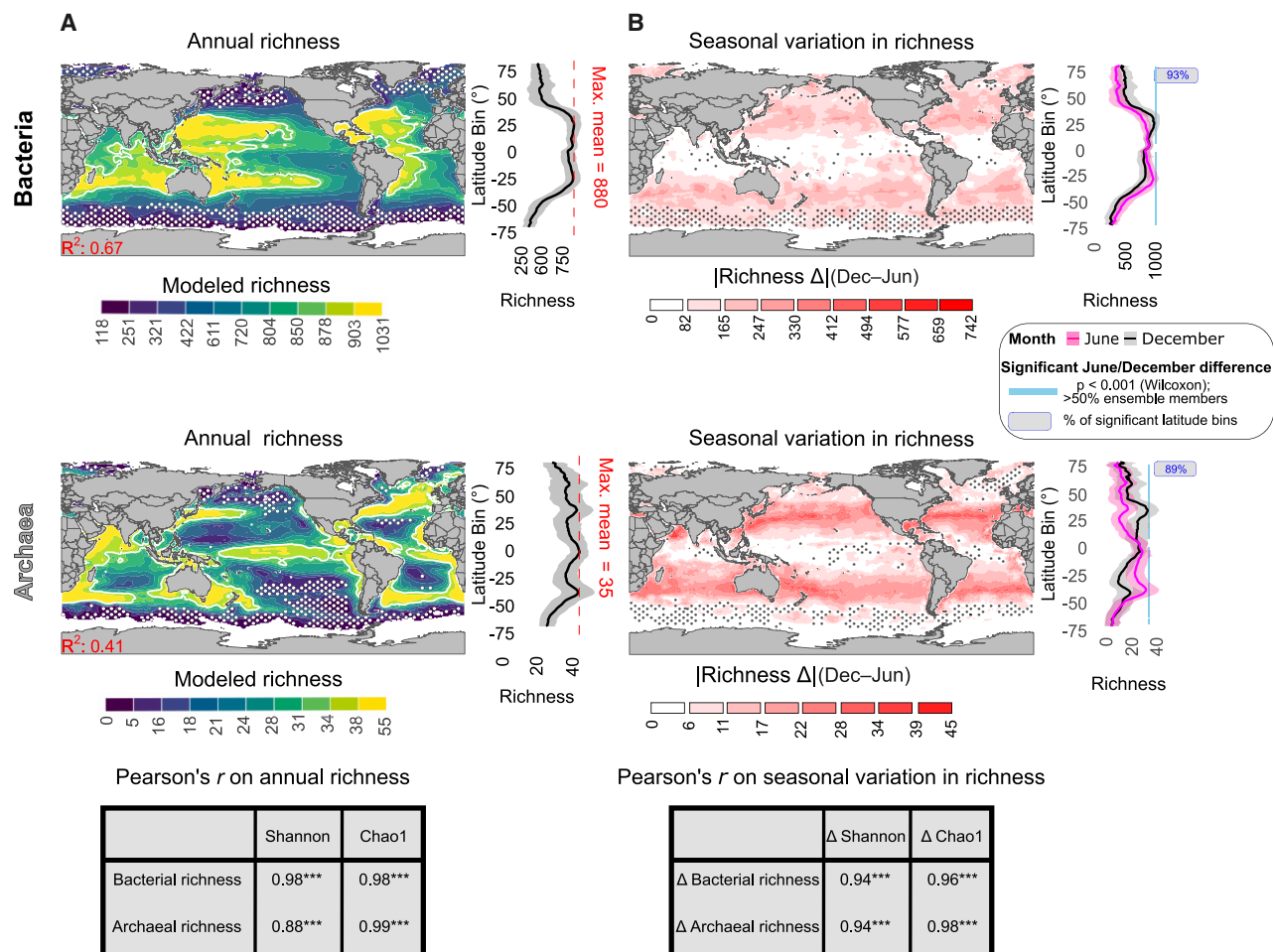


Figure 3. Modeled bacterial and archaeal richness patterns in the surface mixed layer

(A) Global maps display modeled annual richness patterns for Bacteria (top) and Archaea (bottom) in the SML. Areas of high uncertainty are marked by white stippling (coefficient of variation > 20% across model ensemble members). Model predictive power (R^2) is shown in red (lower left). White contours highlight diversity hotspots (regions above the 75th percentile of modeled richness). Latitudinal gradients are shown for the global ocean, with shading indicating model uncertainty ($\pm$ SD) across ensemble members and longitude and dashed red lines with annotation indicating the maximum mean diversity.

(B) Global maps are colored by the magnitude of seasonal variation in richness between December and June for Bacteria (top) and Archaea (bottom), computed as the absolute change in modeled species richness between December and June. Black stippling indicates areas where fewer than 75% of ensemble members agreed on the direction of richness change. Right: latitudinal gradients for June (pink) and December (black) with uncertainty ($\pm$ SD) as shading. Blue labels mark bins with significant seasonal differences (>50% of ensemble members, $p < 0.001$, Wilcoxon test); percentages indicate the fraction of significant bins.

See also Figures S6–S10 and Table S1.

(Bacteria: richness vs. Shannon, $r = 0.98$, and Chao1, $r = 0.98$; Archaea: richness vs. Shannon index, $r = 0.88$, and Chao1, $r = 0.99$; all $p < 0.001$; Figure 3). Across the global ocean, species richness patterns between the two domains showed a moderate correlation ($r = 0.56$, $p < 0.001$; Figure S9A). However, within (sub)tropical regions (0° – 40° absolute latitude), a decoupling of bacterial and archaeal richness was evident ($r = -0.14$, $p < 0.001$; Figure S9B). This low correspondence was consistent across other diversity metrics (Shannon index: $r = -0.04$, $p < 0.001$; Chao1: $r = 0.16$, $p < 0.001$). Together, these results indicate that (sub)tropical bacterial and archaeal communities follow distinct diversity–latitude relationships, suggesting divergent ecological drivers.

The decoupling in annual bacterial and archaeal richness in the SML was also evident in distinct hotspots of diversity,

defined as regions above the 75th percentile of modeled richness (Figure 3A). Bacterial hotspots were identified in oligotrophic gyres ($\sim 25^\circ$ absolute latitude and richness up to 1,031), whereas archaeal hotspots occurred in nutrient-rich upwelling zones (e.g., equatorial divergence, $\sim 40^\circ$ absolute latitude, and richness up to 55). Archaeal richness was markedly lower in oligotrophic regions (richness < 20). Our models showed that LDGs varied not only between but also within ocean basins, e.g., bacterial richness dipped around the equator in the eastern Pacific, whereas this dip was absent in the western Pacific (Figures S10A and S10B). This indicates that sampling transects in different regions and ocean basins can result in differing LDG patterns.

Our habitat-modeling approach revealed seasonal fluctuations in ocean microbiome richness (Figure 3B). For Bacteria,

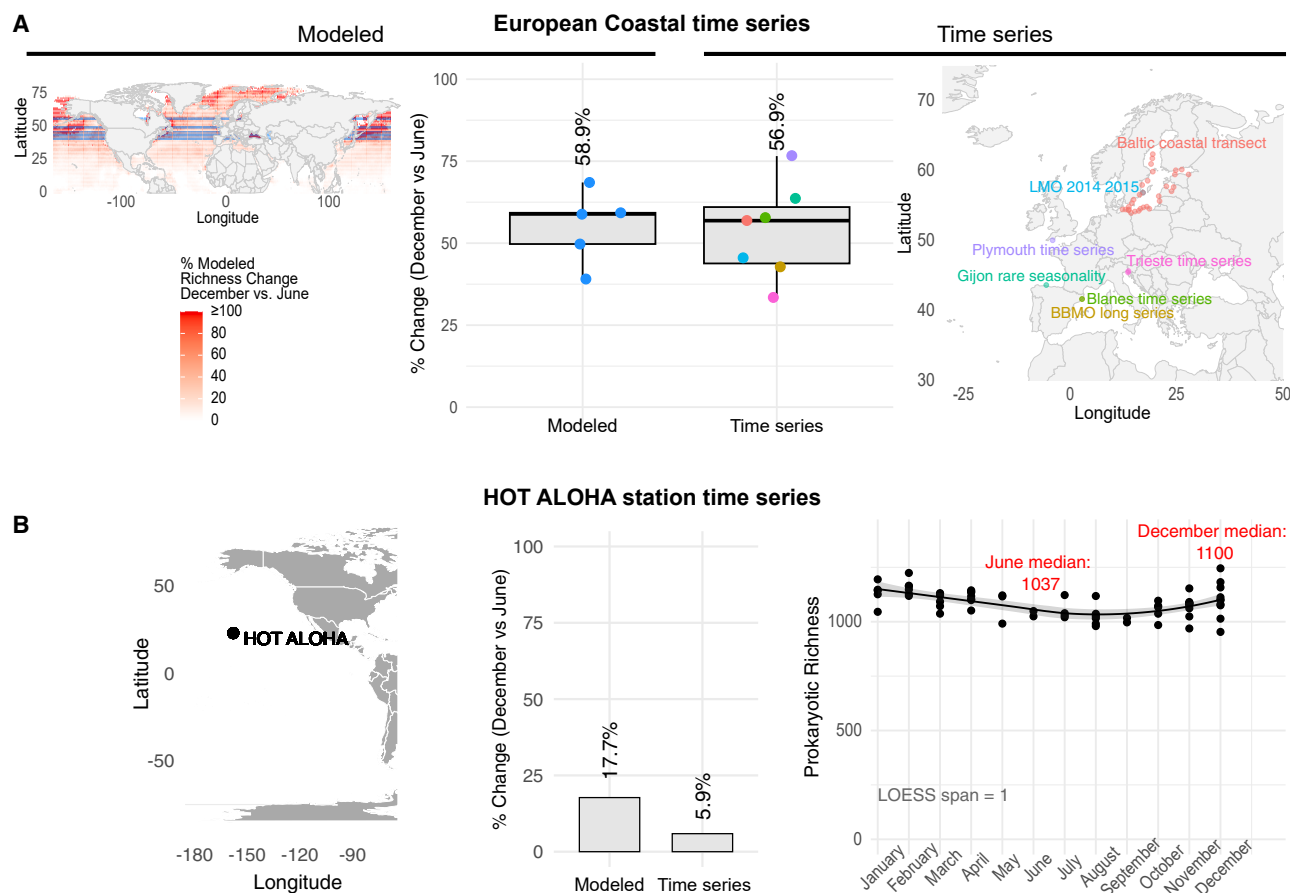


Figure 4. Modeled seasonal richness compared with time series observations

Comparison of the June-to-December change in prokaryotic richness between the model and stationary time series.

(A) European coastal time series are compared with corresponding modeled latitudes. Boxplots compare the symmetric percent difference in prokaryotic richness in December relative to June; text labels indicate the median. The left map shows the latitudes corresponding to the European time series studies, and the coloring indicates the symmetric percent difference in prokaryotic richness of December versus June. The right map shows the locations of the European time series studies.

(B) The map indicates the sampling location of the HOT ALOHA time series (left). The observed seasonal change in prokaryotic richness in the HOT ALOHA time series was compared with the modeled richness change at the corresponding latitude. This comparison is summarized in the bar plot (centre), showing the symmetric percent change in December relative to June, based on the habitat model and the time series observations. The scatterplot with loess fit (right) shows the month-resolved observed richness in SML samples, with text annotations indicating the median observed richness in June and December.

modeled richness increased in winter: in the Northern Hemisphere, richness increased from summer (June) to winter (December) by a median of 17%, corresponding to 131 species (interquartile range, IQR: 41–198), while in the Southern Hemisphere with inverted seasonality, richness declined by 20% or 151 species (IQR: 83–210). Archaea showed similar trends, with higher winter richness. In the Northern Hemisphere, richness increased from June to December by a median of 58% or 11 species (IQR: 4–19) and decreased over the same period in the Southern Hemisphere by 32% or 9 species (IQR: 1–18). Outside equatorial regions, seasonal differences were significant for both bacterial and archaeal richness (Bacteria: 93% of 1° latitude bins; Archaea: 89% of latitude bins). Thus, our results indicate an increase in richness of Bacteria and Archaea in winter compared with summer months, whereas previously reported global diversity maxima at high latitudes during winter¹⁵ are not supported by our findings.

To compare the modeled seasonal changes to time-series observations, we analyzed data from seven European coastal time series stations (Figure 4A). Specifically, we compared the seasonal difference in prokaryotic richness ($\Delta\text{Richness}_{\text{December-June}}$) of the time series with the modeled richness at corresponding latitudes. All coastal time series and open-ocean models showed higher richness in December than in June, with similar median increases (modeled: 58.9% and time series: 56.9%; Figure 4A). For the open ocean, both the Hawaii Ocean Time-series at station ALOHA (HOT ALOHA) at 22.75° latitude ($\Delta\text{Richness}_{\text{December-June}}$: 5.9%) and the modeled December/June richness change at the corresponding latitude (17.7%) suggest that the winter increase in richness is less pronounced near the equator compared with higher latitudes (Figure 4B). This suggests that prokaryotic richness is higher in winter than in summer months and that this variation is modulated by latitude.

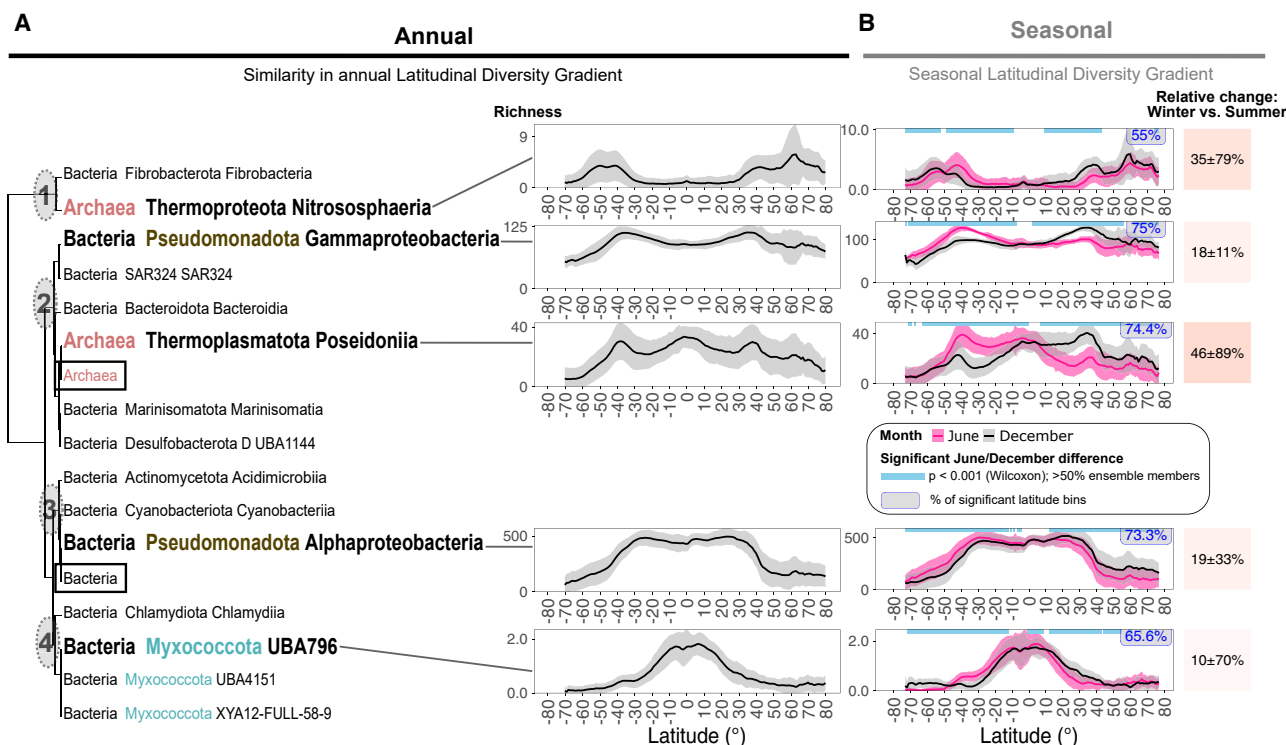


Figure 5. Latitudinal diversity gradients of different taxonomic ranks and across seasonality

(A) Dendrogram showing similarity in modeled annual latitudinal richness patterns across taxa. Mean richness per 1° latitude bin was correlated (Pearson) across taxa (*hclust* and *R stats*). Four distinct clusters of latitudinal diversity gradients (LDGs) were identified. For each cluster, the LDG of the taxon with the highest mean annual richness in the SML is shown, plus the archaeal class with the highest mean richness (Poseidoniiia); solid lines show mean richness per 1° latitude bin; shading indicates $\pm$ SD across ensemble members and longitude.

(B) Left: modeled mean latitudinal richness for June (pink) and December (black). Blue labels mark latitude bins with significant seasonal differences (>50% of ensemble members, $p < 0.001$, Wilcoxon test); percentages indicate the fraction of significant bins. Right: percent change in richness between winter (NH, December; SH, June) and summer (NH, June; SH, December), shown as mean $\pm$ SD across latitude bins.

See also [Figures S11–S14](#).

LDGs vary across taxonomic groups

To gain deeper insights into the structure of bacterial and archaeal richness across the global ocean SML, we modeled species richness at the class and genus levels ([Figures S11 and S12](#)). Although divergent LDGs were already evident at the domain level, this hierarchical approach aimed to assess whether these LDG patterns are internally consistent at lower taxonomic ranks or whether they are composed of increasingly divergent LDG clusters. We further assessed whether similarities in richness distributions align with phylogenetic relationships and finally investigated how seasonal variability contributes to diversity dynamics across taxonomic groups.

At the class level, comparative assessment of annual LDGs revealed four main clusters of diversity gradients ([Figure 5A](#)). The bacterial LDG was highly similar to that of the two richest classes, Alphaproteobacteria ($r = 0.998$, $p < 0.001$) and Cyanobacteriia ($r = 0.970$, $p < 0.001$) (cluster 2; [Figure 5A](#)), highlighting that the overall prokaryotic and bacterial LDGs are primarily shaped by species within these two classes. Similarly, grouping in cluster 4 revealed that the archaeal LDG is highly aligned with the LDG of class Poseidoniiia ($r = 0.976$, $p < 0.001$). Despite variation in gradient shape, most taxonomic groups showed lower diversity at temperate and polar latitudes compared with (sub)-

tropical zones. Notable exceptions included cluster 1, with Archaea of the class Nitrososphaeria and Bacteria of the class Fibrobacteriia both showing increasing diversity toward high latitudes (Nitrososphaeria: $r = 0.71$, $p < 0.001$; Fibrobacteriia: $r = 0.79$, $p < 0.001$). Together, a variety of LDGs exists in the SML, masked by species-rich taxonomic groups, particularly Alphaproteobacteria and Cyanobacteriia.

To evaluate whether additional LDG patterns emerge at higher taxonomic resolution, we analyzed richness-based LDG patterns of domains and classes together with the LDGs of 272 genera. This analysis revealed seven distinct genus-level LDG patterns, the majority of which (5 out of 7) contained at least one of the class-level LDGs ([Figure S12A](#)). The additional variety in LDG patterns resolved at the genus level confirms our findings that the overall prokaryotic LDG is a function of taxonomic resolution and that the number of different LDG patterns increases toward higher taxonomic resolution.

The relative abundance of prokaryotes is frequently skewed toward a few dominant taxa and many less abundant species. We therefore compared Shannon diversity-based LDGs for all modeled genera, which account for relative taxon abundance, with richness-based LDGs and found strong agreement in LDG patterns (median Spearman's $\rho = 0.90$; 71.4% of genera with

$\rho > 0.8$ and $p < 0.001$; Figure S12B). This high correlation indicates that LDG variation persists when accounting for differences in relative abundance of taxa.

Resolving LDGs per genus also revealed that specific genera within Alphaproteobacteria and Cyanobacteria shape the overall prokaryotic and bacterial LDG. Specifically, the species-rich genera *Pelagibacter* and *Prochlorococcus_A* exhibit pronounced richness peaks at (sub)tropical latitudes. Accordingly, their richness patterns closely track overall prokaryotic and bacterial richness (Pearson's $r = 0.98$ for *Pelagibacter* and $r = 0.94$ for *Prochlorococcus_A*, both $p < 0.001$; Figure S12C). This further strengthens the conclusion that a few taxonomic groups disproportionately shape the overall prokaryotic LDG pattern and mask additional LDG variety.

To investigate the relationship between annual LDGs among taxonomic groups and their phylogenetic distances, we compared latitudinal richness distributions to phylogenetic distances (Figure S13). Some classes belonging to the same phylum exhibited similar LDG patterns; for instance, the three Myxococcota classes, UA796, UBA4151, and XYA12-FULL-59-9, all showed an equatorial richness peak. However, alignment of the phylogenetic and LDG dendrograms revealed disparities for several taxonomic groups (entanglement score = 0.33; 0 = complete alignment and 1 = no alignment). For example, although the classes Alphaproteobacteria and Gammaproteobacteria belong to the same phylum, their LDGs differed considerably ($r = 0.71$, $p < 0.001$) and did not cluster together (Alphaproteobacteria: cluster 2, Gammaproteobacteria: cluster 4; Figure 5A). This suggests that observed (dis)similarities in the patterns of latitudinal richness distributions do not merely reflect phylogenetic distance. Even within some classes, we found that different genera can exhibit distinct LDG patterns (Figure S14). For example, within Gammaproteobacteria, genus *BACL14* exhibited the highest richness in (sub)polar regions. The LDG pattern of *BACL14* contrasted the diversity peaks of other gammaproteobacterial genera in intermediate latitudes and was anticorrelated with the LDG of the most species-rich genus, *SAR86A* ($r = -0.91$, $p < 0.001$). Resolving LDGs for genera within classes further supports the finding that a great variety of LDGs exist across taxonomic ranks.

The LDG patterns further exhibited significant seasonal changes in richness across the global ocean, with more than half of all 1° latitudinal bins showing significant monthly variation (Figure 5B). Here, the seasonal change was calculated as the ratio of mean winter-month richness (December in the Northern Hemisphere, June in the Southern Hemisphere) to mean summer richness (June in the Northern Hemisphere, December in the Southern Hemisphere), averaged across all latitude bins. Seasonal changes in richness consistently increased during winter months compared with summer months, across taxonomic groups. The magnitude of seasonal change in richness varied among representative classes, ranging from $57 \pm 49\%$ in Poseidoniiia to $11 \pm 74\%$ in UBA796 (mean $\pm$ SD). Notably, the LDG of class UBA796, which showed the highest richness around the equator, where seasonality is limited, exhibited minimal seasonal change. These results indicate that higher richness in winter is a widespread trend across bacterial and archaeal taxonomic groups. However, the magnitude of seasonal change varied among classes and across latitudes, as indicated by high standard deviations.

Environmental drivers and global diversity hotspots across taxonomic groups

Having identified four main clusters of annual LDGs across taxonomic classes in the SML (Figure 5), we sought to characterize their key environmental drivers and contextualize their diversity hotspots (Figure 6). To disentangle the environmental drivers of prokaryotic diversity, we first assessed correlations among climatological features, which grouped into environmental conditions representing temperature, oxygen, macronutrients, and carbon dynamics (Figure S15). Given the strong covariation among variables in the surface ocean, predictor importance reflects dominant environmental regimes rather than individual variables.

Across LDG clusters, temperature consistently emerged as the most important driver of richness (9 out of 15 classes), particularly for classes within cluster 3 (e.g., Acidimicrobiia: 28%, IQR: 23%–34%, and median and interquartile range) and cluster 4 (e.g., XYA12-FULL-59-9: 38%, IQR: 31%–43%) (Figure 6A). Particulate organic carbon (POC) levels, correlated with primary production ($r = 0.84$, $p < 0.001$; Figure S15), emerged in 8 out of 15 classes as a secondary or tertiary driver and even acted as the strongest predictor in some cases (e.g., cluster 2: POC for Poseidoniiia: 40%, IQR: 35%–45%). Beyond that, phosphate, covarying with other inorganic macronutrients, was identified as a secondary or tertiary driver in 6 classes (e.g., in all classes of cluster 3, ranging from Acidimicrobiia [12%, IQR: 10%–17%] to Alphaproteobacteria [18%, IQR: 7%–23%]). These results highlight that, although temperature exerts a primary influence on richness, lineage-specific sensitivities to macronutrient and carbon gradients could be found, pointing to divergent ecological strategies and the impact of environmental filtering. In contrast, variables related to water-mass dynamics, such as the eddy kinetic energy and the turbulence parameter of the finite-size Lyapunov exponent, were less important predictors (Figure S16), indicating a comparatively weaker influence on richness patterns.

The environmental characteristics and spatial extent of diversity hotspots (area of $> 75^{\text{th}}$ percentile modeled richness; Figures 6B and S11) were complementary to the dominant environmental features identified for each LDG cluster (Figure 5A). Cluster 1 classes (Nitrososphaeria and Fibrobacteria) had richness hotspots in polar and subpolar waters, representing nutrient- and carbon-rich regimes, and their richness hotspots occupied $\sim 36\%$ of the global SML (Figure 6B). Cluster 2 taxa (classes UBA1144, SAR324, Poseidoniiia, Marinisomatia, Gammaproteobacteria, Bacteroidia, and the domain Archaea) exhibited the broadest extent of richness hotspots ($\sim 52\%$ of the global SML), concentrated at mid-latitudes outside the oligotrophic gyre regions, under elevated nutrient concentrations and POC levels (Figure 6C). Taxonomic groups belonging to cluster 3 (Acidimicrobiia, Cyanobacteria, Alphaproteobacteria, and the domain Bacteria) were richest in oligotrophic (sub)tropical waters, with the highest temperatures and lowest phosphate concentrations across all clusters (Figure 6C). Their richness hotspots spanned $\sim 43\%$ of the global ocean but were absent from more nutrient-rich equatorial upwelling zones (Figure 6C). Finally, cluster 4 (class Chlamydia and three Myxococcota classes: UA796, UBA4151, and XYA12-FULL-59-9) was geographically constrained to richness hotspots around the equator

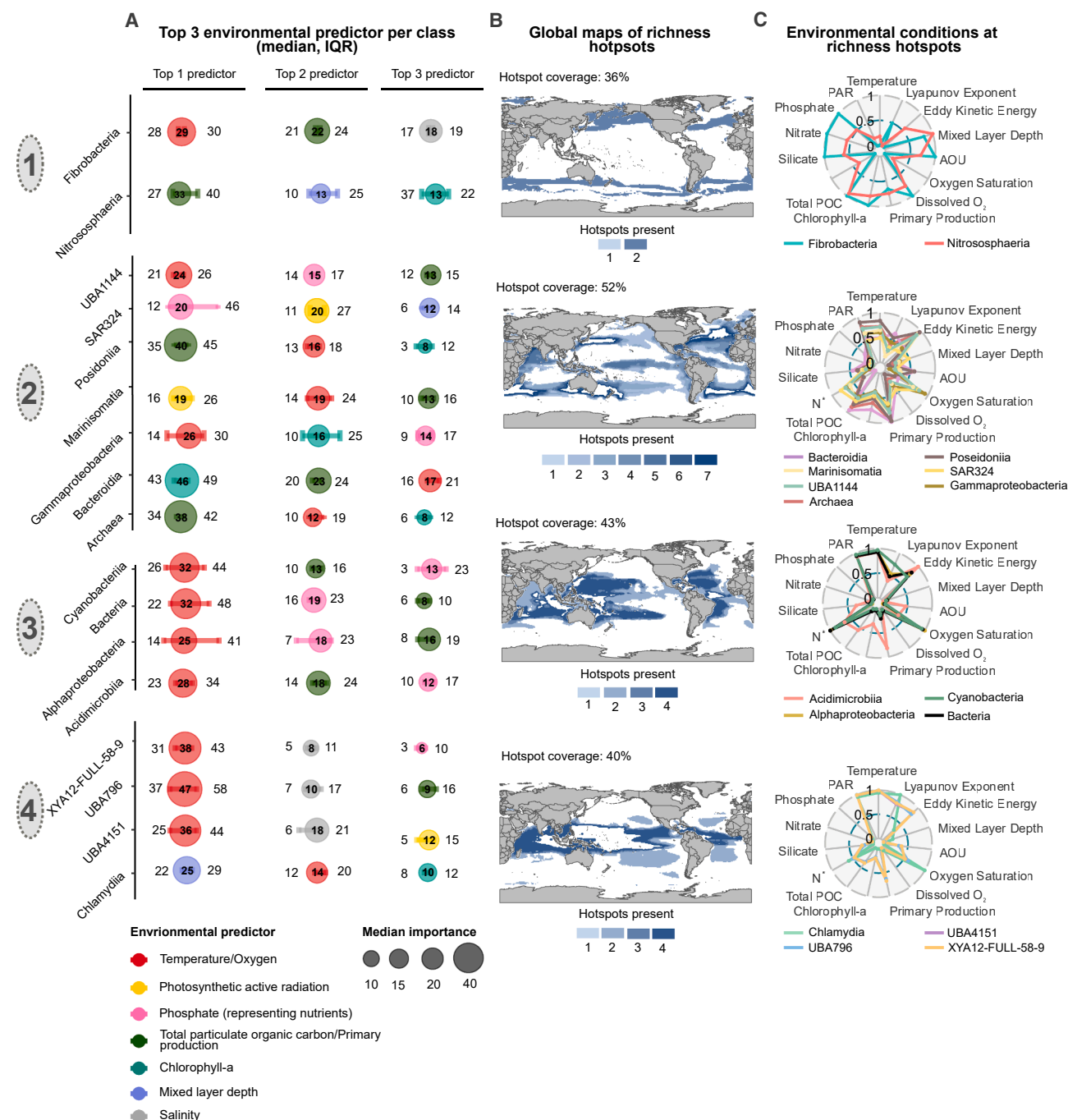


Figure 6. Richness hotspots and environmental drivers in the surface mixed layer across taxonomic groups

(A) Bubble plots show the top three environmental drivers (color coded) of richness for modeled prokaryotic classes and domains. Bubble size shows median variance explained; horizontal bars indicate the interquartile range across ensemble members.

(B) Consensus hotspot maps show, for each LDG cluster (Figure 5), the number of classes with richness hotspots per location (>75th percentile) and the fraction of ocean area covered.

(C) Spider plots depict scaled environmental characteristics (annual mean; PAR, photosynthetically active radiation; N*, excess nitrate relative to phosphate; total POC, particulate organic carbon; AOU, apparent oxygen utilization) across diversity hotspots. Environmental variables were scaled to the range 0–1 using min-max normalization (*rescale* and *R scales*) for comparability. For example, a temperature value of 1 indicates that the richness hotspot for that taxonomic group has the highest median annual temperature compared with all other taxon-specific richness hotspots. Lines are color coded by taxonomic groups.

See also Figures S15 and S16.

(~40% of the global SML), characterized by high photosynthetically active radiation (PAR) and a shallow mixed layer depth (Figure 6C). Taken together, richness hotspots and ultimately LDGs were shaped by lineage-specific associations with environmental gradients, driven primarily by temperature and secondarily by macronutrient and organic carbon availability.

DISCUSSION

Here, we show that the latitudinal structuring of species-resolved diversity in the ocean microbiome is depth dependent and shaped by lineage-specific biogeographic dynamics. Thus, our findings suggest that the diversity of the surface ocean microbiome does not universally conform to the classical LDG perspective but instead is shaped by the interaction between distinct ecological strategies and environmental gradients, resulting in taxon-specific diversity patterns.

The depth-dependent nature of LDGs suggests that microbial diversity is shaped by fundamentally different drivers in the SML and MZ environments. In the SML, environmental conditions, such as temperature, light, and nutrient availability, fluctuate over daily to seasonal timescales⁴ (Figure S6). These variations create heterogeneous ecological opportunities, driving microbial responses that underpin the structuring of diversity over space and time. Accordingly, surface ocean microbiome composition varies along environmental gradients and seasons, whereas MZ microbiome composition remains more stable and is instead influenced by longer-term processes such as water-mass circulation and residence time.^{25,26} Despite strong temporal variability in organic matter input, the relatively uniform physical conditions across latitudes in the MZ likely explain the absence of an LDG. However, limited MZ sampling coverage calls for further investigation to better understand diversity structuring and the processes shaping subsurface microbial communities.

The pronounced LDGs in the SML are structured over both spatial and temporal scales. Our results do not support a seasonal inversion of the bacterial LDG with diversity peaks in (sub-)polar regions in winter months, as previously hypothesized.¹⁵ Instead, our study suggests that the classical LDG pattern (poleward decrease in diversity) holds in the SML throughout the year, but its shape is modulated by seasonal dynamics: in agreement with observations from time series studies,^{23,27–29} our model projects an increase in bacterial and archaeal diversity in winter relative to summer months. A major factor that likely contributes to seasonal variations is the deepening of the SML in winter, which leads to vertical mixing of previously stratified communities, thereby increasing species richness and evenness.^{28,29} Although warm (sub)tropical regions are more diverse than polar regions on a global scale, colder winter months often coincide with higher species richness locally, which likely reflects underlying differences in spatial and temporal scales. Specifically, the elevated richness observed in oligotrophic gyres compared with polar regions may arise from differences in environmental stability and niche partitioning, as persistently low but stable resources in oligotrophic waters can promote the coexistence of many specialized taxa.³⁰ In contrast, polar regions experience strong seasonal extremes and environmental filtering, which may constrain long-term species coexistence despite episodic periods of high productivity.³¹ By capturing spatiotemporal dy-

namics, our findings indicate that previously reported deviations in LDG pattern may be partially explained by seasonal and spatial variability. Our model can serve as a reference to incorporate temporal dimensions into the monitoring of global ocean microbiome diversity.

We identified divergent LDGs at varying taxonomic ranks, such as domain, class, and genus. On the domain level, we found a decoupling of richness between Bacteria and Archaea in the (sub)tropical SML. Although global LDGs have been reported separately for both domains,^{8,10} their spatial decoupling has not previously been highlighted. This bacterial/archaeal decoupling was largely underpinned by species-rich Cyanobacteria (dominated by *Prochlorococcus_A*) and Alphaproteobacteria (dominated by *Pelagibacter*), which dominate the bacterial diversity signal and exhibit richness hotspots in oligotrophic gyres (Figure S12C), consistent with their adaptations to nutrient-scarce, low-productivity environments.^{32,33} Despite their streamlined genomes, *Pelagibacter* and *Prochlorococcus* exhibit diverse ecotypes, reflecting fine-scaled adaptations to stable conditions of light, temperature, and sustained nutrient scarcity in oligotrophic regions.^{34,35} Such functional versatility promotes a high degree of niche partitioning^{30,36} and helps explain the elevated bacterial richness observed in these regions,³⁷ ultimately driving LDG peaks at intermediate latitudes. Archaeal richness, meanwhile, is largely structured by Poseidonii species, which have been linked to productive waters with availability of phytoplankton-derived dissolved organic matter.^{38,39,40} Beyond the domain level, distinct LDG patterns were also evident at the class level. For example, many Bacteroidia species respond to organic matter in upwelling systems,⁴¹ which can explain their LDG pattern that closely follows the gradient of primary production (Figures S6 and S11). Similarly, Gammaproteobacteria show richness hotspots outside oligotrophic gyres, consistent with their classification as copiotrophs that preferentially occupy nutrient-rich environments.^{32,42} The archaeal class Nitrososphaeria displayed elevated richness levels at higher latitudes, in alignment with reports of their prevalence in surface waters around Antarctica.⁴³ Their rare abilities to derive energy from ammonia oxidation and urea degradation⁴⁴ and to withstand freeze-thaw cycles⁴⁵ likely enable their unusual LDG.

The lack of a universal LDG pattern is further amplified at the genus level, where the number of distinct LDG clusters increases to seven (Figure S12A). We found that taxonomic groups with greater phylogenetic relatedness tend to exhibit similar LDGs, as observed, e.g., for the Myxococcota classes (UA796, UBA4151, and XYA12-FULL-59-9; Figure 5) or the genera within class Alphaproteobacteria (*Pelagibacter*, *Pelagibacter_A*, and *AG-337-I02*; Figure S14). This likely reflects the fact that related taxa often inhabit similar ecological niches, known as niche conservatism.⁴⁶ However, this relationship was not consistent across all taxonomic groups. We observed notable disparities between phylogenetic relatedness and LDG pattern at both the class and genus level (Figures S13 and S14). In some cases, related taxa did not exhibit similar LDGs (e.g., genera within Gammaproteobacteria, such as *BACL14* and *SAR86A*; Figure S14), whereas in other cases, phylogenetically distant taxa exhibited similar LDGs (e.g., classes Poseidonii and Bacteroidia; Figure 5). These disparities capture valuable information

on the mechanisms behind global ecological patterns and potentially reflect similar metabolic functions,⁴⁷ explaining why distantly related taxa may converge within the same LDG cluster. Such ecological signatures are only uncovered when viewing the prokaryotic LDG as a function of taxonomic resolution, uncovering diversity patterns masked by species-rich taxonomic groups. Less diverse taxa, although contributing less to overall richness, may nonetheless fulfill important ecological roles and respond differently to environmental change. Taken together, our findings underscore the conclusion that LDGs are not universal features of marine prokaryotes but arise from taxon-specific ecological and evolutionary adaptations to distinct environmental regimes.

Despite such taxon-specific differences, several broader patterns emerge, indicating a degree of generality in the structuring of diversity and its environmental drivers. Most classes share a characteristic decline in diversity toward (sub)polar regions (Figure 5), with temperature identified as a first-order driver (Figure 6), consistent with macroecological principles linking temperature to biodiversity patterns.^{4,5,48} Temperature influences metabolic rates, energy flux, and ecosystem productivity, constraining diversity across latitudes,^{48,49} although it also covaries with other environmental properties. Consequently, associations between temperature and diversity likely reflect both direct physiological effects and indirect associations with co-varying oceanographic and biogeochemical conditions. This temperature-associated pattern aligns with a bimodal structuring of marine diversity, characterized by mid-latitude richness peaks and an equatorial dip,^{8,9,50,51} potentially driven by thermal boundary dynamics and equatorial upwelling acting as ecological filters.^{8,50} Beyond temperature, secondary and tertiary drivers, including the concentration of POC and phosphate, correlated with other macronutrients, were shared across a majority of classes (Figure 6). In line with this, nutrient regimes structure prokaryotic heterotrophs in the surface ocean by latitude, with oligotrophs adapted to nutrient scarcity dominating at low latitudes and copiotrophs with high growth rates dominating at higher-latitude regions.⁵² Recent biogeographic analyses show that microbial functional diversity peaks in nutrient transition zones associated with major circulation fronts, where environmental gradients and resource heterogeneity are strongest.⁵³ Despite previous reports on the potential influence of mixing and connectivity leading to increased diversity,⁵⁴ our environmental driver analysis suggests that environmental filtering plays a more important role in shaping microbial diversity gradients.⁵⁵ However, modeling-derived predictor rankings depend on the scale at which diversity is examined,⁵⁶ with predictors related to global-scale climate indicators such as temperature consistently ranking high in marine plankton studies.^{4,5,57} The observed variations among taxa highlight the limits of universal environmental predictors, showing instead that diversity patterns emerge from taxon-specific adaptations to distinct combinations of temperature, light, nutrients, and carbon dynamics.

Although our global model projections enabled us to disentangle taxon- and depth-specific LDGs within the ocean microbiome and their associated environmental drivers, several limitations remain. A major source of uncertainty stems from the uneven spatial and temporal sampling coverage across the global ocean. This is particularly evident at high latitudes and in the Southern Ocean, where data scarcity restricts our ability

to fully capture prokaryotic diversity dynamics and highlights the need for targeted sampling efforts. Furthermore, while we identified strong associations between environmental variables and diversity patterns, the high degree of covariation among environmental features highlights the challenge of disentangling individual drivers. These relationships should therefore be further explored through experimental and mechanistic studies to better understand the causal mechanisms underlying these observed diversity patterns.

Our results demonstrate that global patterns of ocean prokaryotic diversity are shaped by a few dominant taxonomic groups, whereas variation in LDG patterns is associated with distinct environmental gradients. Consequently, future changes in ocean stratification, nutrient availability, and primary production are expected to impact microbial diversity and ecosystem functions unevenly across taxonomic groups. Given the central role of marine prokaryotes in sustaining biogeochemical cycles, understanding their diversity is critical for assessing the resilience of ocean ecosystems under increasing environmental stress. These findings highlight the need for taxon-resolved, environmentally explicit models to accurately forecast microbiome dynamics and their biogeochemical consequences in a changing ocean.

RESOURCE AVAILABILITY

Lead contact

Requests for further information and resources should be directed to and will be fulfilled by the lead contact, Meike Vogt (meike.vogt@env.ethz.ch).

Materials availability

This study neither utilized nor produced biological or chemical reagents.

Data and code availability

All contextual information for the metagenomic samples, including associated metadata and calculated diversity metrics for each sample, together with the code used to conduct the analyses presented in this work, is available at Github: https://github.com/grp-bork/LDG_Eriksson_Schiller_2025. The code and environmental predictors used to implement the habitat-modeling pipeline are openly available at Zenodo: <https://zenodo.org/records/15168238>.

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AUTHOR CONTRIBUTIONS

D.E., J.S., S.S., N.G., M.V., and P.B. were responsible for the conceptualization of this study, which was further refined by T.P., L.J.U., A.M., and M.K.; supervision was provided by N.G., P.B., S.S., and M.V.; data curation was

conducted by S.M.-V., H.-J.R., and C.C.; analysis and investigation were led by J.S. (diversity metrics) and D.E. (spatiotemporal modeling), with contributions from E.F. and A.M. (European time series and phylogenetic analysis); funding was acquired by P.B., S.S., M.V., and N.G.; bioinformatic methodologies were applied or adjusted by D.E., A.S. (CEPHALOPOD model), J.S. (taxonomic resolution), and S.M.-V., who oversaw resources; visualizations were prepared by D.E. and J.S.; writing was undertaken by D.E., J.S., N.G., S.S., and M.V., with feedback from all other authors.

DECLARATION OF INTERESTS

The authors declare no competing interests.

DECLARATION OF GENERATIVE AI AND AI-ASSISTED TECHNOLOGIES IN THE WRITING PROCESS

During the writing of this work, the authors used ChatGPT (OpenAI) to improve language and readability. After its use, the authors carefully reviewed and edited the text and take full responsibility for the content of the manuscript.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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 - Selection of modeled taxonomic groups
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- **QUANTIFICATION AND STATISTICAL ANALYSIS**
 - Model sensitivity analysis
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SUPPLEMENTAL INFORMATION

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Ocean Microbiomics Database	N/A	https://omdb.microbiomics.io
MicrobeAtlas	Rodrigues et al. ⁵⁸	https://microbeatlas.org/landing
Environmental climatologies	Environmental Physics Group (ETH Zürich)	https://data.up.ethz.ch/shared/bluecloud/OBS/CLIMATOLOGIES/
Global oceans and seas shapefile	Flanders Marine Institute ⁵⁹	https://www.marineregions.org/sources.php#goas
IHO Sea areas shapefile	Flanders Marine Institute ⁵⁹	https://www.marineregions.org/sources.php#goas
Software and algorithms		
CEPHALOPOD	Schickele et al. ¹²	https://github.com/alexschickele/CEPHALOPOD
R package abind 1.4.5	Heideberger and Plate ⁶⁰	https://cran.r-project.org/web/packages/abind/index.html
R package ape 5.8.1	Paradis et al. ⁶¹	https://cran.r-project.org/web/packages/ape/index.html
R package cowplot 1.1.1	Wilke ⁶²	https://cran.r-project.org/web/packages/cowplot/vignettes/introduction.html
R package data.table 1.15.4	Barret et al. ⁶³	https://cran.r-project.org/web/packages/data.table/refman/data.table.html
R package dendextend 1.19.1	Tal Galili ⁶⁴	https://cran.r-project.org/web/packages/dendextend/index.html
R package doParallel 1.0.17	Coporation and Weston ⁶⁵	https://cran.r-project.org/web/packages/doParallel/index.html
R package dplyr 1.1.2	Wickham et al. ⁶⁶	https://cran.r-project.org/web/packages/dplyr/index.html
R package dynamicTreeCut 1.63-1	Langfelder et al. ⁶⁷	https://cran.r-project.org/web/packages/dynamicTreeCut/index.html
R package fmsb 0.7.3	Nakazawa ⁶⁸	https://cran.r-project.org/web/packages/fmsb/index.html
R package foreach 1.5.2	Weston et al. ⁶⁹	https://cran.r-project.org/web/packages/foreach/index.html
R package GGally 2.1.2	Schloerke et al. ⁷⁰	https://cran.r-project.org/web/packages/GGally/index.html
R package ggdendro 0.2.0	de Vries et al. ⁷¹	https://cran.r-project.org/web/packages/ggdendro/index.html
R package ggplot2 3.5.2	Wickham ⁷²	https://cran.r-project.org/web/packages/ggplot2/index.html
R package ggpmisc 0.5.4	Aphalo ⁷³	https://cran.r-project.org/web/packages/ggpmisc/index.html
R package ggradar 0.2.2	Bion ⁷⁴	https://github.com/ricardo-bion/ggradar
R package ggrepel 0.9.6	Slowikowski ⁷⁵	https://cran.r-project.org/web/packages/ggrepel/index.html
R package ggtext 0.1.2	Wilke et al. ⁷⁶	https://cran.r-project.org/web/packages/ggtext/index.html
R package gridExtra 2.3	Auguie ⁷⁷	https://cran.r-project.org/web/packages/gridExtra/index.html
R package hexbin 1.28.3	Carr et al. ⁷⁸	https://cran.r-project.org/web/packages/hexbin/index.html

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REAGENT or RESOURCE	SOURCE	IDENTIFIER
R package Hmisc 5.2-5	Harrell ⁷⁹	https://cran.r-project.org/web/packages/Hmisc/index.html
R package htmlwidgets 1.6.4	Vaidyanathan et al. ⁸⁰	https://cran.r-project.org/web/packages/htmlwidgets/index.html
R package maps 3.4.3	Becker et al. ⁸¹	https://cran.r-project.org/web/packages/maps/index.html
R package mgcv 1.9-4	Wood ⁸²	https://cran.r-project.org/web/packages/mgcv/index.html
R package ncdf4 1.6.0	Pierce ⁸³	https://cran.r-project.org/web/packages/ncdf4/index.html
R package networkD3 0.4.1	Allaire et al. ⁸⁴	https://cran.r-project.org/web/packages/networkD3/index.html
R package parallel 4.6.0	R Core Team ⁸⁵	https://www.r-project.org/
R package phytools 2.5.2	Revell ⁸⁶	https://cran.r-project.org/web/packages/phytools/index.html
R package plyr 1.8.8	Wickham et al. ⁶⁶	https://cran.r-project.org/web/packages/plyr/index.html
R package purrr 1.2.1	Wickham et al. ⁸⁷	https://cran.r-project.org/web/packages/purrr/index.html
R package raster 3.6.26	Hijmans ⁸⁸	https://cran.r-project.org/web/packages/raster/index.html
R package reshape 1.4.4	Wickham ⁸⁹	https://cran.r-project.org/web/packages/reshape2/index.html
R package rnatuarearth 0.3.9	Massicotte and South ⁹⁰	https://cran.r-project.org/web/packages/rnatuarearth/index.html
R package rnatuarearthdata 0.1.0	South ⁹¹	https://cran.r-project.org/web/packages/rnatuarearthdata/index.html
R package scales 1.2.1	Wickham ⁹²	https://cran.r-project.org/web/packages/scales/index.html
R package sf 1.0.14	Pebesma and Bivand ⁹³	https://cran.r-project.org/web/packages/sf/index.html
R package sp 2.1.4	Pebesma and Bivand ⁹⁴	https://cran.r-project.org/web/packages/sp/index.html
R package stats 4.5.2	R Core Team ⁸⁵	https://www.r-project.org/
R package stringr 1.5.0	Wickham ⁹⁵	https://cran.r-project.org/web/packages/stringr/index.html
R package svglite 2.2.2	Wickham et al. ⁹⁶	https://cran.r-project.org/web/packages/svglite/index.html
R package terra 1.7.78	Robert and Hijmans ⁹⁷	https://cran.r-project.org/web/packages/terra/index.html
R package tibble 3.2.1	Müller and Wickham ⁹⁸	https://cran.r-project.org/web/packages/tibble/index.html
R package tidyr 1.3.1	Wickham et al. ⁹⁹	https://cran.r-project.org/web/packages/tidyr/index.html
R package tidyterra 0.4.0	Hernangomez ¹⁰⁰	https://cran.r-project.org/web/packages/tidyterra/index.html
R package treemap 2.4.3	Tennekes ¹⁰¹	https://cran.r-project.org/web/packages/treemap/index.html
R package vegan 2.7-2	Oksanen et al. ¹⁰²	https://cran.r-project.org/web/packages/vegan/index.html
R package viridis 0.6.5	Garnier et al. ¹⁰³	https://cran.r-project.org/web/packages/viridis/index.html
R package viridisLite 0.4.2	Garnier et al. ¹⁰⁴	https://cran.r-project.org/web/packages/viridisLite/index.html

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REAGENT or RESOURCE	SOURCE	IDENTIFIER
R package webshot 0.5.5	Chang ¹⁰⁵	https://cran.r-project.org/web/packages/webshot/index.html

METHOD DETAILS

Metagenomic sample selection

Metagenomic data were obtained from the Ocean Microbiomics Database (OMDB; <https://omdb.microbiomics.io>), which compiles marine metagenomic datasets from publicly available studies and BioProjects registered in the European Nucleotide Archive (ENA). Only metagenomic data used in published studies or shared via personal communication were included. For the diversity analysis of marine microbial communities, we excluded samples from coastal environments (within 20 km of the shoreline) to minimize the confounding effects of eutrophic and dynamic coastal processes and further excluded samples from the enclosed basins, the Baltic and Mediterranean Seas. Additionally, samples collected in response to specific events (e.g., algal blooms, pollution events) and those with a minimum filter size > 0.8 μm were removed to discard samples that exclude the free-living prokaryotic community, retaining samples with lower filter size thresholds of 0.2–0.8 μm . For SML analyses, we retained samples from within the mixed layer depth at each location, with mixed layer depth information derived from the World Ocean Atlas 2018 (WOA18).¹⁰⁶ Samples collected from depths between 200 and 1,000 m, and located below the SML, were classified as mesopelagic.

Generation of taxonomic profiles

For the selected samples, taxonomic profiles were generated using the mOTUs4 profiler with default parameters.^{17,107} The profiler uses the mOTUs marker gene database as reference, which comprises species-level units defined by ten universal single-copy phylogenetic marker genes¹⁰⁸ derived from isolate reference genomes, single-cell amplified and metagenome-assembled genomes, and environmental assemblies.¹⁰⁷ Metagenomic reads are directly aligned to these markers, and relative species abundances are estimated from marker gene coverage, approximating the relative copy number of genomes per species present in each sample. Marker genes that cannot be assigned to any species-level unit are used to quantify the fraction of uncharacterized genomes (“unsigned”), allowing consistent relative abundance estimates across samples.¹⁰⁹

Diversity indices

Species diversity was calculated after accounting for inter-sample differences in sampling effort and sequencing depth, by rarefying mOTUs counts to equal counts per sample (*rarefy* function, *vegan* R package). Rarefaction was conducted with two different sample sizes (1,000 and 5,000 mOTU counts), considering only samples with mOTU counts above the respective threshold. Rarefaction was repeated 200 times per sample. At each rarefaction repetition, the rarefied mOTUs table was subsetted to species belonging to the same taxonomic rank (domain, phylum, class, order, family, genus), and diversity metrics (richness, Shannon index, Chao1) were calculated (*diversity* function, *vegan* R package). Final diversity values per sample and taxonomic group represent the mean of the 200 repetitions. Genus diversity (Figure S4) was calculated similarly, except that counts of species belonging to the same genus were first aggregated prior to rarefaction.

Environmental features

Environmental parameters used to model prokaryotic diversity indices capture physical, chemical, and biological characteristics of the marine environment, serving as key environmental features of prokaryotic diversity.^{6,8,9} Biological variables include chlorophyll-*a* concentration (mg m^{-3}), a proxy for phytoplankton biomass, and primary production ($\text{mg C m}^{-2} \text{ day}^{-1}$), both sourced from GIMS climatologies.^{110,111} Physical parameters encompass sea surface temperature ($^{\circ}\text{C}$) from the World Ocean Atlas 2018¹⁰⁶ and photosynthetically active radiation ($\text{Ein m}^{-2} \text{ day}^{-1}$) from the Global Marine Information System¹¹¹ as well as oceanographic dynamics metrics such as Eddy Kinetic Energy ($\text{cm}^2 \text{ s}^{-2}$)¹¹² and the Finite-Size Lyapunov Exponent (days^{-1} ; obtained from AVISO).¹¹³ Chemical environmental features include nitrate, phosphate, and silicate concentrations ($\mu\text{mol kg}^{-1}$) from the World Ocean Atlas 2018, along with derived stoichiometric indices such as N^* ($[\text{nitrate}] - 16^*[\text{phosphate}]$) and Si^* ($[\text{silicate}] - [\text{nitrate}]$) to assess nutrient limitation patterns. Oxygen-related variables, including concentration ($\mu\text{mol kg}^{-1}$), fractional saturation (%), and apparent oxygen utilization ($\mu\text{mol kg}^{-1}$), are also sourced from the World Ocean Atlas 2018.¹¹⁴ Additionally, particulate organic carbon concentrations (mg C m^{-3}) were derived from Stramski et al.¹¹⁵ All climatologies have a monthly spatial resolution of 1° by 1° longitude and latitude, and annual means alongside seasonal latitudinal variations are visualized in Figure S6. Although this monthly resolution does not capture finer temporal dynamics of marine microbial communities, it has proved effective to represent major seasonal trends^{111,112} and allows the use of robust climatology datasets that enhance the signal-to-noise ratio in downstream analyses. We further evaluated the correlation between in situ environmental variables measured during the Tara Ocean expedition²⁴ and the climatological parameters used in our study (Figure S7). Because our models are trained exclusively on open-ocean samples within the SML, we excluded samples from marginal seas, including the Mediterranean Sea, Red Sea, Baltic Sea, Black Sea, Persian Gulf, and Gulf of Aden. Seven environmental parameters were available for comparison, including physical variables (temperature ($^{\circ}\text{C}$), photosynthetically active radiation

(Ein m⁻² day⁻¹), and mixed layer depth (m)), nutrient concentrations (nitrate (μmol L⁻¹), phosphate (μmol L⁻¹), and silicate (μmol L⁻¹), and the biological variable, chlorophyll-a (mg m⁻³).

Habitat modeling framework

To model microbial diversity patterns, we employed CEPHALOPOD (Comprehensive Ensemble Pipeline for Habitat modelling Across Large-scale Ocean Pelagic Observation Datasets),¹² a state-of-the-art, standardized, and highly automated habitat modeling framework designed to produce intercomparable outputs across scarce observation datasets, and observation types, such as metagenomics. CEPHALOPOD follows an ensemble modeling approach, including regression and machine learning algorithms, evaluated by an explicit traffic-light quality check system that ensures robust predictions of the biological target(s), which in this study were the diversity metrics richness, Shannon index, and Chao1. Here, we briefly recall the main steps of CEPHALOPOD and refer to Schickele et al.¹² for detailed methods and quality check benchmarks.

First, CEPHALOPOD matches metagenomic observations to the resolution of the environmental features to ensure spatial and temporal consistency between the biological target(s) and the environmental conditions in which they were observed. If several observations fall into the same monthly grid cell (1° by 1° spatial resolution), an average across the observations is computed and used for modeling. Second, features showing negligible association with the target variables are discarded. Then, CEPHALOPOD only retains the most informative environmental features among groups of intercorrelated ones. Finally, CEPHALOPOD performs a recursive feature elimination procedure, only retaining the minimal, non-redundant set of environmental features best explaining the variance in the target. At this stage, we retain a robust, non-collinear, non-redundant, and parsimonious set of environmental features, to best model diversity metrics.

The selected features were then used in a standardized ensemble habitat modeling approach, balanced across regression (GLM; GAM), tree-based (RF, XGBoost), and machine learning algorithms (SVM, MLP). To mitigate the effects of spatial autocorrelation, which can bias algorithm performance evaluation, and to optimize both algorithm training and hyperparameter tuning, CEPHALOPOD implements a spatial block cross-validation procedure. This provides an effective balance between spatial independence and sufficient sample size for algorithm calibration and evaluation. Algorithm performance is then assessed by comparing predicted and observed target values across the evaluation folds, while the variance explained by each feature is quantified to assess model interpretability. Both performance and feature importance are associated with quality checks (i.e., $R^2 > 0.25$ and top 3 features > 50% variance explained). To propagate uncertainty to the projections, CEPHALOPOD generates bootstrap replicates across all algorithms, passing the above-mentioned quality checks. Finally, the variability in the projections, across bootstraps and algorithms, is associated with a final quality check (i.e., normalized standard deviation < 0.5). This ensures that only robust and interpretable algorithm outputs are considered in subsequent analyses.

Selection of modeled taxonomic groups

Annual and seasonal diversity distribution in the ocean SML was modeled across taxonomic ranks. We restricted this to taxonomic groups that successfully passed the four sequential CEPHALOPOD quality criteria for continuous target variables, including a priori predictor testing, predictive performance ($R^2 \geq 0.25$), cumulative variable importance and projection uncertainty.¹² If the class-level annual LDG was highly correlated with that of its corresponding phylum (Pearson's $r > 0.9$), we only showed the lower taxonomic rank (class level) to avoid redundancy (Figure 5). For each modeled phylum with $R^2 \geq 0.25$ ($n = 11$ phyla), the annual LDG of at least one corresponding class was highly correlated with the annual LDG of its corresponding phylum.

European time series studies - Seasonality

All data used for the seasonal analysis of European time series were obtained from the MicrobeAtlas⁵⁸ download section (Table S1). Richness was calculated from operational taxonomic unit (OTU) read counts (97% sequence identity) using the *rarefy* function of the R *vegan* package. For each sample, the OTU read counts were rarefied to 3,000 observations with 20 repetitions. Final richness values were obtained by calculating the median richness of the 20 rarefaction iterations. Within each study, we summarized richness by sampling month (median) and then calculated the relative change between December and June (Figure 4).

QUANTIFICATION AND STATISTICAL ANALYSIS

Model sensitivity analysis

In order to quantify the influence of coastal sample inclusion on the modeling of prokaryotic diversity, we iteratively excluded samples based on their distance from the coast to assess model stability (from 5 km to 1,400 km). To assess the sensitivity of the inferred diversity patterns to uneven geographic sampling, we implemented a basin-stratified subsampling analysis. Samples from each major ocean basin were randomly downsampled using basin-specific sample-size thresholds before model fitting (ranging from 350 to 10 samples per basin). For each threshold T , basins with more than T observations were randomly reduced to T observations (without replacement), whereas basins with T or fewer observations were retained unchanged. This procedure was repeated 100 times per threshold to generate balanced realizations of the dataset. Each subsampled dataset was propagated through the full modeling pipeline,¹² allowing us to quantify uncertainty arising from unequal sample representation. The coefficient of variation (CV) across the model outputs with varying thresholds is summarized to visualize geographic regions that are mostly influenced by uneven sampling distribution.

Statistical testing of seasonal variation in latitudinal diversity gradients

To assess seasonal variations in marine prokaryote diversity along latitudinal gradients, richness data for December (winter in the Northern Hemisphere; summer in the Southern Hemisphere) and June (winter in the Southern Hemisphere; summer in the Northern Hemisphere) were extracted from ensemble mean outputs of diversity models. These data were grouped into 1° latitude bins, and mean richness values were calculated for each bin and month. Variability around the mean was quantified as ± 1 standard deviation (SD). Statistical differences in richness between December and June across latitude bins were evaluated using the Wilcoxon test, implemented via the *wilcox.test* function from the *stats* package in R. Latitude bins with significant differences ($p < 0.001$) across $> 50\%$ of model ensemble members were identified, and their significance was visually distinguished by horizontal blue labels. In detail, we evaluated seasonal differences in richness across individual ensemble members, defined by unique combinations of bootstrap resampling and algorithm choices. Instead of relying solely on the ensemble mean, Wilcoxon tests were performed separately for each ensemble member within 1° latitude bins, allowing a more comprehensive assessment of variability. The proportion of ensemble members displaying significant seasonal differences ($p < 0.001$) was then calculated to quantify the robustness of observed patterns across models. This approach ensures that conclusions about seasonal richness shifts are not overly influenced by any single modeling choice but instead reflect consistent patterns across a diverse set of predictive algorithms and resampling strategies. Visualization of results included both 1° latitudinal mean richness estimates and variability across ensemble members, with shaded confidence regions representing the range of model outputs. The resulting modeled latitudinal diversity gradients were visualized using the R *ggplot2* package, where solid lines represented mean richness values, and shaded ribbons depicted variability ($\pm$ SD).