Contrasting processes drive gradients in phylodiversity across shallow and deep seafloors

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Our knowledge of the distribution and evolution of deep-sea life is limited, impeding our ability to identify priority areas for conservation. Here we analyse, for the first time, large integrated phylogenomic and distributional datasets of seafloor fauna from the equator to pole for an entire class of invertebrates. We find that ubiquitous latitudinal diversity gradients are assembled through contrasting evolutionary processes for shallow and deep seas. In the shallow-water tropical-temperate realm, speciation, extinction and migration rates are broadly consistent with an "out of the tropics" process [1]. Speciation rates are reversed for the realm containing the deep sea and Antarctica, being highest at polar and lowest at tropical latitudes, and net migration is from high to low latitudes. The tropical upper bathyal (200-700 m deep), with its rich ancient phylodiversity, is characterised by relatively low background extinction rates. Conversely, the specialised Antarctic fauna is rebounding from episodic extinction events associated with the rapid cooling of polar waters over the mid-Cenozoic.

The decline of species richness with latitude is so prevalent across taxonomic groups and biomes that it has been called the first-order pattern of biodiversity across the planet [2]. However, elucidating the

mechanisms that create such patterns remains a major challenge [3]. Different combinations of speciation, extinction and range expansion rates can result in high and low diversity regions. The high diversity tropics are characterised as being a 'cradle' (resulting from high speciation rates) or 'museum' (an accumulation zone with low extinction rates) [4]. Based on marine bivalve fossil data, Jablonski et al. [1] hypothesised an 'out of the tropics' process with lineages originating in the tropics then expanding their range to include both tropical and higher latitudes, the tropics thus being both a cradle and a museum. However, this mechanism has been since investigated only in shallow marine and terrestrial ecosystems. The deep sea (below 200 m) is an important third ecosystem that differs from other environments in that the distribution of life is not primarily driven directly by thermal energy [5,6]. Moreover, it continuously covers a broad range of latitudes. Testing evolutionary and ecological hypotheses in unique environments like the deep sea offers the potential to disentangle some of the numerous interacting variables that potentially affect the distribution of biodiversity [3]. However, until now we have lacked the comprehensive phylogenetic data to investigate these patterns.

Here we combine substantial distributional (160k records) and DNA sequence data (596 species, 267kb) across an entire taxonomic class of invertebrates (Ophiuroidea) to test the 'out of the tropics' hypothesis from shallow to deep-sea environments, from the equator to Antarctica across the Indo-Pacific southern hemisphere (Extended Data Fig. 1). Ophiuroids, or brittle-stars, have become a useful model for examining large-scale patterns of marine biogeography as they occur abundantly on the seafloor of most oceans [6-8]. Specifically we test the 'out of the tropics' prediction [3] that speciation rates are higher and extinction rates lower in tropical compared to temperate and polar regions, for both shallow water (0-200 m) and deep-sea systems (> 200 m).

We find a marine latitudinal diversity gradient of varying profile at all depths and at various levels of evolutionary differentiation (Fig. 1 and Extended Data Fig. 2). High species richness occurs at sublittoral (0-200 m) and upper bathyal (200-700 m) depths at tropical latitudes (0-35°S) with moderate richness in

temperate (34-46°S) and mid-bathyal (700-2000 m) zones, and a steep decline to Antarctica and the abyss. At the shallowest level (0-100 m) there is a pronounced latitudinal peak south of the equator (13-23°S) while with increasing depths it is more broadly tropical. A non-equatorial peak of richness for shallow marine fauna has been observed for many marine datasets [9]. Across all latitudes the bathymetric peak is in the upper to mid bathyal, shifting southwards with depth. Bathymetric peaks of species richness in the Indo-Pacific at tropical upper bathyal depths have been recorded for other eurybathyal invertebrate groups, such as azooxanthellate scleractinian corals, turrid molluscs, and galatheid crustaceans [10-12]. The deeper temperate latitudinal peak (~1000 m) is compatible with the reported mid-bathyal peak in richness from the northern Atlantic Ocean [5]. With increasing depth, and phylogenetic scale, the gradients become more step-like and pushed further south. Horizontal gradients in the lower bathyal and abyss (>2000 m) differ in being relatively consistent over tropical and temperate latitudes, then gradually declining across the Southern Ocean. Family-level taxa (~110 my) are widespread [14], declining most rapidly at high latitudes and lower bathyal depths (Extended Data Fig. 3a).

Patterns of phylogenetic diversity (PD) are broadly similar, but with the peak restricted to the upper bathyal. Other phylogenetic diversity indices including relative PD (RPD), evolutionary distinctness (ED) and mean lineage diversification rate, highlight the differences between the species diversity and underlying phylogenetic structure. Species with the highest ED, a measure of how isolated they are on the phylogenetic tree, are also concentrated in the tropical upper bathyal. Relative Phylogenetic Diversity (RPD, Fig. 1c), the ratio of observed PD to PD expected from species richness, is significantly low ($p < 0.01$, Extended Data Fig. 3d) in Antarctic waters and the tropical shallows, indicative of phylogenetic clustering or discrete origins and extensive recent speciation (Fig. 2). Conversely, the tropical deep sea, as species rich as the shallows, has a relatively high RPD ($p > 0.95$) reflecting numerous diverse lineages spread across the phylogeny (Fig. 2). Mean lineage diversification rates (Fig. 1d) distinguish the relatively recent phylogenetic radiations evident in Antarctic and older radiations in tropical sublittoral regions.

Simpson's phylo beta diversity ($p\beta_{Sim}$ [15,16]) measures the turnover in phylogenetic composition across the study region. Peak $p\beta_{Sim}$ occurs across a depth gradient between 100 and 300 m at tropical and temperate latitudes (Fig. 1f and Extended Data Fig. 3f). This bathymetric turnover is so pronounced that the seafloor fauna should be considered to form two biological realms, (1) tropical-temperate shallow water (0 to 200-300 m) and (2) the deep sea plus Antarctica. Notable latitudinal compositional changes also occur around 54°S, 45°S and 34°S, allowing five distinct biomes to be defined from multivariate analyses of $p\beta_{Sim}$ across our study region: tropical shallow, temperate shallow, tropical deep sea, temperate deep sea and Antarctica (Fig. 1g). The five bioregions have divergent signatures of speciation, extinction and migration (Fig. 3) that are robust to randomised trials and incomplete sampling (Extended Data Table 4, Extended Data Fig. 5).

The tropical shallows are more a 'cradle' than a 'museum', with moderate rates of speciation but low rates of extinction, generating high endemic species richness clustered into large discrete radiations (Fig. 2, 3). The temperate shallows are less phylogenetically clustered, have lower speciation rates and higher extinction rates, resulting in reduced species richness despite ongoing exchange between the tropical and temperate shallows (Fig. 3d and Extended Data Table 6). Transition rates between these shallow biomes and Antarctica approximate zero. The temperate shallow water biome currently ends at the southern end of Australia and New Zealand, although it may have continued to 61°S prior to the development of Oligocene polar ice-caps [17]. In summary, faunal distribution across the temperate-tropical shallow water realm is not inconsistent with the 'out of the tropics' scenario reported for marine bivalves [1] and various terrestrial clades [18,19]. However, the shallow Antarctic ophiuroid fauna is not part of this process, being phylogenetically related to deep-sea lineages.

The deep-sea and Antarctic realm has an entirely different pattern. The tropical deep sea, with high species diversity but low speciation rate, is a 'museum' or accumulation biome, rather than a 'cradle'. It

is phylogenetically dispersed, containing a diverse assemblage of ancient lineages, where both speciation and extinction rates are relatively low but the net diversification rate is still positive, and with low to intermediate rates of immigration respectively from the tropical shallow and temperate deep-sea biomes (Extended Data Table 4). The temperate deep sea is a 'flux' biome, containing a transitional fauna, with low net diversification (moderate speciation and high extinction rates) and intermediate to high rates of migration across neighbouring deep-sea latitudes. Net migration is from south to north, both in terms of rate and number of transitions (Extended Data Table 6). Explaining the tropical-temperate transition in the deep sea is one of the unresolved problems of marine biogeography [7], as isotherms occur more or less horizontally from the equator, across both tropical and temperate latitudes, before shoaling in subantarctic waters (Extended Data Fig. 7). Contrary to the hypothesis that thermal energy promotes diversification [20], the Antarctic has the highest rate of speciation of all our biomes, four times the rate of the tropical deep sea. Thus the 'cradle' and 'museum' are reversed for the deep sea, and regional rates of speciation, extinction and migration do not conform to the predicted 'out of the tropics' mechanism. The latitudinal biodiversity gradient in the deep sea has been created or is being maintained by other processes.

Antarctica has a short-branched phylogenetically-clustered ophiuroid fauna indicative of a recent (post mid-Cenozoic) radiation. Numerous ophiuroid families are absent (Extended Data Fig 2, 3) but background extinction rate estimates are only a fifth of the speciation rate (Fig. 3), suggesting other process may account for the current diversity. Fossil evidence indicates that there were elevated rates of extinction in several marine faunal groups coincident with rapidly cooling polar seas, in particular during the development of polar ice-caps at the Eocene-Oligocene (41-34 my) transition, and with a pronounced strengthening of the Antarctic Circumpolar Current during the Middle Miocene climatic transition (14-12 my) [21]. Remaining fauna had to evolve tolerance to cold water, the presence of ice, and marked seasonal primary productivity. Eurybathy is now a feature of the Antarctic fauna [22] and some deep-sea clades appear to have expanded their range into shallow water. Radiation of surviving lineages

would have been facilitated by a combination of vacant niches, removal of predation pressure, and creation of intermittent ice-sheet dispersal barriers [21,23]. Thus the pattern of high speciation rate but modest species diversity for ophiuroids is consistent with a rebound response to episodic extinction events. The Antarctic biome may not be at evolutionary equilibrium.

The low speciation rate for the tropical deep-sea biome is unexpected. Our data is not consistent with hypotheses that the richness is derived from increased speciation rates, generated either from elevated habitat heterogeneity or along the extreme pressure and thermal gradients that characterise the upper oceans [13]. Instead, we argue that low extinction rates and relatively high accumulation rates maintain the high phylodiversity. We hypothesise that the upper-mid bathyal (200-2000 m) has been a stable complex environment and long term refuge for deep-sea animals. Indeed, microfossil ophiuroid assemblages from the late Cretaceous Blake Nose deposits (114 my, palaeo-depth of 800-1500 m), contain the same families as habitats at similar depths in the modern Atlantic Ocean [24]. Upper bathyal waters are the tropical rain forests of the sea, preserving a rich ancient fauna, and a reservoir of phylogenetic diversity. This fauna has not been emphasized in conservation assessments to date.

Conversely, the abyss (> 3500 m) is characterised by low richness for ophiuroids (Fig. 1) and many other faunal groups [25]. This decline has been related to long term environmental drivers (e.g. reduced carbon flux, temperature and increased pressure [6]) or from oceanographic events such as the intermittent development of widespread anoxic conditions in the deep oceans [26]. Unlike for Antarctica, we find that abyssal taxa amount to a small diverse subset of the bathyal lineages, with little evidence for endemic speciation except in polar areas (Fig. 1c-d, 2), suggesting multiple infrequent migrations from bathyal to the abyss. Similar patterns have been found in other animal groups [13,27].

Contrasting patterns and processes in the shallow and deep marine environments suggest reconsideration of conservation priorities. The United Nation's Sustainable Development target 5 goal 14

and Aichi biodiversity target 11 specify that only 10 percent of the coastal and marine areas should be conserved, without consideration of the strong bathymetric and latitudinal turnover in phylodiversity. It may not be appropriate to use extensive deep-sea marine protected areas as a biodiversity offset against lack of shallow water protection. The blue planet requires a global approach to long term marine conservation that addresses the dynamics of oceanic biodiversity.

1 Jablonski, D., Roy, K. & Valentine, J. W. Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science* **314**, 102-106, doi:10.1126/science.1130880 (2006).

2 Krug, A. Z., Jablonski, D., Valentine, J. W. & Roy, K. Generation of Earth's First-Order Biodiversity Pattern. *Astrobiology* **9**, 113-124, doi:DOI: 10.1089/ast.2008.0253 (2009).

3 Brown, J. H. Why are there so many species in the tropics? *J Biogeogr* **41**, 8–22, doi:10.1111/jbi.12228 (2014).

4 Stebbins, G. L. *Flowering Plants: Evolution above the Species Level*. (Belknap, 1974).

5 Rex, M. A. & Etter, R. J. *Deep-sea biodiversity: Pattern and scale*. (Harvard University Press, 2010).

6 Woolley, S. N. C. *et al.* Deep-sea diversity patterns are shaped by energy availability. *Nature* **533**, 393–396, doi:10.1038/nature17937 (2016).

7 O'Hara, T. D., Rowden, A. A. & Bax, N. J. A southern hemisphere bathyal fauna is distributed in latitudinal bands. *Curr Biol* **21**, 226-230, doi:10.1016/j.cub.2011.01.002 (2011).

8 Stöhr, S., O'Hara, T. D. & Thuy, B. Global diversity of brittle stars (Echinodermata: Ophiuroidea). *PLoS ONE* **7**, e31940, doi:10.1371/journal.pone.0031940 (2012).

9 Chaudhary, C., Saeedi, H. & Costello, M. J. Bimodality of latitudinal gradients in marine species richness. *Trends Ecol Evol* **31**, 670-676, doi:10.1016/j.tree.2016.06.001 (2016).

10 Bouchet, P., Lozouet, P. & Sysoev, A. An inordinate fondness for turrids. *Deep Sea Res II* **56**, 1724-1731, doi:10.1016/j.dsr2.2009.05.033 (2009).

11 Macpherson, E. *et al.* Biogeography of the deep-sea galatheid squat lobsters of the Pacific Ocean. *Deep Sea Res I* **57**, 228-238, doi:10.1016/j.dsr.2009.11.002 (2010).

12 Cairns, S. Deep-water corals: An overview with special reference to diversity and distribution of deep-water Scleractinian corals. *Bull Mar Sci* **81**, 311-322 (2007).

13 Brown, A. & Thatje, S. Explaining bathymetric diversity patterns in marine benthic invertebrates and demersal fishes: physiological contributions to adaptation of life at depth. *Biol Rev Camb Philos Soc* **89**, 406-426, doi:10.1111/brv.12061 (2014).

14 O'Hara, T. D., Hugall, A. F., Thuy, B., Stöhr, S. & Martynov, A. V. Restructuring higher taxonomy using broad-scale phylogenomics: the living Ophiuroidea. *Mol Phylogenet Evol* **107**, 415-430, doi:10.1016/j.ympev.2016.12.006 (2017).

15 Graham, C. H. & Fine, P. V. A. Phylogenetic beta diversity: linking ecological and evolutionary processes across space in time. *Ecol Lett* **11**, 1265–1277, doi:10.1111/j.1461-0248.2008.01256.x (2008).

16 Leprieur, F. *et al.* Quantifying Phylogenetic Beta Diversity: Distinguishing between 'True' Turnover of Lineages and Phylogenetic Diversity Gradients. *PLoS ONE* **7**, e42760, doi:10.1371/journal.pone.0042760 (2012).

17 Aronson, R. B. & Blake, D. B. Global climate change and the origin of modern benthic communities in Antarctica. *Am Zool* **41**, 27-39, doi:10.1093/icb/41.1.27 (2001).

18 Jansson, R., Rodríguez-Castañeda, G. & Harding, L. E. What can multiple phylogenies say about the latitudinal diversity gradient? A new look at the tropical conservatism, out of the tropics, and diversification rate hypotheses. *Evolution* **67**, 1741-1755, doi:10.1111/evo.12089 (2013).

19 Rolland, J., Condamine, F. L., Jiguet, F. & Morlon, H. Faster speciation and reduced extinction in the tropics contribute to the mammalian latitudinal diversity gradient. *PLoS Biology* **12**, e1001775, doi:10.1371/journal.pbio.1001775 (2014).

20 Rohde, K. Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* **65**, 514–527, doi:10.2307/3545569 (1992).

21 Rogers, A. D. Evolution and biodiversity of Antarctic organisms: a molecular perspective. *Phil Trans R Soc B* **362**, 2191-2214, doi:10.1098/rstb.2006.1948 (2007).

22 Brey, T. *et al.* Do Antarctic benthic invertebrates show an extended level of eurybathy? *Antarct Sci* **8**, 3-6, doi:10.1017/S0954102096000028 (1996).

23 Clarke, A. & Crame, J. A. Evolutionary dynamics at high latitudes: speciation and extinction in polar marine faunas. *Phil Trans R Soc B* **365**, 3655–3666, doi:10.1098/rstb.2010.0270 (2010).

24 Thuy, B. *et al.* Ancient origin of the modern deep-sea fauna. *PLoS ONE* **7**, e46913, doi:10.1371/journal.pone.0046913 (2012).

25 Vinogradova, N. G. Vertical zonation in the distribution of deep-sea benthic fauna in the ocean. *Deep Sea Res* **8**, 245-250, doi:10.1016/0146-6313(61)90025-9 (1962).

26 Jenkyns, H. C. Geochemistry of Oceanic Anoxic Events. *Geochem Geophys* **11**, 1-30, doi:10.1029/2009GC002788 (2010).

27 McClain, C. R. & Hardy, S. M. The dynamics of biogeographic ranges in the deep sea. *Proc Roy Soc B* **277**, 3533-3546, doi:doi: 10.1098/rspb.2010.1057 (2010).

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Methods

Datasets. This study analysed distributional (occurrence) and phylogenetic data of ophiuroids (brittle stars). The global distributional dataset contains over 160,000 collection records, derived and validated from museum databases, the global OBIS database, and literature sources [6-8]. After discarding outliers, three-dimensional species ranges were created by interpolating between minimum/maximum latitudinal, longitudinal and bathymetric distributional extents. The deep sea is vast and incompletely sampled (Extended Data Fig. 1) so interpolation was required. We finally used species ranges rather than more complex species distributional (SDM) models as many phylogenetically important species did not have sufficient distribution records to train complex models.

In order to maximise the overlap between biogeographic and phylogenetic datasets while retaining a broad scope, the study area was constrained to marine environments from 70°S to 0°N and 0 to 4,000 m depth. Longitudinal limits were increased with every degree of latitude to ensure a linear latitudinal scale and equal cell areas symmetrical around 150°S, e.g. extending from 109-191°E at 0°S, 100-200°E at 35°S, and 34-267°E at 70°S (Extended Data Fig. 1a). A species or family was recorded as present in a cell if any location in a cell was within its known latitudinal, longitudinal and bathymetric range. This region includes 828 named species, of which 596 (72 %) were represented in the phylodiversity analyses. The number of species sequenced that occurred in each grid cell ranged from 41-94% (Extended Data Fig. 1c).

The phylogeny used here is an extension of the tree used by Bribiesca-Contreras et al. [28] and built using the same methodology [14,29]. Briefly, a RAxML (v8.1.20) [30] bootstrap consensus tree was inferred from a phylogenomic data matix of 265kb of exon data and the mitochondrial COI gene for 781 taxa, 708 of

which have both exon and COI and 73 with only COI data. This tree was then converted into an ultrametric chronogram using Penalized Likelihood Rate Smoothing (PLRS; r8s v7.3) [31] using 12 fossil based calibration points [14]. This methodology has been found to produce robust trees, broadly congruent with Bayesian (BEAST [32]) analyses of the same data, but with fewer computational constraints [14,29,33]. A subtree of 596 taxa from our study region (Fig. 2) was then pruned from this larger reference tree. A single tree was used because uncertainty in absolute age was not important to the analyses herein. We used a new phylogenetically-based taxonomic classification of the Ophiuroidea [14] to map major lineage (~110 mya) distribution patterns. These families form three approximately equal-sized clades (A, B and C) [14,33] each contributing to the overall pattern in varying ways (Fig. 2 and Extended Data Fig. 8).

Environmental plots (seafloor bathymetry, temperature (°C), salinity (‰), oxygen (ml/l), organic carbon flux (g/m^{2}year)) were derived following Woolley et al. [6]. Names of water masses are derived from Tomczak & Godfrey [34].

Phylodiversity analyses. Phylogenetic diversity (PD) calculations summed tree branch lengths for all taxa present in a grid cell [35]. Relative PD [36,37] was calculated by dividing observed PD by the mean from a null model, generated by randomising species present in each cell while retaining cell species richness (1,000 replicates). This index produces similar results to mean phylogenetic pairwise distance between species (MPD or Δ^+ [38,39] normalised by the mean distance among all species, Extended Data Fig. 3c). Evolutionary distinctness (ED) scales PD by the number of terminal lineages subtending the branch, thus measuring a species' contribution to the total evolutionary history of its clade [40,41]. However, this index is therefore sensitive to the presence of unknown cryptic species, which appear to be prevalent in the oceans [42]. Therefore, each lineage less than 10 my (4% of tree height) was counted as only one terminal for the purposes of calculating ED. We mapped the top 10% of species with the highest levels of ED [43]. The mean lineage diversification rate (Fig. 1d) [44] is the inverse of mean ED [41,43].

We calculated beta diversity (based on morpho species) and phylogenetic beta-diversity (based on phylogenetic branch lengths) [15] following Baselga [45] and Leprieur et al. [16]. For each pair of grid cells we calculated 1) β_{Sor} (Sorensen's dissimilarity index) and β_{Sim} (Simpson's dissimilarity index), and 2) their phylogenetic equivalents ($p\beta_{Sor}$, $p\beta_{Sim}$) for species on our tree. We analysed the resulting dissimilarity matrices in two ways, using 1) ordination and classification to identify spatial clusters of ophiuroid phylodiversity (Extended Data Fig. 9), and 2) a neighbourhood approach (comparing focal cells with their immediate latitudinal and bathymetric neighbours) to investigate fine scale turnover of beta diversity (Fig. 1f, Extended Data Fig. 3e-f). Non-parametric Multidimensional Scaling Ordination was performed using the R function metaMDS() in the 'vegan' v2.4-5 package [46]. Various agglomerative hierarchical and non-hierarchical clustering algorithms were trialled [47] as implemented in the R-package 'cluster' v2.0.1 [48], using mean silhouette scores to discriminate supported clusters.

For further phylogenetic diversification analyses, we defined phylo-regions (or biomes) based on a UPGMA (unweighted Pair-Group Method using arithmetic Averages) cluster analysis of the $p\beta_{Sim}$ dissimilarities, on the basis that it emphasised compositional change rather than species-richness gradients, produced well-supported geographically-cohesive groups, and reasonably reflected the neighbourhood turnover plot. We selected the five cluster solution (Fig. 1g) as a balance between the complexity of the study region and the requirements of multi-state phylogenetic models (see below), including the need to limit the number of parameters being estimated and reduce the unevenness in the numbers of species per state [49]. In particular, abyssal clusters were characterised by very low species richness and we used combined bathyal-abyssal biomes for subsequent analyses. Simpson's beta phylo diversity between biome faunas confirms the distinction between the tropical-temperate shallow water realm and the deep sea+Antarctic realm (Extended Data Fig. 10).

Multiple State Speciation and Extinction (MuSSE) models [50] were fitted across our phylogenetic tree to estimate speciation, extinction and transition rates associated with the five biomes. We used the R package 'diversitree' v0.9-10 [50] to report both Maximum Likelihood and Bayesian results (exponential prior, ML solution start, 10,000 MCMC sampled steps, 100 step burnin for chain tuning).

We corrected for incomplete sampling [51,52] by specifying the ratio of species in our tree to all known species for each phylo-region (Antarctica = 85%, temperate shallow = 80%, temperate deep= 80%, tropical shallow = 75%, and tropical deep= 70%). We assigned a single state to each species in the MuSSE analysis by selecting the biome with the maximum number of collection events for that species. We did not cater for multiple states per species, despite some of our species occurring in two (n=123) or three biome (n=2), because 1) current shared-state models (e.g. GeoSSE [53]) can only model two regions, and 2) the addition of multi-regional states to the MuSSE analysis would greatly increase the number of parameters being estimated. Instead, in order to test the robustness of our single biome state assignment, we compared the result against 100 trials of re-sampling species states according to their frequencies of occurrence in each region. These re-sampling rates essentially matched our single state assignment results, indicating its adequacy. As a final check we conducted 100 trials randomising the tree tip states. The lack of any correlation of these random to our observed results (mean Pearson correlation=0.05) further indicated the results were not merely a product of relative biome richness [51]. Results of these re-sampling and randomization analyses are summarized in Extended Data Table 4 and Extended Data Fig. 5.

Biome transition rates were further corroborated [49-52] through the use of ancestral state reconstructions generated from All Rates Determined (ARD) and Equal Rates (EQ) Maximum Likelihood models using the ace(type="discrete") function in the R package 'ape' v5 [54]. The number of cladogenetic biome transitions were calculated from 1,000 stochastic maps sampled from the ARD marginal state probabilities using the

R function make.simmap(Q="empirical") in the package phytools v0.6-44 [55]. For phylogenetic visualisations (Fig. 2), nodes were determined to be decisive if the ER state probability was >= 95%.

28 Bribiesca-Contreras, G., Verbruggen, H., Hugall, A. F. & O'Hara, T. D. The importance of offshore origination revealed through ophiuroid phylogenomics. *Proc Roy Soc B* **284**, 20170160, doi:10.1098/rspb.2017.0160 (2017).

29 Hugall, A. F., O'Hara, T. D., Hunjan, S., Nilsen, R. & Moussalli, A. An exon-capture system for the entire class Ophiuroidea. *Mol Biol Evol* **33**, 281–294, doi:10.1093/molbev/msv216 (2015).

30 Stamatakis, A. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* **22**, 2688-2690, doi:10.1093/bioinformatics/btl446 (2006).

31 Sanderson, M. J. R8s: inferring absolute rates of molecular evolution and divergence times in the absence of a molecular clock. *Bioinformatics* **19**, 301–302, doi:10.1093/bioinformatics/19.2.301 (2003).

32 Drummond, A. J. & Rambaut, A. BEAST:Bayesian evolutionary analysis by sampling trees. *BMC Evol Biol* **7**, 1–8, doi:10.1186/1471-2148-7-214 (2007).

33 O'Hara, T. D., Hugall, A. F., Thuy, B. & Moussalli, A. Phylogenomic resolution of the Class Ophiuroidea unlocks a global microfossil record. *Curr Biol* **24**, 1874-1879, doi:10.1016/j.cub.2014.06.060 (2014).

34 Tomczak, M. & Godfrey, J. S. *Regional Oceanography: An Introduction*. 2nd improved edition edn, (Daya Publishing House, 2003).

35 Faith, D. P. Conservation evaluation and phylogenetic diversity. *Biol Conserv* **61**, doi:10.1016/0006-3207(92)91201-3 (1992).

36 Davies, R. G. *et al.* Environmental predictors of global parrot (Aves: Psittaciformes) species richness and phylogenetic diversity. *Glob Ecol Biogeogr* **16**, 220-233, doi:10.1111/j.1466-8238.2007.00282.x (2007).

37 Webb, C. O., Ackerly, D. D., McPeek, M. A. & Donoghue, M. J. Phylogenies and Community Ecology. *Annu Rev Ecol Syst* **33**, 475-505, doi:10.1146/annurev.ecolsys.33.010802.150448 (2002).

38 Clarke, K. R. & Warwick, R. M. A taxonomic distinctness index and its statistical properties. *J Appl Ecol* **35**, 523-531, doi:10.1046/j.1365-2664.1998.3540523.x (1998).

39 Tucker, C. M. *et al.* A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biol Rev Camb Philos Soc* **92**, 698-715, doi:10.1111/brv.12252 (2017).

40 Vane-Wright, R. I., Humphries, C. J. & Williams, P. H. What to protect? Systematics and the agony of choice. *Biol Conserv* **55**, 235–254, doi:10.1016/0006-3207(91)90030-D (1991).

41 Jetz, W. *et al.* Global Distribution and Conservation of Evolutionary Distinctness in Birds. *Curr Biol* **24**, 919-930, doi:10.1016/j.cub.2014.03.011 (2014).

42 Miglietta, M. P., Faucci, A. & Santini, F. Speciation in the sea: Overview of the symposium and discussion of future directions. *Integr Comp Biol* **51**, 449-455, doi:10.1093/icb/icr024 (2011).

43 Isaac, N. J. B., Turvey, S. T., Collen, B., Waterman, C. & Baillie, J. E. M. Mammals on the EDGE: Conservation Priorities Based on Threat and Phylogeny. *PLoS ONE* **2**, e296, doi:10.1371/journal.pone.0000296 (2007).

44 Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. & Mooers, A. O. The global diversity of birds in space and time. *Nature* **491**, 444, doi:10.1038/nature11631 (2012).

45 Baselga, A. Partitioning the turnover and nestedness components of beta diversity. *Glob Ecol Biogeogr* **19**, 134-143, doi:10.1111/j.1466-8238.2009.00490.x (2010).

46 vegan: Community Ecology Package. R package version 2.3-5. http://CRAN.R-project.org/package=vegan (2016).

47 Kreft, H. & Jetz, W. A framework for delineating biogeographical regions based on species distributions. *J Biogeogr* **37**, 2029–2053, doi:10.1111/j.1365-2699.2010.02375.x (2010).

48 cluster: Cluster Analysis Basics and Extensions. R package version 2.0.1. (2015).

49 Davis, M. P., Midford, P. E. & Maddison, W. P. Exploring power and parameter estimation of the BiSSE method for analyzing species diversification. *BMC Evol Biol* **13**, 38, doi:10.1186/1471-2148-13-38 (2013).

50 FitzJohn, R. G. Diversitree: comparative phylogenetic analyses of diversification in R. *Methods Ecol Evol* **3**, 1084–1092, doi:10.1111/j.2041-210X.2012.00234.x (2012).

51 Rabosky, D. L. & Goldberg, E. E. Model inadequacy and mistaken inferences of trait-dependent speciation. *Syst Biol* **64**, 340-355, doi:10.1093/sysbio/syu131 (2015).

52 FitzJohn, R. G., Maddison, W. P. & Otto, S. P. Estimating trait-dependent speciation and extinction rates from incompletely resolved phylogenies. *Syst Biol* **58**, 595-611, doi:10.1093/sysbio/syp067 (2009).

53 Goldberg, E. E., Lancaster, L. T. & Ree, R. H. Phylogenetic Inference of Reciprocal Effects between Geographic Range Evolution and Diversification. *Syst Biol* **60**, 451-465, doi:10.1093/sysbio/syr046 (2011).

54 Paradis, E., Claude, J. & Strimmer, K. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, doi:10.1093/bioinformatics/btg412 (2004).

55 Revell, L. J. phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol Evol* **3**, 217-223, doi:10.1111/j.2041-210X.2011.00169.x (2012).

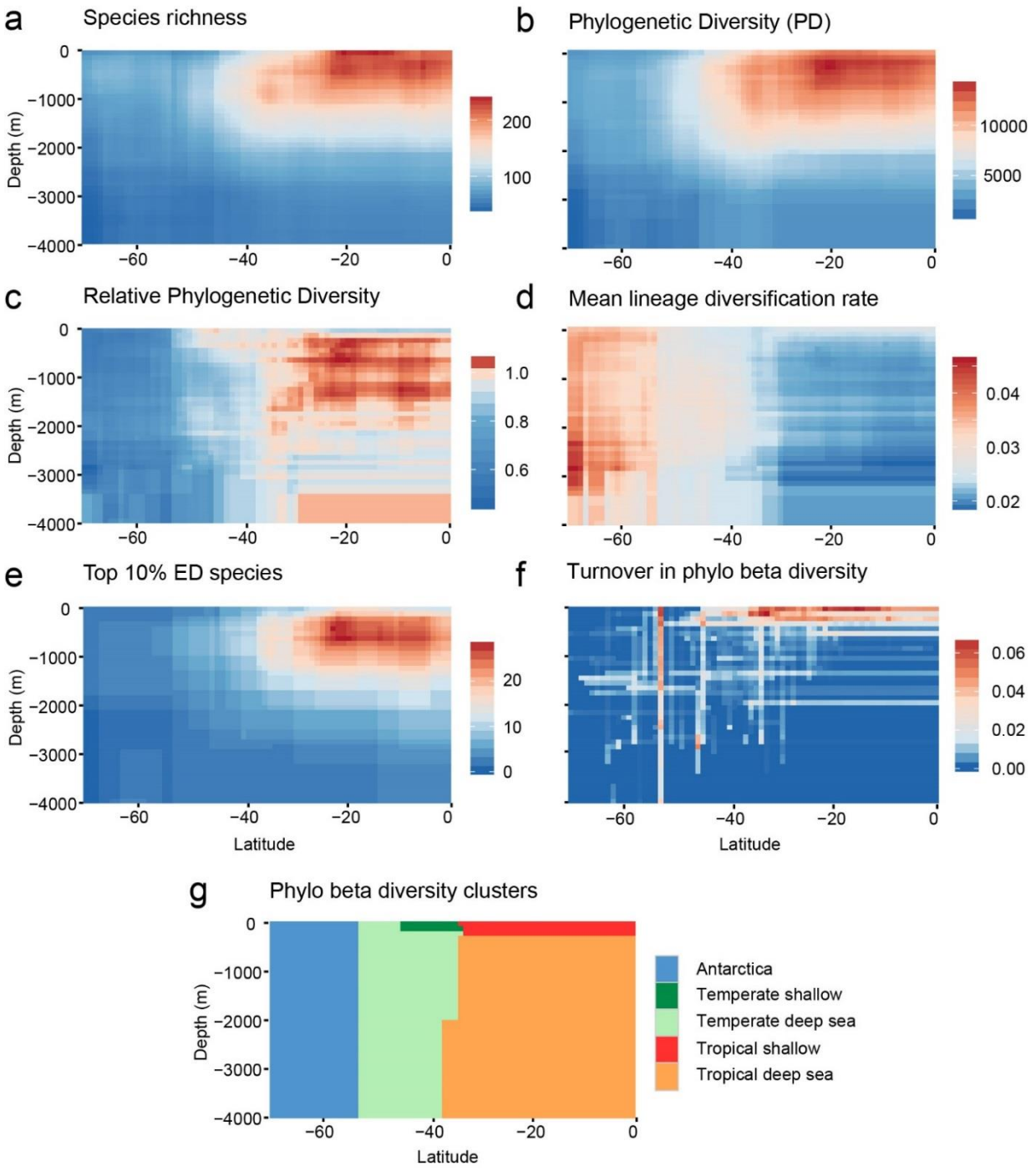


Figure 1 | **The shape of phylodiversity across the seafloor**. (a) Species richness is concentrated in tropical shallow water regions with a steep decline to Antarctica and the abyss. Phylogenetic metrics are all high at tropical latitudes, although they emphasise different aspects of evolutionary assembly with depth. (b) Total Phylogenetic Diversity (PD) peaks at upper bathyal depths. (c) Relative PD given species richness is high at mid bathyal depths and low in Antarctica and tropical shallows. (d) Mean lineage diversification rates are highest in Antarctica and the tropical shallows. (e) Numbers of species with the highest ED peaks in the tropical upper bathyal. (f) Turnover in Simpson's phylogenetic beta diversity (pB_{Sim}) between neighbouring cells is highest across depth in tropical shallow water and across latitudes between temperate and Antarctic latitudes. (g) Latitudinal/bathymetric representations of five clusters derived from pB_{Sim} dissimilarity coefficients.

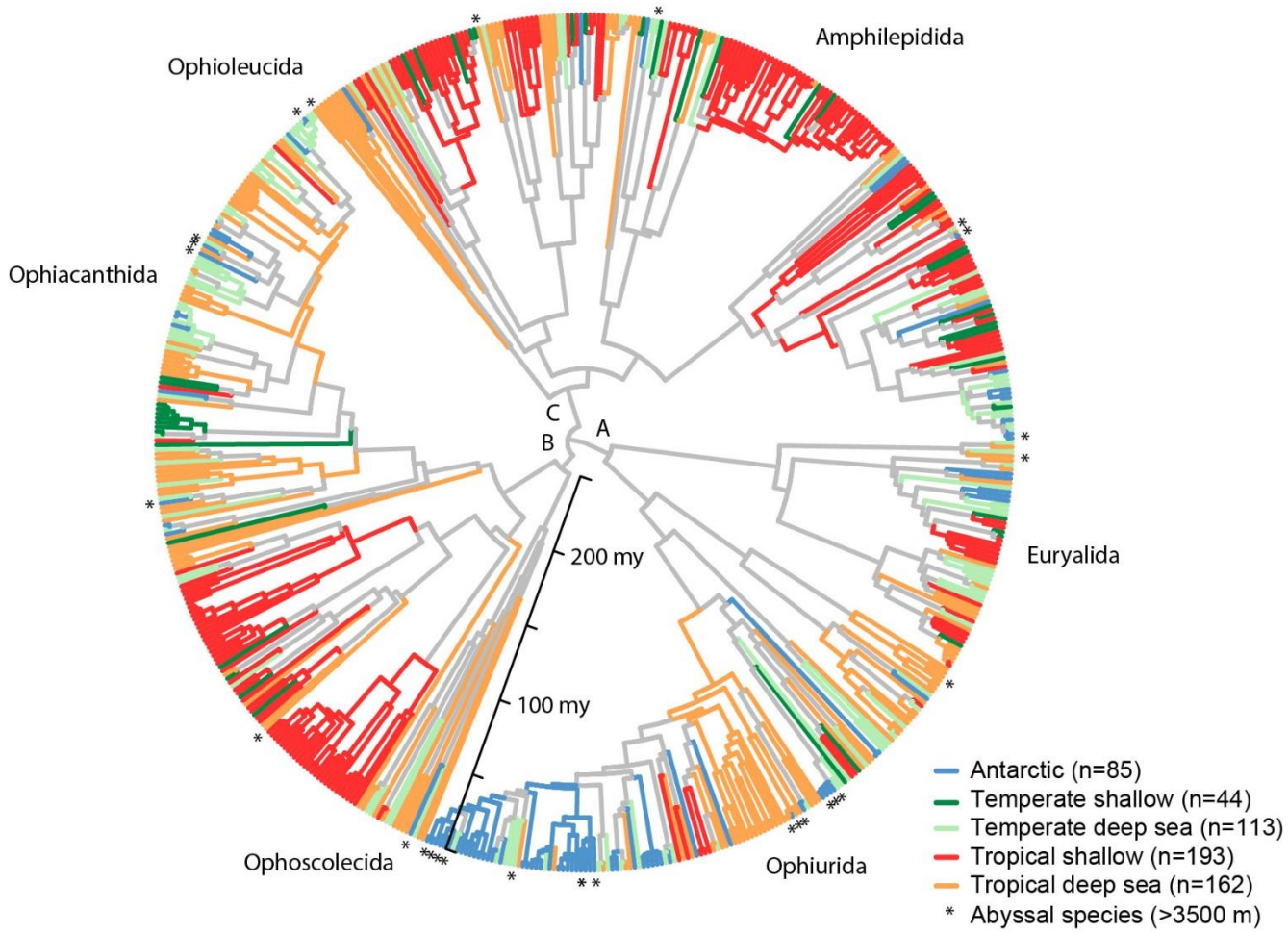


Figure 2 | **Biomes possess divergent phylogenetic signatures.** Maximum Likelihood ancestral state reconstruction shows lineages (n=596) from tropical shallow and Antarctic biomes are phylogenetically clustered compared to those in other biomes. Branch colours on the phylogenomic chronogram follow Fig. 1g, grey indicates indecisive nodes (<95% probability). The three primary clades (A-C) and six orders are indicated, and abyssal taxa marked by asterisk.

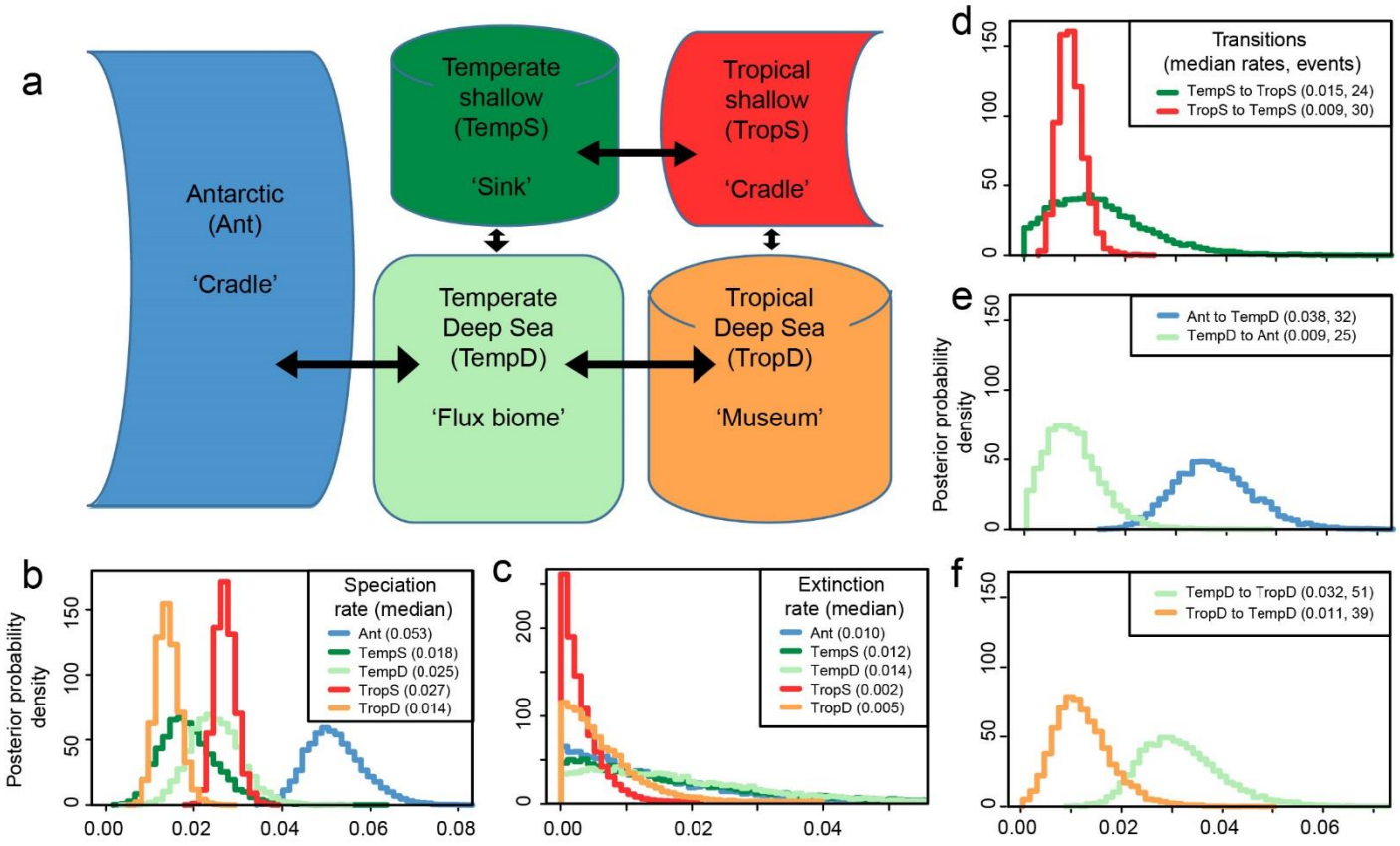
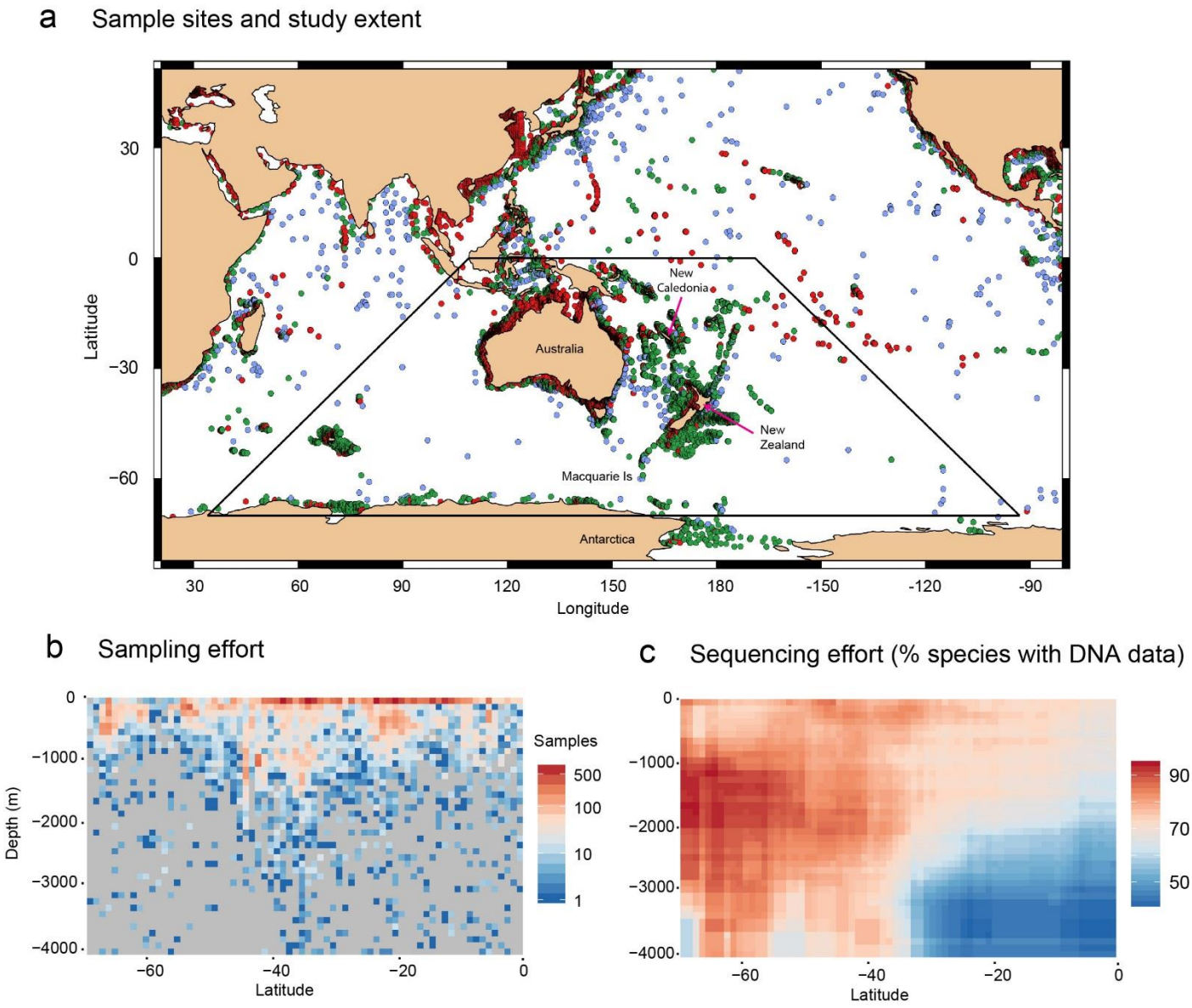
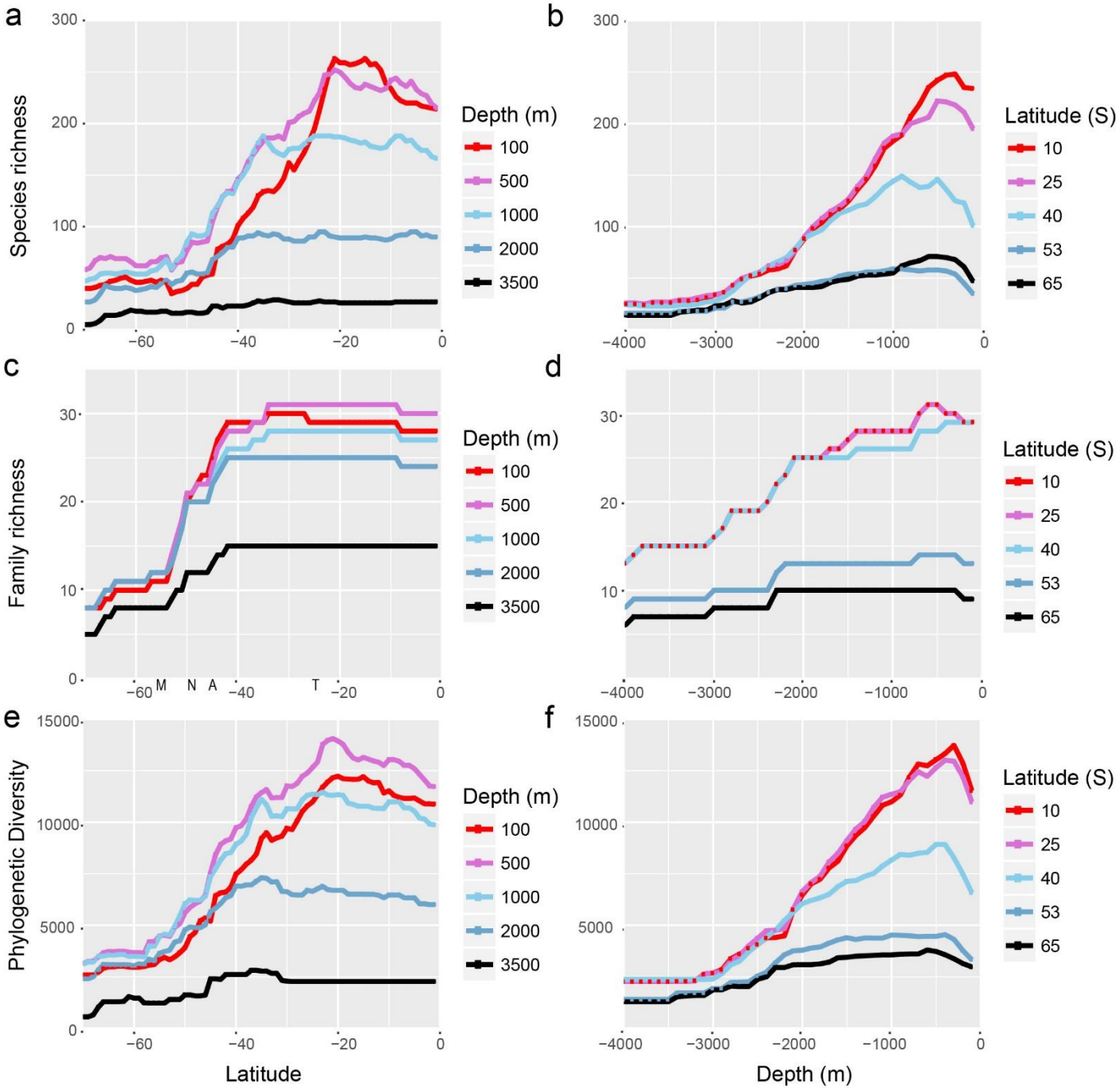


Figure 3 | **Distinct pathways of diversification and migration occur in shallow and deep seas** (a) Schematic of biome interactions from the MuSSE/ARD stochastic mapping analyses, showing the predominately latitudinal pattern of interchange (arrows scaled to the median number of stochastic map events), with Antarctica coupled to deep sea rather than shallow biomes. (b) Speciation rates are highest for the Antarctic biome and lowest for the tropical deep sea. (c) Extinction rates are elevated for temperate and Antarctic biomes and low for tropical ones, with negligible net diversification in temperate biomes. Net migration between neighbouring biomes is similar at shallow depths (d) but towards the tropics in the deep sea (e-f). See Extended Data Tables 4, 6 for full details.

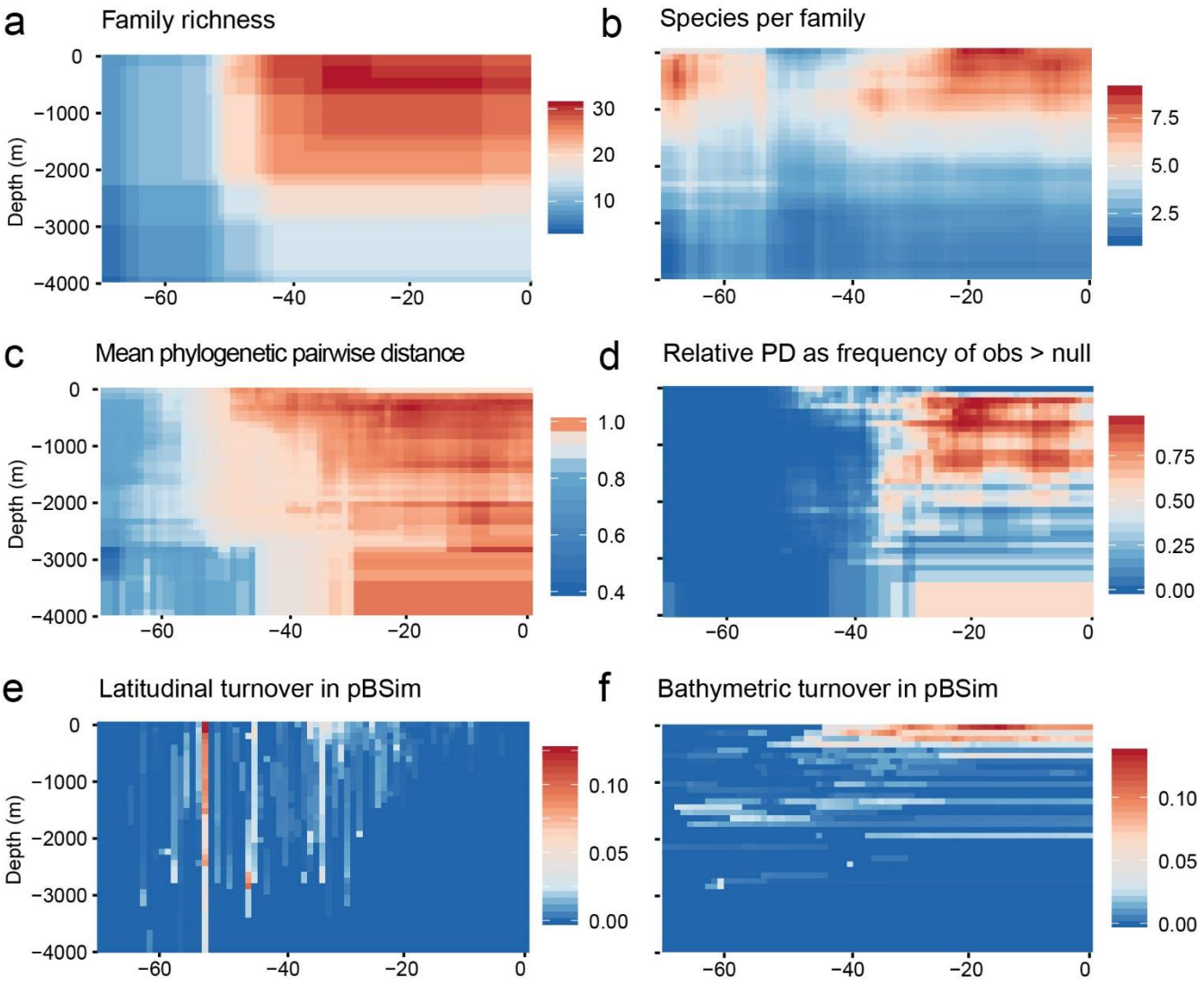
Extended Data



Extended Data Figure 1 | Maps and plots of collection and sequencing effort. (a) Map of sample sites across the study area. The study area, a trapezoid shape on this geographical projection, contains equal area polygons per latitude spaced either side of 150°S. Red dots indicate shallow sites (0-200 m), green are from the upper to mid bathyal (200-2000 m) and blue from the lower bathyal and abyss (>2000 m); many sites overlap. Sampling over our study area has been concentrated around continental margins with few expeditions to the abyssal plain or mid-ocean ridges. Collection effort (e.g. numbers of trawls, dredges, RoV collections) over our study area (b) was, as expected, highest in shallow water (0-100 m) followed by cells at upper to mid bathyal depths. Variation in collection effort does not explain the latitudinal gradient of species richness for this data [6]. Although, collection effort was much lower at lower bathyal and abyssal depths (2000-4000 m), this was offset by a general increase in size of observed species ranges with depth. Many abyssal ophiuroids were widespread across temperate and tropical latitudes. Percentage of species with DNA data (c) was high (>70 %) over the entire study area, except below 2000 m across tropical latitudes (mean 52 %, min 41 %). However, these depths are relatively species poor and sequencing effort across the entire tropical deep sea biome (as defined in Fig. 1g) exceeded 70 %.



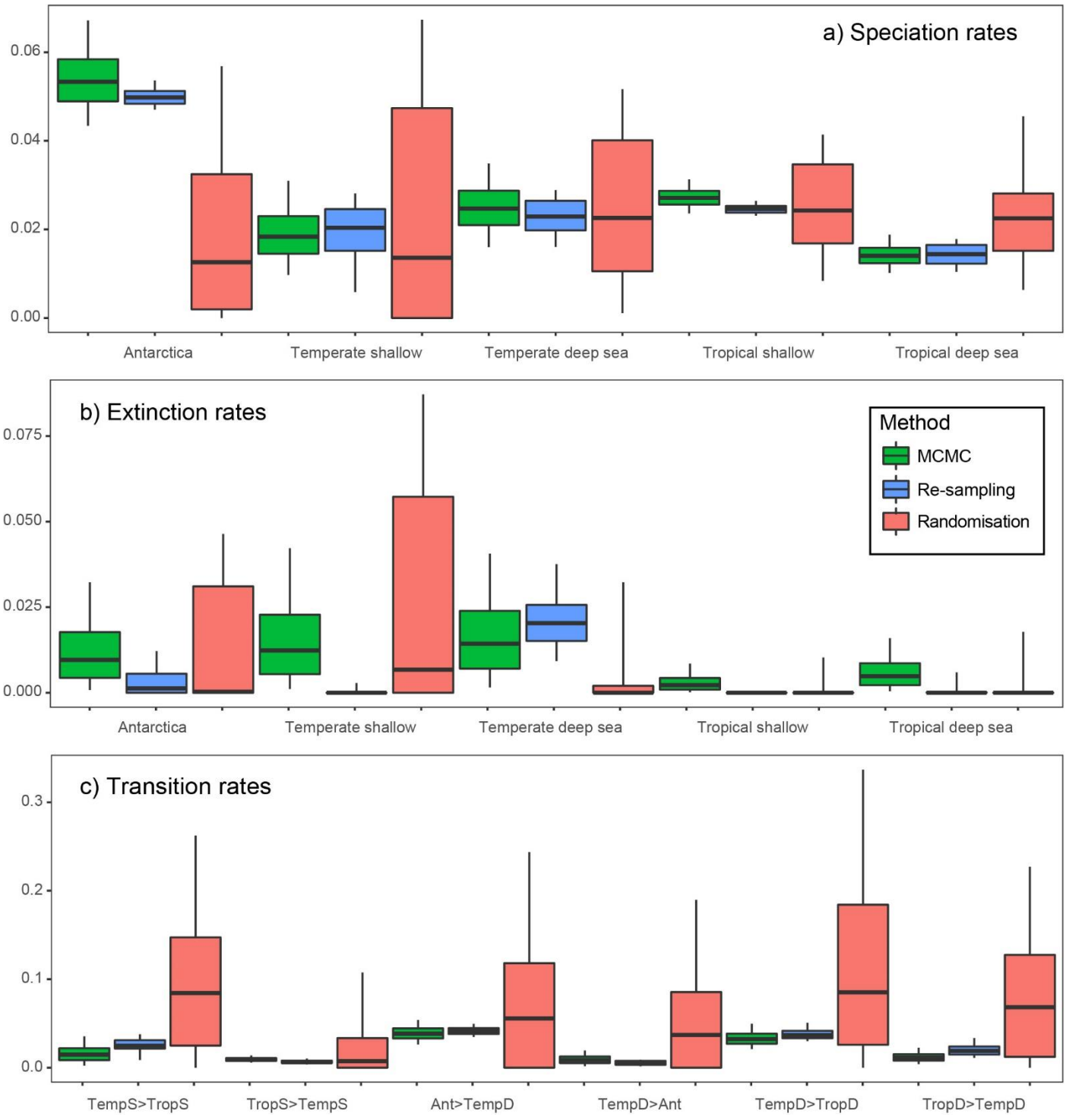
Extended Data Figure 2 | Latitudinal and Bathymetric gradients. Diversity peaks between 13 and 23°S and between 200 and 600 m depth, declining into polar regions and abyss. Reports (e.g. [5]) that the global ocean fauna exhibit a mid-bathyal species richness (2000 m) are based on a misreading of Vinogradova [25], who included only species occurring below 2000 m in her analysis of the abyssal decline in richness, thus generating an artificial peak of richness at 2000 m. T-Tropical-Temperate transition, A-end of Australian continental shelf, B-end of New Zealand continental shelf, M-Macquarie Island.



Extended Data Figure 3 | **Additional latitudinal/bathymetric plots of diversity indices.** (a) High levels of family-level richness extend into temperate regions and mid bathyal depths. Phylogenetic radiations (b) are concentrated in tropical shallow habitats and Antarctica. (c) Patterns of normalised mean phylogenetic pairwise distance between cells is similar to relative PD (Fig. 1c). (d) The frequency that observed PD exceeded null models that randomised species present in each cell while retaining cell species richness. Simpson's beta phylodiversity turnover (Fig. 1f) factored into latitudinal (e) and bathymetric (f) components.

Rate	Biome(s)	MuSSE rates: ML	MCMC median	Tip state re-sampling (n=100)	Tip randomisation (n=100)	Stochastic map events from ARD ML ancestral state model (n=1000): Mean	SD
Speciation	Antarctica (Ant)	0.050693	0.053309	0.049784	0.013245		
	Temperate shallow (TempS)	0.016091	0.018360	0.020361	0.013721		
	Temperate deep sea (TempD)	0.027735	0.024691	0.022906	0.022841		
	Tropical shallow (TropS)	0.025076	0.027110	0.024599	0.024398		
	Tropical deep sea (TropD)	0.012104	0.014036	0.014409	0.022491		
Extinction	Antarctica (Ant)	0.008355	0.009586	0.001280	0.000363		
	Temperate shallow (TempS)	0.000006	0.012346	0.000000	0.005197		
	Temperate deep sea (TempD)	0.016715	0.014348	0.020324	0.000000		
	Tropical shallow (TropS)	0.000000	0.002225	0.000000	0.000000		
	Tropical deep sea (TropD)	0.000924	0.004813	0.000001	0.000000		
Biome transition	Ant>TempS	0.000002	0.000923	0.000997	0.000000	0.7	0.8
	Ant>TempD	0.039868	0.038453	0.041098	0.052866	32.6	5.9
	Ant>TropS	0.000000	0.000942	0.000000	0.080543	0.4	0.7
	Ant>TropD	0.000003	0.002259	0.000000	0.091123	11.4	4.0
	TempS>Ant	0.000098	0.002101	0.001007	0.022291	2.2	1.2
	TempS>TempD	0.017291	0.012074	0.008190	0.038603	9.3	3.0
	TempS>TropS	0.017048	0.014675	0.024850	0.084110	24.3	6.1
	TempS>TropD	0.004020	0.006957	0.000001	0.074225	7.6	3.2
	TempD>Ant	0.008814	0.008677	0.005229	0.033824	24.1	4.1
	TempD>TempS	0.001091	0.001240	0.000406	0.002308	3.4	1.6
	TempD>TropS	0.002933	0.001606	0.000000	0.109594	4.1	2.0
	TempD>TropD	0.029547	0.032253	0.036919	0.084304	51.9	8.1
	TropS>Ant	0.000000	0.000299	0.000000	0.024469	1.3	1.0
	TropS>TempS	0.008712	0.009134	0.006551	0.008052	29.9	3.8
	TropS>TempD	0.000002	0.000725	0.000001	0.052294	7.4	2.6
	TropS>TropD	0.001751	0.001617	0.004036	0.173270	16.5	3.9
	TropD>Ant	0.002534	0.002803	0.002961	0.038863	9.2	2.7
	TropD>TempS	0.000592	0.001009	0.000001	0.004054	5.3	2.0
	TropD>TempD	0.010703	0.011255	0.019104	0.066857	39.2	6.0
	TropD>TropS	0.000851	0.001137	0.002733	0.195992	14.5	3.6
Log Likelihood (LnL)		-3473.45	-3399.53	-3484.50	-3755.13		

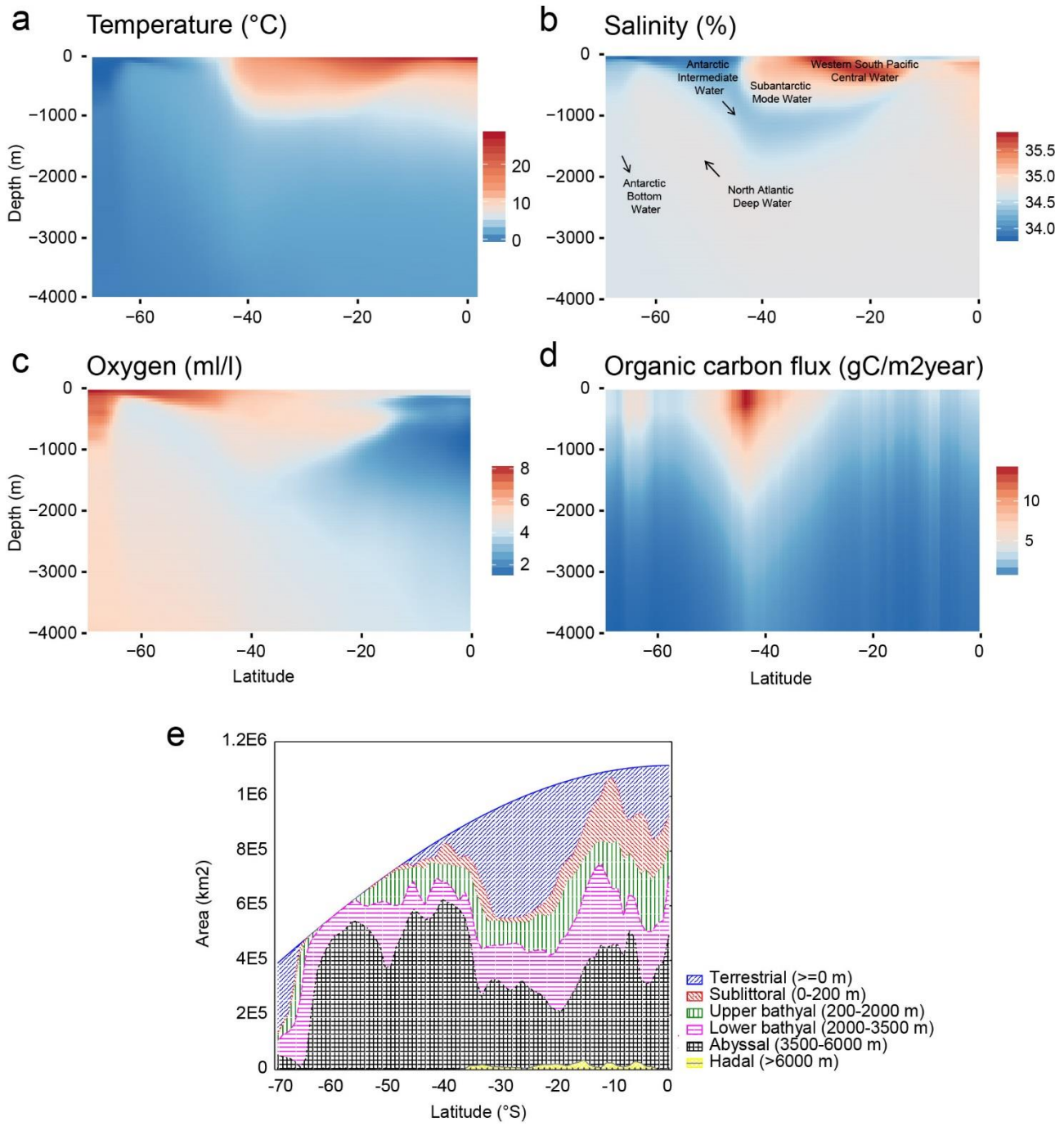
Extended Data Table 4 | MuSSE and stochastic map parameter estimates. MuSSE speciation, extinction and biome transition rates calculated from Maximum Likelihood (ML) and Bayesian (MCMC) methodologies for the entire dataset, and state resampling trials (ML median values), followed by mean and standard deviation of the number of cladogenetic transition events calculated from stochastic maps of marginal All Rates Determined (ARD) ML ancestral state reconstructions. Cells are ranked by colour (Red>White>Blue) independently for each column and rate type. Distributions of MuSSE rates are shown in Extended Data Fig. 5. The rank order of speciation, extinction and transition rates were broadly similar for both Maximum Likelihood (ML) and Bayesian MuSSE methodologies. However, ML extinction rates were considerably lower than the MCMC equivalents, probably due to their wide confidence intervals.



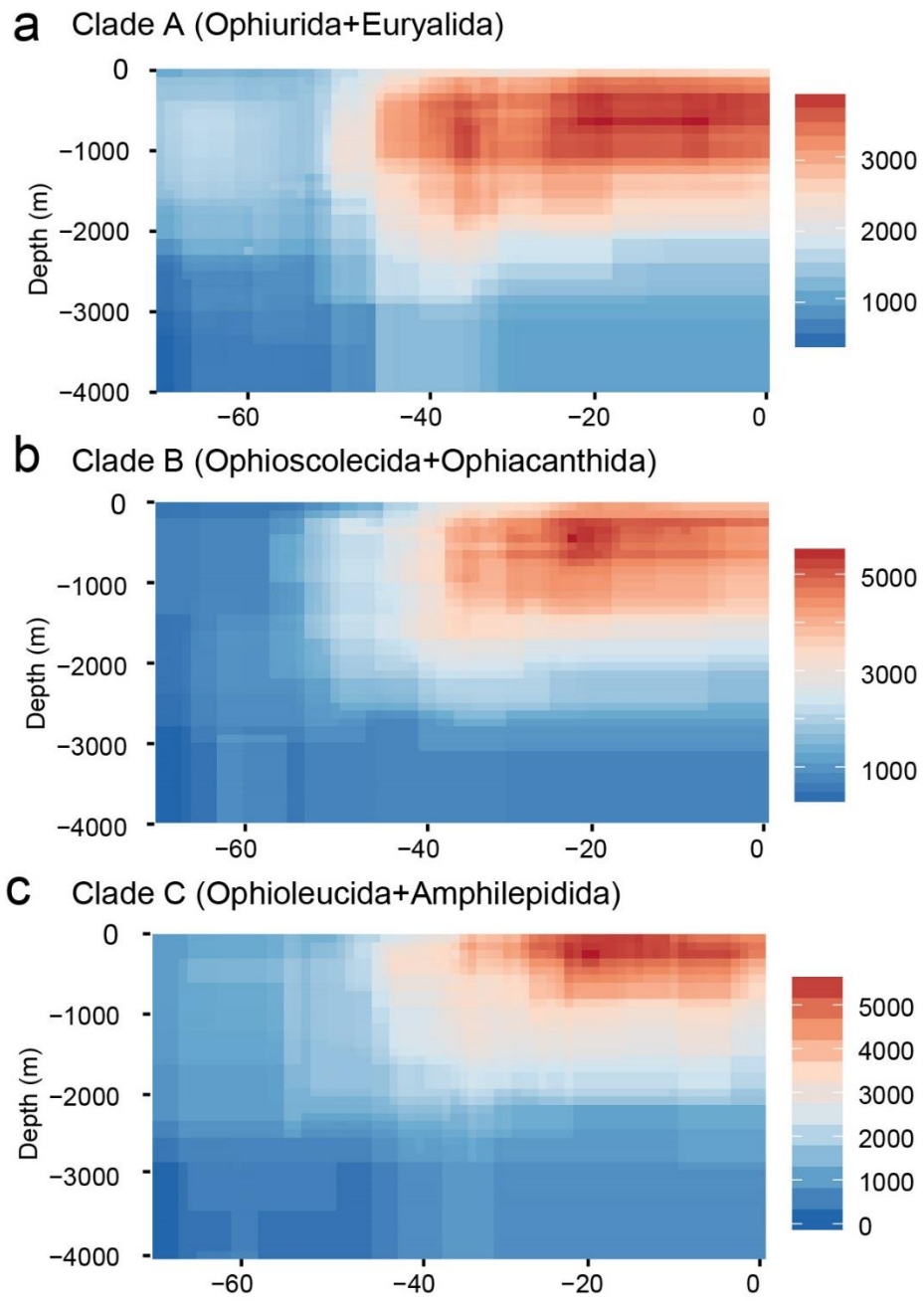
Extended Data Figure 5 | MuSSE randomisation trials. Comparison of (a) speciation, (b) extinction and (c) transition rates generated from our MuSSE Bayesian MCMC analysis compared to ML analyses that i) resampled states (biomes) within species with multi-biome distributions, and ii) randomised tip states while retaining biome richness. The re-sampling results are broadly similar to the original MCMC run, indicating biome misclassification did not significantly affect the results. One exception is the Temperate shallow (TempS) to tropical shallow (TropS) transition rates, which were significantly different for re-sampling due the occurrence of subtropical species across the transition zone. Tip state randomisation produced wide confidence limits as expected, indicating that the results were not merely a product of relative biome richness or chance association.

Parameter significance tests	MuSSE MCMC rate	ARD stochastic mapping events
Antarctic with highest speciation rate	0.9978	-
Ant>TempB greater than TempB>Ant	1.0000	0.860
TempD>TropD greater than TropD>TempD	0.9980	0.879
TropS>TempS greater than TempS>TropS	0.2683	0.771

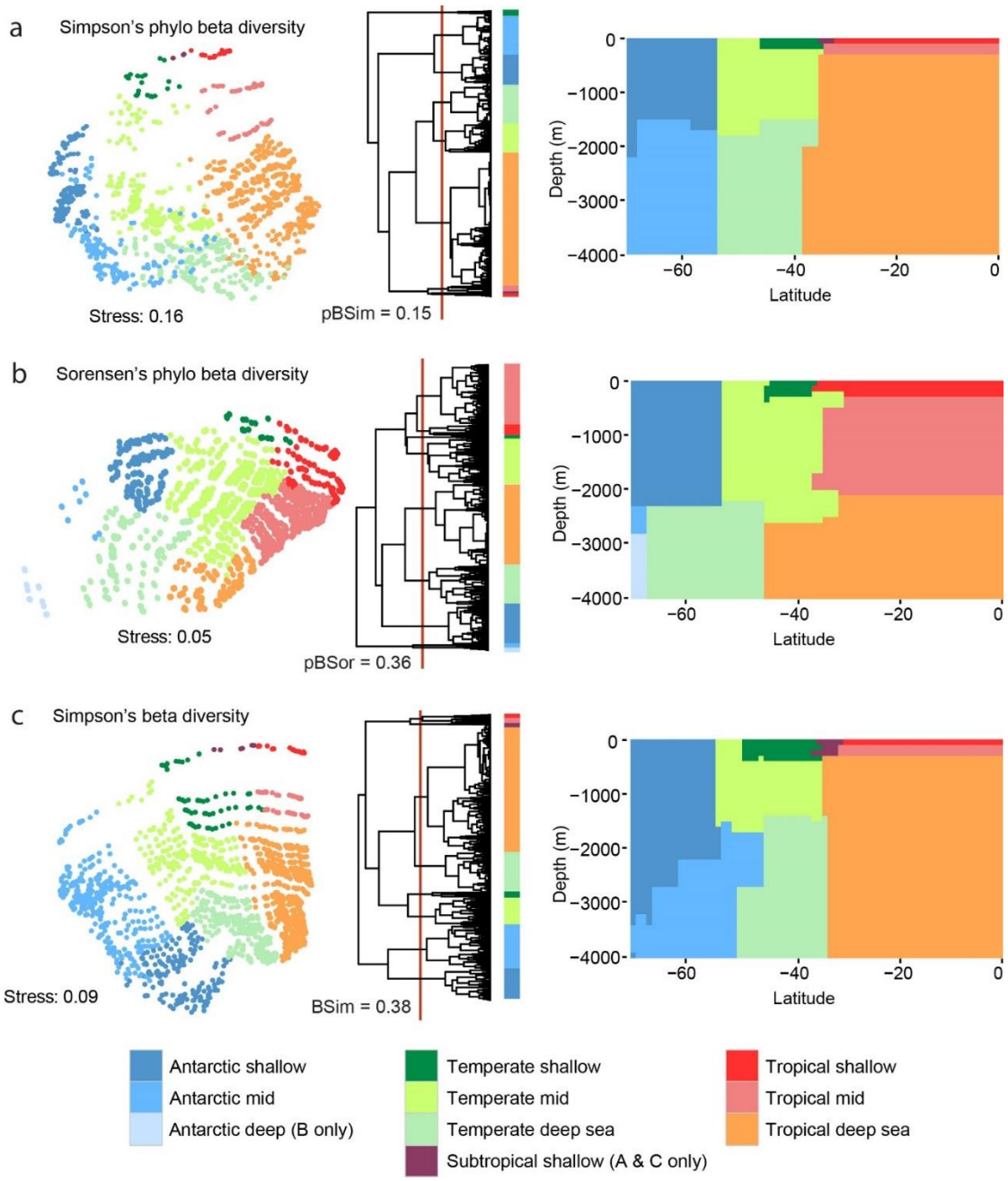
Extended Data Table 6 | Comparison of selected parameters from both the set of 10,000 MuSSE MCMC steps and number of events from 1,000 All Rates Determined stochastic maps. The Antarctic biome had significantly higher speciation rate than the other four biomes. In the deep sea, the net transition across the three biomes (Antarctica to temperate deep sea to tropical deep sea) was from south to north. In shallow water, although the number of north to south events were generally higher, the rates were lower reflecting inequality in species richness; the direction of transition was not significant at α=0.05.



Extended Data Figure 7 | Environmental patterns. Mean annual environmental data (a-d) for each latitudinal (1.0°) and bathymetric (100 m) cell across our study area for comparison with phylodiversity analyses. A lens of relatively hot (a) salty (b) water occurs at shallow depths across tropical and temperate latitudes (0-40°S). Antarctic Intermediate Water sinks at subantarctic latitudes and flows north to subtropical latitudes (20°S) at mid-bathyal depths (~1000 m). Deoxygenated (c) 'deep' water flows southwards from the northern hemisphere at lower bathyal depths, shoaling off the Antarctic continent. Cold dense oxygen-rich 'bottom' water sinks near Antarctica, flowing northwards at abyssal depths. Yearly net primary production (d) peaks at temperate latitudes over the study area, driving elevated carbon flux to the seafloor; Antarctic production is highly seasonal. Area of depth strata per degree of latitude across the study region (e), calculated by counting the number of cells of each category for each degree of latitude in the ETOPO1 raster GIS layer (0.01º resolution) and adjusting for the reducing circumference of the Earth with increased latitude. There is limited terrestrial, sublittoral and upper bathyal habitat in the Southern Ocean between the Australian/New Zealand continental masses and Antarctica.



Extended Data Figure 8 | P**hylodiversity plots of ophiuroid subclades.** The three major clades of extant Ophiuroidea (following O'Hara et al. [14,33]) contribute differently to overall patterns of phylogenetic diversity (PD) across our five biomes (Fig. 2). (a) Clade A is rich in deep-sea and Antarctic species, although individual families had divergent distributions. The Antarctic is dominated by the Ophiopyrgidae while the Ophiomusaidae, Ophiosphalmidae, Astrophytidae and Euryalidae are largely absent from there. Clade A has low species richness in the two shallow water biomes. (b) Clade B is rich in the tropical shallow, tropical deep sea and temperate deep sea biomes. It consists of one suborder (Ophiodermatina) that is heavily represented in tropical shallow water biome and another (Ophiacanthina) that is largely present in deep sea habitats, particularly on hard substrata such as seamounts. (c) Clade C on the other hand is rich in tropical and temperate shallow water biomes, including the families Ophiolepididae, Ophionereididae, Amphiuridae and Ophiotrichidae, and has relatively few lineages in the deep sea or Antarctica.

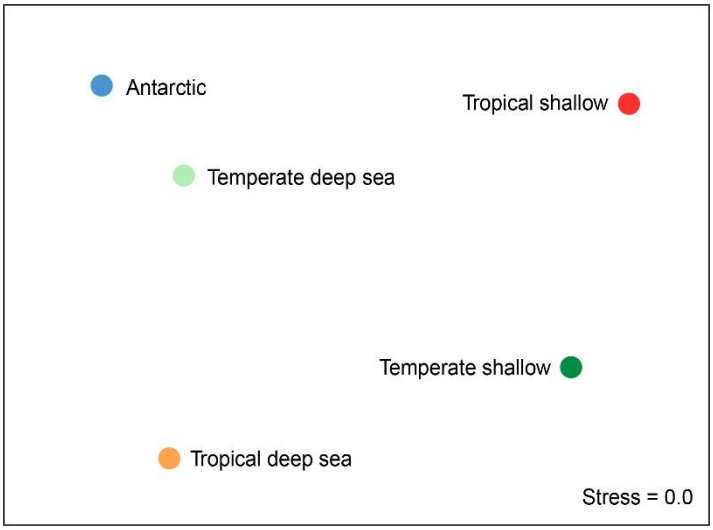


Extended Data Figure 9 | Beta diversity and phylo beta diversity. Ordinations (nMDS), cluster dendrograms (UPGMA) and Latitudinal/bathymetric representations of (phylo) beta diversity clusters for each 1.0° latitude x 100 m depth cell across our study region. (a) Simpson's phylo beta diversity (pB_{Sim}), (b) Sorensen's phylo beta diversity (pB_{Sor}), and (c) Simpson's beta-diversity of presence-absence of species (B_{Sim}). Nine clusters (vertical red lines) are coloured to highlight coherent patterns across latitude and depth. The three methods showed broad similarities in grouping the fauna into tropical, temperate and polar regions and sublittoral, upper bathyal, and lower bathyal/abyssal depth strata, although the cluster hierarchy can differ. The pB_{Sim} and B_{Sim} plots emphasised the strong compositional turnover between 100-300 m at tropical and temperate latitudes (Fig. 1f, ED Fig. 2e). pB_{Sor}, which emphasises species richness gradients in addition to compositional turnover, clustered upper bathyal cells (200-2000 m) separately from those in the lower bathyal/abyss (>~2000 m), reflecting a zone of higher species richness and relative PD (Fig. 1). The pB_{Sim} and B_{Sim} analyses also identified a small shallow water subtropical cluster reflecting the heightened latitudinal turnover between 30-40°S [7]. The pB_{Sor} analysis separated two species poor Antarctic deep-sea regions. The extent of the temperate sublittoral zone varied among analyses, possibly due to it being a small zone of admixture and turnover. The number of clusters was reduced to five (Fig. 1g) for the MuSSE analyses (see methods for rationale).

a

	Antarctica	Temperate shallow	Temperate deep sea	Tropical shallow
Temperate shallow	0.746			
Temperate deep sea	0.392	0.595		
Tropical shallow	0.709	0.394	0.668	
Tropical deep sea	0.491	0.541	0.475	0.770

b



Extended Data Figure 10 | Simpson's phylo beta diversity (pB_{Sim}) between biome faunas. (a) pB_{Sim} results, and (b) a resulting non-parametric MDS. Both the tropical/temperate shallow water biomes and the Antarctic/tropical deep sea/temperate deep sea biomes are compositionally similar (i.e. with low values of pB_{Sim}), consistent with the MuSSE and ARD stochastic map biome transition results (Fig. 3 and Extended Data Table 4).