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Biogeography of polychaete worms (Annelida) of the world

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ABSTRACT: The global biogeography of polychaete worms has never been assessed previously. In the present study, we studied the world distribution patterns of polychaetes based on datasets obtained from the Global Biodiversity Information Facility, the Ocean Biogeographic Information System, and the authors' recently published checklist of Indonesian polychaete species. Polychaete biogeographic regions were visualized using 'Infomap Bioregions', and the latitudinal species richness gradient was examined using three metrics, i.e. alpha, gamma and estimated species richness (the last metric was adjusted for sampling bias). We identified 11 major polychaete biogeographic regions. The North Atlantic, Australia and Indonesia were the top three species-rich biogeographic regions in the world. The total polychaete species was higher in the southern hemisphere (about 2100 species, 67 families) than in the northern one (about 1800 species, 75 families) despite significantly more data in the latter (over 500,000 records compared to over 26,000 records). Contrary to the classical idea of a unimodal distribution pattern, the latitudinal gradient of polychaetes was generally bimodal with a pronounced dip north of the Equator (15° N). We suggest the slightly higher peak of species richness in the southern (30° S) than northern (60° N) hemispheres reflects higher southern endemisms. These patterns are unlikely to be due to sampling bias but rather a natural phenomenon, and we found them most significantly correlated with sea temperature.

KEY WORDS: Biodiversity, endemism, global distribution, latitudinal diversity gradient, Polychaeta

1. INTRODUCTION

Understanding of the world's biodiversity requires biogeographic knowledge, i.e. why species occur where they do. Identifying biogeographic regions, i.e. areas of endemism, is thus the first step in protecting areas with high biodiversity and endemism.

Historically, the first biogeographic schema focused on terrestrial fauna (mainly vertebrate species) such as those of Sclater (1858) and Wallace (1876). Wallace's Line is one of the oldest boundaries in biogeography and divides the Asian from the Australian fauna (Wallace 1860). In the marine realm, the evidence for biogeographic boundaries was first considered unclear (e.g. Ekman 1953, Briggs 1974). However, Spalding et al. (2007) proposed 12 coastal realms

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1 based on expert opinion, and more recently Costello et al. (2017) published a map of 18 and 12
2 coastal and offshore realms of the world based on species distribution data analysis.

3 The latitudinal distribution of the world's species was generally believed to show a unimodal
4 pattern, whereby species richness increases from the polar to tropical regions with a peak
5 around the Equator (e.g. Kaufman 1995, Gaston 2000). As latitude is strongly correlated with
6 temperature, temperature-driven hypotheses have been proposed to explain the underlying
7 mechanisms behind these patterns, including *the species-energy hypothesis*, which asserts that
8 faster metabolic and speciation rates in warmer temperatures have contributed to higher species
9 numbers in the tropics (e.g. Kaspari et al. 2004), and *the species-productivity hypothesis*, which
10 states that greater primary productivity has supported more individuals in the tropics (e.g.
11 Rosenzweig 1995, Chase & Leibold 2002).

12 Contrary to the classical unimodal paradigm, Chaudhary et al. (2016) found the latitudinal
13 gradient of marine species richness to be bimodal with a dip around the Equator. The pattern
14 was considered due to sampling bias by Fernandez & Marques (2017) and Menegotto & Rangel
15 (2018). However, Chaudhary et al. (2017) used a rarefied species richness estimator to show
16 that the pattern was unlikely to be due to sampling bias. The latitudinal diversity gradient
17 pattern, in fact, can vary between taxa. Razor clams (Mollusca), for example, shows a strong
18 bimodal pattern (Saeedi et al. 2017), whereas the pattern for planktonic radiolarians appears to
19 be unimodal (Boltovskoy & Correa 2016, 2017).

20 Polychaete worms (phylum Annelida, class Polychaeta) are ubiquitous in virtually all marine
21 and estuarine habitats, at all latitudes, and from the supra-littoral to abyssal waters. They
22 typically dominate macrofaunal assemblages in sedimentary environments, representing 25-
23 63% of all species and 39-73% of all individuals (Hutchings 1998). The group also has a high
24 tolerance towards extremes of temperature, salinity and oxygen availability. Some species
25 occur near hydrothermal vents with extremely high temperatures and low available oxygen

1 (McHugh & Tunnicliffe 1994), and others occur in fresh or near-fresh waters (Glasby & Timm
2 2008).

3 Since the middle of the 18th century, about 11,500 polychaete species (about 1400 genera,
4 85 families) have been described and accepted (Pamungkas et al. 2019). Over this period,
5 numerous marine expeditions and investigations have been carried out at regional scales. Many
6 polychaete datasets generated from these studies have been archived in the Global Biodiversity
7 Information Facility (GBIF) and Ocean Biogeographic Information System (OBIS). Despite
8 the availability of these datasets, the global biogeography of polychaetes has never been
9 assessed. In this paper, we investigate the geographic world distribution of polychaetes,
10 including regions of endemism and latitudinal diversity gradient patterns, identify gaps in the
11 distributional data, and compare our findings with those of other marine groups. We thus test
12 whether or not the geographic world distribution of the taxon is similar to that of all marine
13 taxa together as studied by Costello et al. (2017). Also, we ask whether polychaetes, like many
14 other marine organisms, show the classical unimodal diversity gradient pattern with peak
15 species richness at the Equator, as suggested by the taxon-limited polychaete study of
16 Giangrande & Licciano (2004). In addition, we determine the primary environmental variables
17 responsible for shaping polychaete distributional patterns and species richness.

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2. MATERIALS & METHODS

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2.1. Dataset collection and quality control

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The datasets used in the present study were primarily obtained from GBIF and OBIS,
downloaded on 10 June 2018 (Ref. S1). In addition to these, we added Indonesian polychaete
records published in Pamungkas & Glasby (2019) as most records in that geographic region
were not in GBIF and OBIS (records uploaded to OBIS Indonesia at
http://obis.lipi.go.id:8080/ipt/resource?r=polychaeta_pamungkas_2019). Each dataset from

1 GBIF and OBIS was first prepared by removing records without a species name or
2 geocoordinates. To ensure the use of data with high coordinate accuracy, we omitted records
3 without coordinate uncertainty or with coordinate uncertainty of more than 10 km. This 10 km
4 figure is a compromise between retaining existing record accuracy (most records have less than
5 1 km of coordinate uncertainty), recognizing small islands, and keeping each record within one
6 degree of latitude, i.e. about 111 km. Duplicated records with the same species name, latitude
7 and longitude, depth and collection date, were also removed (Tables S1 & S2). Both datasets
8 were then merged, and duplicates between the two datasets were removed (Table S3). World
9 Register of Marine Species (WoRMS) was used as a basis for the higher classification and, to
10 reconcile synonyms and misspellings, the nomenclature of polychaete species names was
11 verified using ‘Taxon match’ (datasets with invalid species names were only used after the
12 names were corrected). The final dataset used for analyses in this study is available at
13 https://auckland.figshare.com/articles/dataset/Global_polychaete_data_csv/12401993.

14

15 **2.2. Polychaete biogeographic regions and indicator species**

16 All polychaete occurrence records were mapped using ArcGIS version 10.4.1. Records that
17 were mapped inland were either corrected (based on the locality information given in the
18 dataset) or removed (if no locality information was given). The interactive web application
19 ‘Infomap Bioregions’ (<http://bioregions.mapequation.org>) was then used to identify polychaete
20 biogeographic regions objectively based on latitude-longitude coordinates for all species
21 records (Edler et al. 2016). The analysis was run with the following settings: for the spatial
22 resolution, we used grid cells of 4° to reflect spatial differences in data density – the maximum
23 and the minimum cell capacities were set to 100 and 50 occurrence records, respectively; and
24 for the clustering algorithm, we set the numbers of trials and cluster cost to 1 and 1.5,
25 respectively, to identify major polychaete biogeographic regions. ‘Infomap Bioregions’ uses

1 neural network theory to map the similarity of cells based on their species composition. In doing
2 so, it identified the most common and indicative polychaete species in each biogeographic
3 region. Because we focussed on major biogeographic regions only, we made no attempt to
4 recognize any hierarchy among the regions (e.g. realms, provinces etc.), and isolated cells were
5 removed. In addition, we calculated the percentage of endemic polychaete species in each
6 region.

7

8

2.3. Analyses

9 Following the methods of Chaudhary et al. (2017), the latitudinal gradient was examined
10 using three metrics, i.e. alpha, gamma and estimated species richness. As alpha and gamma
11 species richness were biased by uneven numbers of records between latitudinal bands (Fig. S1),
12 we performed the rarefaction method of Hurlbert (1971) in R version 3.5.3 (R Core Team,
13 2013) using the ‘vegan’ package (Table S4). The analysis calculated the expected number of
14 species in each 5° latitudinal band per repeatedly sampled 50 occurrence records, i.e. the so-
15 called E(S50). The equation used was:

16

$$E(S_n) = \sum_i [1 - (N - N_i)^n / N^n]$$

17 where **E(S_n)** is defined as the expected number of species in a sample of (**n**) records, selected
18 randomly from a sample containing (**N**) records and (**S**) species. E(S50) was much less biased
19 by sampling effort (Fig. S1). We then ran a Generalised Additive Model (GAM) using R (Table
20 S5) to define the best non-linear model fitting the latitudinal gradients in species richness
21 (Hastie & Tibshirani 1990), i.e. whether it shows a uni-, bi- or multimodal pattern.

22 We investigated a range of environmental variables shown by previous studies (Smith et al.)
23 to be correlated with taxon occurrences, i.e. sea surface and bottom temperatures, salinity,
24 primary productivity, particulate organic carbon, depth, slope, distance from land and sea-to-
25 land ratio. Environmental datasets were downloaded on 6 November 2019 from the Global

1 Marine Environment Datasets (GMED) (Basher et al. 2018) and analysed using MATLAB
2 R2018. Using the non-parametric Spearman rank correlation analysis, we correlated E(S50)
3 and E(S30) values with a number of environmental variables for each 5° latitudinal band and
4 5° cell, respectively.

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6

3. RESULTS

7

3.1. Geographical distribution

8 Most polychaete species records, i.e. over 75%, were coastal (Fig. 1) and within 2.5 km of
9 land (Fig. 2); this, in part, is likely related to greater accessibility of coastal area for sampling.
10 Consequently, fewer species were found in latitudinal bands with a higher sea-to-land ratio,
11 reflecting the lesser coastal area (Fig. S2). The number of species tended to decline with depth
12 (Fig. 2). The coasts of some temperate and subtropical regions, i.e. Europe, Australia and New
13 Zealand, had the most species records. In the tropics, most species records were centred in
14 Indonesia, and in polar waters more occurred in the Antarctic than Arctic (Fig. 1). Of all
15 polychaete families, spionids had the most records (over 62,000 records), followed by serpulids
16 and terebellids with over 28,000 records each (Table S6).

17 We identified 11 major polychaete biogeographic regions (Fig. 1). Regions with the most
18 polychaete species records were, in order, the North Atlantic (including eastern and western
19 parts of Mediterranean Sea), Australia and Indonesia, whereas regions with the least species
20 records were the eastern Pacific Ocean, Caribbean Sea and Atlantic Ocean (Table 1). Despite
21 being the region with the most polychaete species, the North Atlantic had the lowest indicative
22 species score (1), whereas Indonesia had the highest indicative species score (291) (Table 1).
23 These scores mean that the indicative species of the North Atlantic have the same frequency of
24 occurrence there as in other regions, whereas those of Indonesia are 291 times more frequent in
25 this biogeographic region than in other regions (the species of Indonesia are, as a whole, far

1 more distinctive than those of the North Atlantic). Of the 11 biogeographic regions, seven
2 regions had more than 50% endemism of polychaete species (Table 1). The eastern part of the
3 Pacific Ocean and the Central Mediterranean Sea had the highest (100%) and the lowest (5%)
4 percentage of endemic polychaete species, respectively (Table 1) (here, we define ‘endemic
5 species’ as species unique to a biogeographic region as defined in this study).

6 **3.2. Latitudinal distribution**

7 The analysis of over 550,000 cleaned polychaete occurrence records (3415 species, 77
8 families) (Tables S3 & S6) showed significantly more records in the northern (over 500,000
9 records) than the southern hemisphere (over 26,000 records) (Fig. 3A). Similarly, the average
10 number of polychaete species, including the data variance, was generally higher in the northern
11 than the southern hemisphere (Fig. 3A). However, the total number of species was higher in the
12 southern (about 2100 species, 67 families) than the northern (about 1800 species, 75 families)
13 hemisphere (Fig. 3B). A similar pattern of slightly higher species numbers in the southern
14 hemisphere was also observed for each of the two subclasses (i.e. Errantia and Sedentaria),
15 although Sedentaria appeared to be relatively less speciose than Errantia between 5° N and 10°
16 S (Fig. 3C).

17 The latitudinal gradient of alpha species richness (average per latitudinal band) was bimodal
18 and much higher in the northern than southern hemisphere (Figs 3A & 4A). Gamma (total)
19 species richness for all errant and sedentary species was more symmetrically bimodal with a
20 peak at around 55°N and slightly higher one at 35°S, and a dip north of the Equator between
21 15°N and 30°N (Figs 3B, C & 4B). We found that both alpha and gamma species richness were
22 highly correlated ($p < 0.0001$) with the number of occurrence records (Fig. S1), suggesting that
23 the pattern was driven by uneven sampling effort. Although E(S50) was also correlated with
24 the number of records (Fig. S1), it was far less so ($p \leq 0.01$). Nevertheless, our rarefaction
25 analysis, which adjusted for the uneven sampling effort across latitudinal bands, found that the

1 latitudinal species richness gradient of polychaetes, i.e. the E(S50), remained bimodal with the
2 peaks at around 60°N and 30°S, and a dip at around 15°N (Fig. 3D). Supporting this, our GAM
3 also showed the pattern to be bimodal (Fig. 4C). This further indicates that the bimodality is
4 unlikely to be due to sampling bias, and that the southern hemisphere has higher species
5 richness than the northern one.

6 There were significant correlations between the E(S30) and all environmental variables in
7 each 5° cell, except particulate organic carbon and slope (Fig. 2). All correlation coefficients
8 were positive and weak except the coefficients for depth and distance from land (Fig. 2). For
9 latitudinal bands, there was a moderate positive correlation between the E(S50) and the sea
10 surface temperature and salinity, and a negative correlation with the sea-to-land ratio (Fig. S2).

11

12

4. DISCUSSION

13

4.1. Geographical distribution

14 We found that Europe and its surroundings had the most records – and therefore have
15 published (in a broad sense) the most polychaete data – followed by Australia and New Zealand.
16 More records were also found in Antarctic than Arctic waters and in the tropics, Indonesia had
17 more records than other equatorial regions (Fig. 1). That most polychaete records were coastal
18 is in line with the general pattern for marine species found in comparable online-data based
19 biogeographic studies (Costello et al. 2015, Costello & Chaudhary 2017).

20 The 11 polychaete biogeographic regions identified in this study largely coincide with the
21 marine biogeographic regions proposed by Spalding et al. (2007) and determined from data
22 analysis by Costello et al. (2017). They also closely coincide with the 24 biogeographic regions
23 outlined by Glasby (2005), which were based on sponge and polychaete distributions, albeit
24 some adjacent regions of Glasby (2005) were combined in the present study (e.g. temperate and
25 tropical Australia). However, due to insufficient data, particularly for Africa, South America

1 and the deep sea in general, the present study did not recover previously defined biogeographic
2 regions such as the Arctic Seas, Black Sea (studies by Arvanitidis et al. (2002, 2009), Surugi
3 et al. (2010) & Costello et al. (2017) found the Black Sea to be a distinct from the Mediterranean
4 Sea), Chile, Inner Baltic Sea, North American Boreal, Northwest Pacific, offshore Indian
5 Ocean, middle east Pacific, South Atlantic and West Pacific Oceans, South Africa, Tasman Sea,
6 Tropical East Atlantic as well as the Western Indo-Pacific (Table 1). Further, some
7 biogeographic regions recognized in this study were subdivided into smaller units in other
8 studies. For example, biogeographic region 6, i.e. Antarctica and the southern coast of
9 Argentina (which here includes the entire Southern Ocean), comprised several distinct regions
10 including East Antarctic, West Antarctic – South Georgia, and Magellan, in the polychaete
11 biogeography study of Glasby & Alvarez (1999) and Glasby (2005). Our recognition of region
12 6, nevertheless, agrees with several all-taxa studies considering the Antarctic and Southern
13 Ocean to be one biogeographic region (Ekman 1953, Spalding et al. 2007, Costello et al. 2017).
14 Reasons for the recognition of a combined Antarctic plus Southern Ocean area seem to reflect
15 the larger amount of data available (Glasby & Alvarez (1999) and Glasby (2005) only analysed
16 six families and ten clades of polychaetes, respectively); it may also reflect spatial biases where
17 particular geographic areas may have been sampled differently (e.g. sediments or epifauna).
18 Obtaining polychaete data from poorly-known areas and utilizing all available data using a
19 standard biogeographic methodology are thus a priority for further research.

20 Biogeographic region 1, i.e. the North Atlantic excluding the coast of Spain and France
21 facing Biscay Bay, was found to be the region with the most polychaete species reflecting its
22 large area and survey effort. Yet, the score of the indicative species of this region was the lowest
23 among all biogeographic regions (Table 1) as polychaete species from the North Atlantic
24 occurred also in many other geographic regions. By contrast, Indonesia (region 3) had the
25 highest score and was the third most species-rich biogeographic region in the world despite a

1 relatively low number of records (Table 1). The high polychaete species richness and
2 endemicity in this area is not surprising as the region is part of the Coral Triangle (CT), so
3 named because it is a globally rich region for corals (Veron et al. 2009), fish and other species
4 (e.g. Asaad et al. 2018).

5 Despite located near region 1, the Bay of Biscay coast of Spain and France (region 5) and
6 the central part of the Mediterranean Sea (region 7) were identified as distinct biogeographic
7 regions. However, we caution recognition of the indicative species of these regions as endemic
8 because the data were taken from 42 locations only. To the best of our knowledge, almost all
9 of the indicative species of both regions have not been reported elsewhere since their first
10 descriptions. Further, occasionally species in both regions have been reported a considerable
11 distance away – for example, one of the indicative species of region 5, i.e. *Microrbinia linea*,
12 was also reported in the China Sea (Liu & Liu 2008). This outlier, and others, may represent
13 misidentifications; taxonomic revisions are the basis to improving the accuracy of species
14 names in global datasets. Thus, regions 5 and 7 may be part of region 1, following the warm-
15 temperate Lusitania Region proposed by Briggs & Bowen (2012), which includes largely
16 coastal areas of southern Britain and Ireland, extending south to southern Morocco, and
17 eastwards through the Mediterranean Sea. Similarly, Spalding et al. (2007) considered coastal
18 Europe (including Bay of Biscay) and Mediterranean Sea as one marine biogeographic region
19 (i.e. Temperate Northern Atlantic), albeit comprising six smaller regions. Also, the species
20 distribution data analyses by Costello et al. (2017) defined the North East Atlantic and
21 Mediterranean as one biogeographic region.

22 Further, we found that most of the polychaete biogeographic regions were coastal, but some
23 were offshore, such as those situated in the offshore northern Atlantic, Antarctic and eastern
24 Pacific Oceans (regions 11, 6 and 9, respectively) (Fig. 1). These biogeographic regions were
25 dominated by deep-sea polychaete species associated with hydrothermal vent habitat. In fact,

1 all indicative species of region 11 were described from the deep-sea environment of the area,
2 and four of the five species were obtained from hydrothermal vents (Zibrowius 1972,
3 Desbruyères & Hourdez 2000, Sigvaldadóttir & Desbruyères 2003, Paxton & Morineaux 2009).
4 Similarly, all indicative species of region 9 were originally described from a similar
5 hydrothermal vent habitat (Pettibone 1984a,b, 1985a,b, 1986, Blake 1985,1991, Desbruyères
6 & Laubier 1986, ten Hove & Zibrowius 1986, Hourdez et al. 2006), all of whose species were
7 not recorded elsewhere (Table 1). Whether these regions are really biogeographic regions or
8 reflect sampling of unique deep-sea habitats merits further research comparing data from vents
9 and non-vent habitats in these biogeographic regions.

10

11

4.2. Latitudinal distribution

12 The total number of polychaete species was slightly higher in the southern hemisphere despite
13 about twenty times more samples in the northern than southern hemispheres (Fig. 3A-C). This
14 finding contradicts the pattern of most marine taxa where species richness generally peaks in
15 the northern hemisphere (Chaudhary et al. 2016, 2017; Chaudhary 2019), but is similar to the
16 pattern of a few taxa such as fish, shark and rays, stony corals (Chaudhary 2019) and amphipods
17 (Arfianti & Costello, 2020) when sampling bias is accounted for (Table S7). In our case, we
18 suspected that elevated polychaete species richness in the southern hemisphere may be driven
19 by high endemism as species richness and endemism have been found to be positively
20 correlated (e.g. Costello et al. 2017). Moreover, when the brackish Black and Baltic Seas are
21 excluded, an all-taxon study that mapped global biogeographic ‘Realms’ equivalent to
22 polychaete biogeographic regions in our study suggested that endemism may be higher in the
23 southern than northern hemisphere (47% vs 40%) (Costello et al. 2017). Indeed, comparison of
24 the number of endemic species (per biogeographic region) in the present study shows about

1 1300 endemic species occur in the southern hemisphere compared to about 870 endemics in the
2 northern one (62% vs 48%).

3 A less likely explanation for the greater number of polychaete species in the southern than
4 northern hemisphere is the adoption of northern hemisphere species names by polychaete
5 workers of the southern hemisphere (see a review by Hutchings & Kupriyanova 2018). This
6 may have, in small part, artificially inflated the number of species in the southern hemisphere,
7 and at the same time hidden the distinctive, largely endemic fauna in the southern hemisphere,
8 which was first revealed in revisionary morphological taxonomic studies (Hutchings & Glasby
9 1991), and more recently by molecular studies. Also, our analysis of species occurring in both
10 hemispheres indicated that less than 1% (5 of about 500) of species occurring in both
11 hemispheres are the result of suspected misidentification (Table S8), so taxonomic bias would
12 appear to have little influence on the patterns observed in this study. However, the number of
13 polychaete species documented in the present study (i.e. about 3400 species) is much less than
14 the total named species (i.e. nearly 11,500). Therefore, the use of a larger sample of polychaete
15 species, underpinned by improved taxonomy, will undoubtedly provide additional insights into
16 the large-scale biogeography of polychaetes.

17 The bimodal latitudinal gradient in alpha, gamma and E(S50) species richness for
18 polychaetes (Figs 3 & 4) supports the findings of Chaudhary et al. (2016, 2017) of bimodality
19 of overall marine species. Our results are thus in line with the latitudinal species richness
20 gradient of various marine groups such as amphipods (Arfianti & Costello 2020), bivalves
21 (Crame 2000, 2001, 2002), brachiopods (Shen & Shi 2004), planktonic organisms (Brayard et
22 al. 2005), razor clams (Saeedi et al. 2017), sea anemones (Fautin et al. 2013), seaweeds (Bolton
23 1994, Kerswell 2006) and zooplankton (Rutherford et al. 1999), as well as with the latitudinal
24 species richness gradient of some terrestrial groups like amphibians, reptiles, birds and
25 mammals (McCoy & Connor 1980, Currie 1991, Sax 2001). However, most of the authors of

1 these studies did not explicitly state the pattern to be bimodal, either because the pattern was
2 not noticed, or the drop in species richness near the Equator was considered to be due to a lack
3 of data. The pattern was first noticed and reinterpreted to be bimodal by Chaudhary et al. (2016).

4 The results of the present study thus strongly contradict the findings of other studies focussed
5 on polychaetes suggesting that the latitudinal gradient species richness either does not exist
6 (Gobin & Warwick 2006) or is unimodal (Giangrande & Licciano 2004). The former study had
7 only 14-77 polychaete species from 15 sampling sites at four geographic locations (so the
8 different pattern found in that study may simply reflect a lack of sufficient data), and the latter
9 study was limited to 428 species of the Sedentaria family Sabellidae (so the differences with
10 the bimodal pattern finding in our study are more surprising given that we found the Sedentaria
11 to be relatively less speciose than Errantia in the vicinity of the tropics, specifically between
12 5°N and 10°S). The greater taxon sampling in our study – about 3400 species in 85 families
13 sampled across 10,000 sampling sites around the globe – resulted in a bimodal pattern in
14 polychaete species richness. We show that alpha and gamma species richness-based latitudinal
15 gradients are biased by uneven sampling effort across the globe (Fig. S1). However, our
16 rarefaction index E(S50) and GAM, which corrected for sampling effort, demonstrated that the
17 pattern remains bimodal (Fig. 4C). This indicates that the bimodal pattern in polychaete species
18 richness is not an artefact, but rather a natural phenomenon.

19 Chaudhary et al. (2016) proposed that sea surface temperature was the primary factor
20 causing the dip in marine species richness in the tropics. That is, the equatorial region may
21 already be too hot from climate warming; some marine species may have been lost and/ or
22 moved to higher latitudes as has been observed for marine fish (e.g. Perry et al. 2005, Nye et
23 al. 2009, Last et al. 2011), echinoderms and decapods (O'Hara & Poore 2000) as well as some
24 algae (Phillips 2001). At local scales, polychaete species composition is influenced by a range
25 of abiotic factors such as food availability (e.g. Snelgrove & Butman 1994, Haedrich et al.

1 2008), sediment type (Etter & Grassle 1992), habitat complexity (Serrano & Preciado 2007),
2 salinity (Stephenson et al. 1979) and environmental disturbances (Gray 1997). However, these
3 factors influence distributions of marine species at local habitat scales rather than biogeographic
4 scales. Sea temperature, in contrast, influences both local and global distributions of marine
5 species due to its pervading effects on individual growth, reproduction and physiology, as well
6 as the limits of species geographic distributions. Of all the potential environmental variables
7 that may affect the latitudinal distribution of the animals (Fig. 2), sea surface temperature is the
8 only one that is relatively symmetrical with latitude, and is possibly the primary factor shaping
9 the bimodal pattern in polychaete species richness, whether due to ecological, environmental
10 and/ or evolutionary factors.

11 Further, that polychaete species number tends to decrease with depth (Fig. 2) support the
12 findings of studies by Carvalho et al. (2013) and Gunton et al. (2015) for polychaetes, and
13 Costello & Chaudhary (2017) for marine species in general. Poor food supply in the deep-sea
14 environment (we define ‘deep-sea environment’ as the pelagic and benthic zones below 200
15 m), which results in low environmental disturbance, growth and competitive displacement
16 rates, may be an explanation (Cosson-Sarradin et al. 1998). Habitat homogeneity and lower
17 temperatures have also been linked to lower species richness in the deep sea compared to
18 continental shelves (Costello & Chaudhary 2017). We also note that deep-sea species are in
19 general poorly-documented (Smith et al. 2006). In many parts of the world’s oceans, as our data
20 indicated, no deep-sea species have even been reported. Information gaps in Earth’s polychaete
21 diversity can, therefore, be filled by further targeting collecting of this data-poor habitat, as well
22 as other habitats with high marine species richness such as coral reef ecosystems. Moreover,
23 researchers and research institutions need to make their datasets publicly available – this ideally
24 includes data of published literature – so that other scientists can make use of them to better
25 study the distribution of marine species (e.g. Costello 2009, Costello et al. 2013). More detailed

1 morphological and molecular studies are also likely to reveal a large increase in polychaete
2 diversity not only in poorly-studied areas, but also in well-studied areas. For example, Lavesque
3 et al. (2017) identified a large intertidal polychaete as a new *Marphysa* species from *M.*
4 *sanguinea* complex collected from a well-studied area, i.e. Bay of Biscay, Northeast Atlantic.
5 Indeed, when the data gaps from poorly-sampled geographic areas are filled, and datasets are
6 made fully available as we found by compiling data for Indonesia, and more detailed taxonomic
7 studies are conducted, it may provide new insights into the latitudinal gradients and
8 biogeographic regions recognized here.

9

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15

16

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Biogeography of polychaete worms

1 Table 1. The major polychaete biogeographic regions mapped (sorted on species richness) in comparison with marine regions outlined by Spalding et al. (2007) and Costello et
 2 al. (2017). A cell represents an area with 4° grid-cell resolution.
 3

Region	Location(s)	Records	Species	Cells	Most common species (record)	Most indicative species (score)	% endemic species	Spalding et al. (2007)	Costello et al. (2017)
1	North Atlantic & eastern and western parts of Mediterranean	494766	1144	41	<i>Lanice conchilega</i> (11004)	<i>Pygospio elegans</i> , <i>Nephtys cirrosa</i> , <i>Pholoe baltica</i> , <i>Pseudopolydora pulchra</i> , <i>Scalibregma celticum</i> , <i>Ophelia borealis</i> , <i>Polycirrus norvegicus</i> , <i>Dipolydora caulleryi</i> , <i>Ampharete falcata</i> , <i>Paranaitis kosteriensis</i> (1)	62.4	Temperate Northern Atlantic	Northeast Atlantic, Norwegian Sea & Mediterranean
2	Australia	13292	1111	24	<i>Aglaophamus australiensis</i> (295)	<i>Longicarpus modestus</i> , <i>Pista australis</i> , <i>Spio blakei</i> , <i>Armandia intermedia</i> , <i>Nephtys inornata</i> , <i>Micronephthys oculifera</i> , <i>Galeolaria gemineoa</i> , <i>Prionospio tridentata</i> , <i>Mediomastus australiensis</i> (37)	65.9	Central Indo-Pacific & Temperate Australasia	Coral Sea & South Australia
3	Indonesia	1571	513	11	<i>Leodice antennata</i> (38)	<i>Ceratonereis tentaculata</i> , <i>Tomopteris nationalis</i> , <i>Leanira coeca</i> , <i>Glycera longipinnis</i> , <i>Opisthosyllis australis</i> , <i>Phyllochaetopterus claparedii</i> , <i>Polyodontes atromarginatus</i> , <i>Lumbrineris latereilli</i> , <i>Loimia nigrifilis</i> , <i>Lysidice oele</i> (291)	62.3	Central Indo-Pacific	Indo-Pacific Seas & Indian Ocean
4	New Zealand	5659	381	10	<i>Hyalinoecia tubicola</i> (193)	<i>Armandia maculata</i> , <i>Asychis trifilosus</i> , <i>Scolecopides benhami</i> , <i>Boccardia syrtis</i> , <i>Sthenelais chathamensis</i> , <i>Lepidonotus polychromus</i> , <i>Pomatoceros caeruleus</i> , <i>Phylo novaezealandiae</i> , <i>Neosabellaria kaiparaensis</i> , <i>Paradiopatra minuta</i> (57)	35.5	Temperate Australasia	New Zealand

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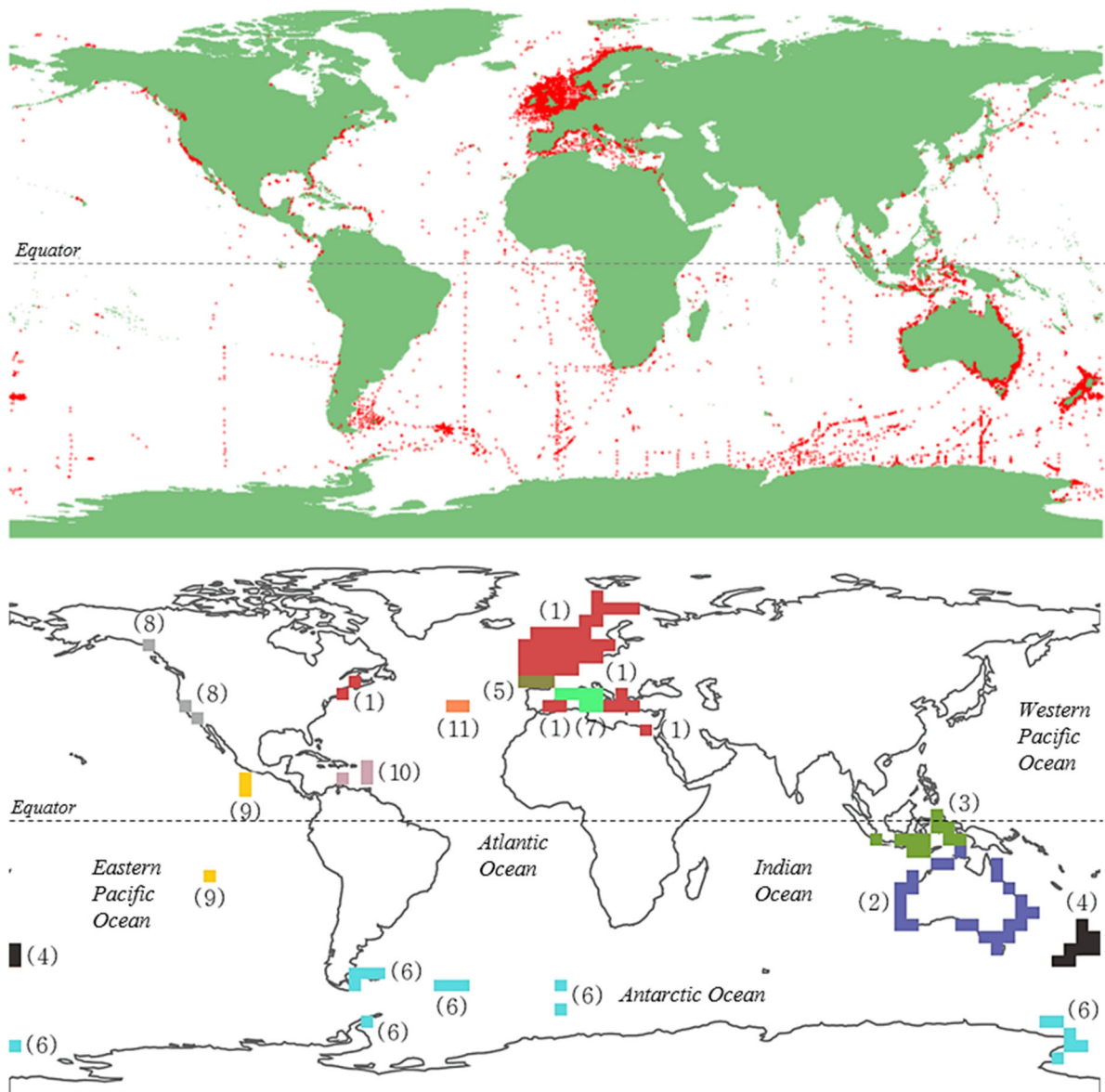
5	The Atlantic coasts of Spain & France	928	216	3	<i>Glycera papillosa</i> (46)	<i>Lumbrinerides laubieri</i> , <i>Poecilochaetus fulgoris</i> , <i>Paradoneis abranchiata</i> , <i>Exogone furcigera</i> , <i>Sclerobregma branchiata</i> , <i>Microrbinia linea</i> , <i>Paraonides rubriceps</i> , <i>Lumbrineriopsis gasconiensis</i> , <i>Diplobranchia capillaris</i> , <i>Bonellia plumosa</i> (240)	20.7	Temperate Northern Atlantic	Northwest North Atlantic
6	Antarctica & the southern coast of Argentina	1983	207	17	<i>Pelagobia longicirrata</i> (103)	<i>Spiophanes tcherniai</i> , <i>Amythas membranifera</i> , <i>Polycirrus kerguelensis</i> , <i>Lanicides vayssierei</i> , <i>Genetyllis polyphylla</i> , <i>Epigamia charcoti</i> , <i>Ophryotrocha notialis</i> , <i>Capitella perarmata</i> , <i>Thelepides koehleri</i> , <i>Terebellides</i> spp. (107)	50.8	Southern Ocean & Temperate South America	Southern Ocean & Argentina
7	Central Mediterranean Sea	5066	197	6	<i>Sabella spallanzanii</i> (631)	<i>Perinereis macropus</i> , <i>Protobonellia brevirhynchus</i> , <i>Spirobranchus lima</i> , <i>Adercodon pleijeli</i> (18)	5.1	Temperate Northern Atlantic	Mediterranean
8	The western coast of the USA	419	87	3	<i>Phragmatopoma californica</i> (156)	<i>Phyllodoce medipapillata</i> , <i>Dorvillea moniloceras</i> , <i>Pareurythoe californica</i> , <i>Pista pacifica</i> , <i>Spirobranchus spinosus</i> , <i>Megasyllis nipponica</i> , <i>Glycera robusta</i> , <i>Odontosyllis phosphorea</i> , <i>Lepidonotus spiculus</i> , <i>Hermadionella truncata</i> (71)	77.4	Temperate Northern Pacific	North Pacific

Biogeography of polychaete worms

9	The eastern part of the Pacific Ocean	574	31	3	<i>Paralvinella grasslei</i> (52)	<i>Branchinotogluma sandersi</i> , <i>Branchiplicatus cupreus</i> , <i>Branchipolynoe symmytilida</i> , <i>Paralvinella pandorae</i> , <i>Thermiphione risensis</i> , <i>Protis hydrothermica</i> , <i>Lepidonotopodium riftense</i> , <i>Nicomache arwidssoni</i> , <i>Sirsoe hessleri</i> , <i>Malacoceros samurai</i> (213)	100	Tropical Eastern Pacific & Eastern Indo-Pacific	Southeast Pacific & Gulf of California
10	Caribbean Sea	243	16	3	<i>Spirobranchus giganteus</i> (67)	<i>Notaulax nudicollis</i> , <i>Eupolymnia crassicornis</i> , <i>Notopygos caribea</i> , <i>Hydroides mongeslopezi</i> (165)	44.4	Tropical Atlantic	Caribbean & Gulf of Mexico
11	Atlantic Ocean	254	15	2	<i>Branchipolynoe seepensis</i> (80)	<i>Lepidonotopodium jouinae</i> , <i>Prionospio unilamellata</i> , <i>Laonice asaccata</i> , <i>Ophryotrocha fabriae</i> , <i>Neomicrorbis azoricus</i> (138)	62.5	Temperate Northern Atlantic	Offshore & Northwest North Atlantic

1 Biogeographic regions for which our study lacked data are: Arctic, Western Indo-Pacific and Temperate Southern Africa (in Spalding et al. 2007), as well as Arctic Seas, Gulf
 2 of Aqaba, Aden, Suez & Red Sea, South Africa, Black Sea, Chile, Inner Baltic Sea, North American Boreal, Northwest Pacific, Offshore Indian Ocean, Offshore middleeast
 3 Pacific, Offshore South Atlantic, Offshore West Pacific, Tasman Sea and Tropical East Atlantic (in Costello et al. 2017). Biogeographic regions that were relatively data-poor
 4 in the study of Glasby (2005) included Southwest Atlantic, Red Sea, Greater New Zeland, Peruvian, Magellan, and West Atlantic and South Georgia, which all had fewer
 5 than 2% of the total number of species records in the study.

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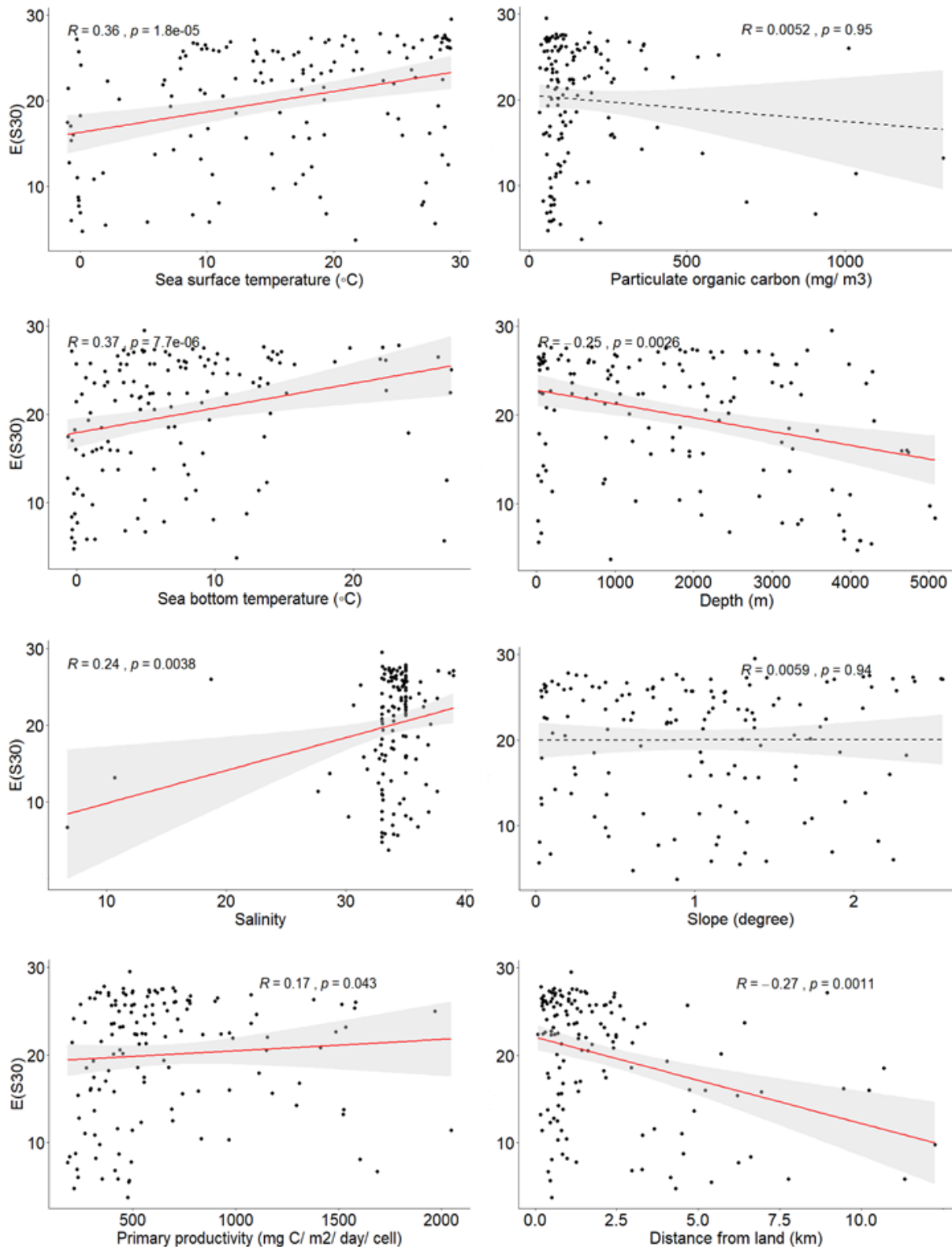


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2 Fig. 1. Map of polychaete occurrence records (above) and biogeographic regions (below). Species records were
 3 based on GBIF and OBIS datasets, plus the authors' recently published checklist of Indonesian polychaete species.
 4 Biogeographic regions were generated by uploading the records to the interactive web application 'Infomap
 5 Bioragions' (see Table 1 for the details).

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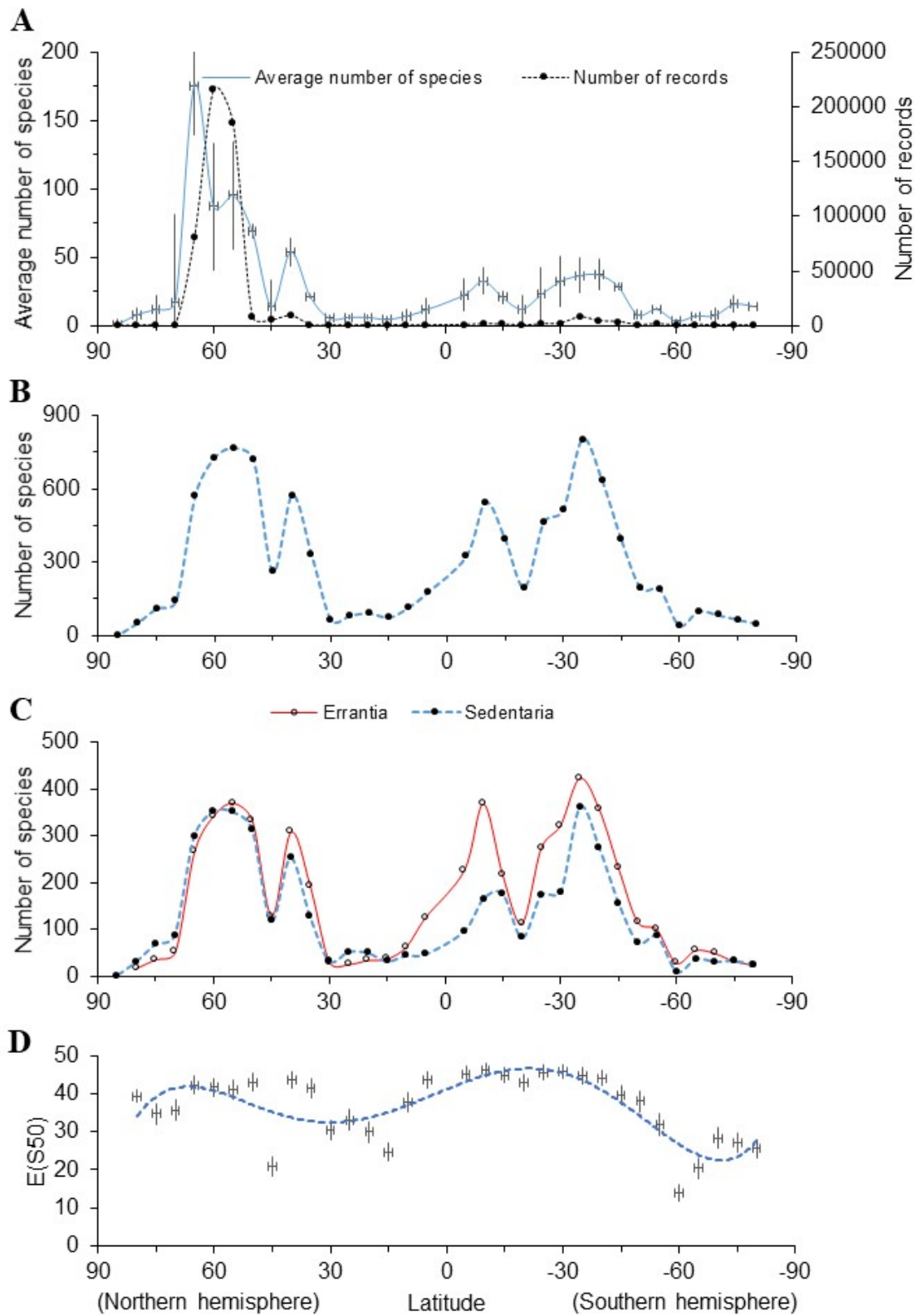
Biogeography of polychaete worms



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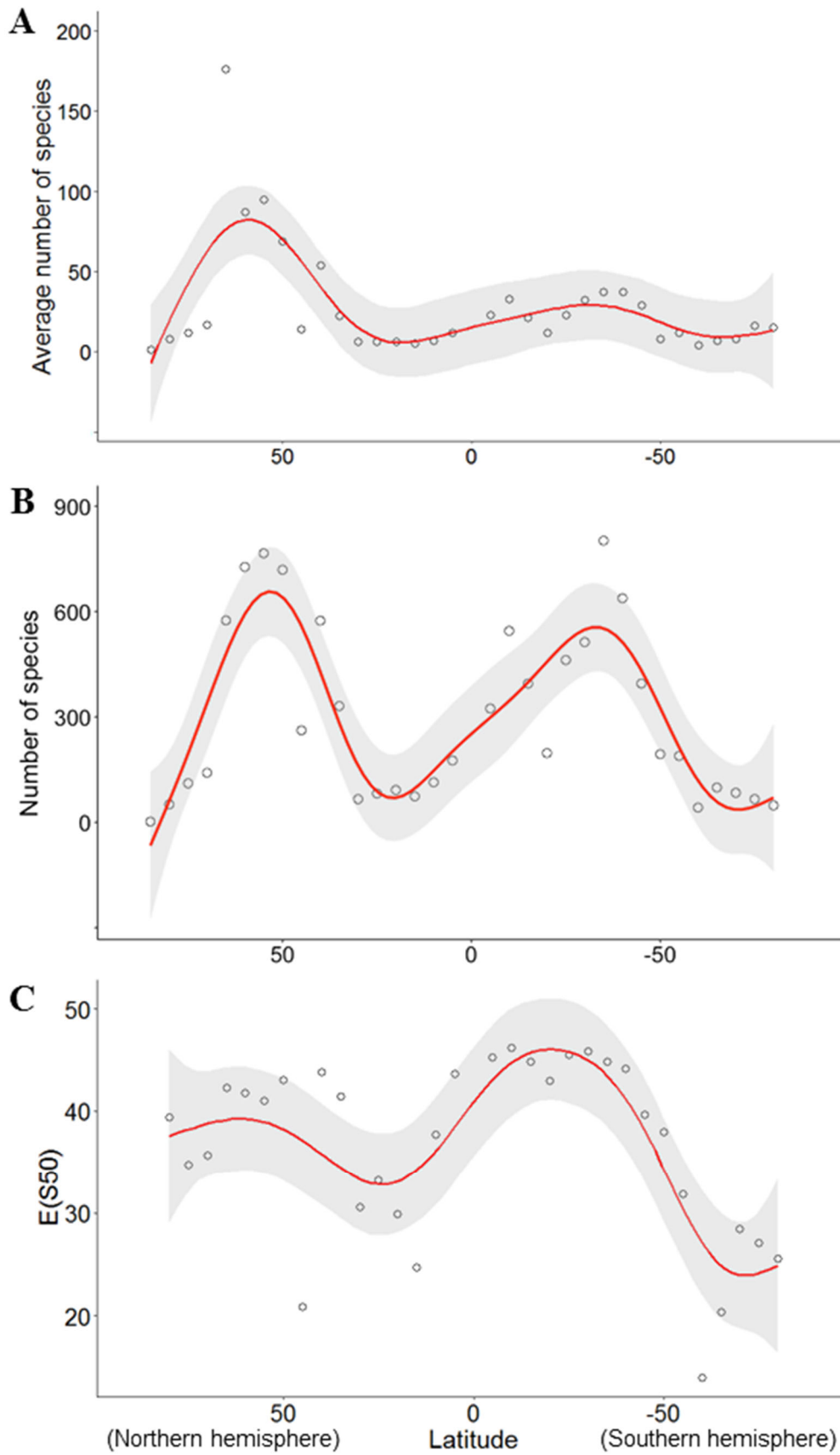
2 Fig. 2. Spearman correlation analyses between the E(S30) and various environmental variables in each 5° grid-cell
 3 resolution. R is the Spearman's correlation coefficient. The analysis is significant and very significant when p
 4 value < 0.05 and < 0.01 or < 0.001 , respectively. Visually, red-solid and black-dashed linear regression lines also
 5 indicate significant and non-significant analysis results, respectively. Grey shadings are the standard errors.

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2 Fig. 3. (A) Alpha species richness (calculated as means of species number \pm standard errors with two-point moving
 3 average trend line) and record numbers. (B) Gamma species richness (all species). (C) Gamma species richness
 4 (errant and sedentary species). (D) $E(S50)$.



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2 Fig. 4. GAMs of the (A) alpha species richness, (B) gamma species richness and (C) E(S50). The solid red lines
 3 are the best non-linear models, smoothed using the Restricted Maximum Likelihood (REML) method (see Table
 4 S4). Grey shadings are the standard errors, whereas empty circles are the data points.