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ORIGINAL RESEARCH

Global Leptocheliidae diversity: environmental drivers and richness hotspots

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Abstract

Human-driven environmental changes in the ocean are reshaping the diversity and distribution of coastal organisms. Understanding species diversity is essential for assessing threats, predicting impacts, and guiding conservation planning. Our study focuses on the family Leptocheliidae (Crustacea: Tanaidacea), a suitable model for investigating diversity and distribution in low-mobility crustaceans. This family, abundant in shallow waters and sensitive to environmental shifts, was analyzed at global scale using literature, databases, and unpublished data from Australian coral reefs. Species richness, estimated richness, and sampling effort were calculated organizing data into latitudinal bands and ca. 800,000 km hexagonal cells. Cluster analysis by biogeographic provinces was used to identify distinct species assemblages Generalized Linear and Additive Models (GLM, GAM) assessed environmental drivers, including temperature, productivity, chlorophyll, dissolved oxygen, salinity, silicate, phytoplankton, nitrate, and phosphate. Results revealed a bimodal species richness pattern, with diversity peaking in lower latitudes and declining at the equator. Biodiversity hotspots were identified in the Indo-Australian region, central Indo-Pacific, Gulf of Mexico, and Caribbean, with high estimated richness in the Mediterranean and SE Australia. The subpolar region displayed distinct, but low-diversity assemblages. Among the environmental variables, dissolved oxygen was identified as the most important factor influencing species diversity and estimated diversity across latitudes, followed by temperature. Models incorporating salinity were the most reliable for species diversity within hexagonal regions.

Keywords Crustacea · Tanaidacea · Distribution · Oxygen · Temperature · Salinity

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Introduction

Understanding how marine species are distributed across ecosystems remains a central question in ecology and biogeography (Rao 1997; Podesta et al. 1993; Saeedi et al. 2019, 2020, 2022a, b). Despite decades of the extensive research, the mechanisms shaping spatial diversity remain only partly understood largely due the complexity of habitats and interactions among multiple abiotic and biotic factors. Species ranges are shaped by geological history, physicochemical conditions, and ecological interactions (Poore and O'Hara 2007; Butler et al. 2010; Bowen et al. 2013). Geological processes, such as tectonic activity, volcanism and land formation, create topographic barriers that enhance environmental heterogeneity, promote niche speciation and drive regional endemism (Zaffos et al. 2017; Pellissier et al. 2018). Among physicochemical variables, temperature, oxygen availability, and energy supply are consistently identified as key drivers of marine biodiversity, although their relative influence varies across depth zones (Wooley et al. 2016; Deutsch et al. 2020; Borges et al. 2022). In shallow-water taxa, temperature often dominates affecting metabolic rates and selective pressure (Morley et al. 2016; Saeedi et al. 2022a, b), whereas in the deep sea, characterized by stable low temperatures, food availability becomes the constraint (Buhl-Mortensen et al. 2010; Knauber et al. 2023).

Contemporary biodiversity patterns are being reshaped by human activities. Rising temperatures, ocean acidification, pollution, habitat degradation, and biological invasions alter biogeographic dynamics and forcing species shift their ranges (Harley et al. 2006; Saeedi et al. 2017a, b; Hobday and Matear 2020; Simões et al. 2021). Low-dispersal taxa, are particularly vulnerable because they have narrow ecological tolerances and limited capacity to track shifting environmental optima (Feder et al. such as peracarids2010; Ingels et al. 2012). Habitat loss in such groups can rapidly declines population structure and under severe conditions lead to localized extinctions (Travis 2003; Airoldi et al. 2009). Anticipating these changes and integrating them into conservation planning strategies requires understanding of both species distribution and the environmental drivers.

Tanaidacea are small benthic crustaceans of the suborder Peracarida that, like other peracarids, lack a planktonic larval stage. Their early development occurs within a brood pouch, releasing juveniles directly to benthic habitat. Post-released juveniles typically settle near the maternal individual, where they construct protective tubes (Johnson and Atsettle near the maternal individual, constructitramadal 1982; Larsen 2005). This life history, combined with sedentary adult behavior, results in dense local population occasionally comprising thousands of individuals per square meter (Błażewicz and Jażdżewski 1996; Larsen 2005) highly dependent on local food availability (Jakiel et al. 2020).

Leptocheliidae is one of the most abundant and diverse tanaidacean family, comprising 140 described species found mainly on continental shelves of tropical, subtropical, and temperate regions, where it encounters a wide range of environmental conditions including fluctuations in temperature, salinity, or oxygen levels (e.g., Larsen and Rayment 2002; Bamber 2007; Błażewicz-Paszkowcz and Bamber 2012). Occasionally leptochellids were recorded below the shelf break (e.g. Lang 1973; Larsen 2003), and a few in polar regions (Błażewicz-Paszkowycz et al. 2012). Leptochellids occupy diverse shelf substrates from coral, macroalgae to sandy and muddy bottoms, and often exhibit narrow habitat preferences (Edgar 2012; Guţu 2016). These traits, together with their common abundance, taxonomic diversity, and

sensitivity to environmental changes make them promising bioindicators of environmental and anthropogenic changes.

Despite their potential importance, global diversity patterns in the family Leptocheliidae remain poorly explored due to historical taxonomic ambiguities, and uneven sampling efforts, especially outside well studied regions. Consequently, most existing studies have focused on local species descriptions and taxonomic resolution, with relatively few efforts to synthesize broader biogeographic patterns (Bamber 2010; Guţu 2016; Iwasa-Arai et al. 2024). Our work addresses this gap by exploring a global dataset of Leptocheliidae occurrences: (1) identifying hotspots of species richness; (2) modelling the influence of environmental variables shaping the species richness; and (3) delineating regional assemblages characteristic to particular habitats and regions. We aim to evaluate the potential of Leptocheliidae as indicators of environmental and anthropogenic changes in coastal marine ecosystems. Future analyses utilizing this group could serve as a valuable tool for assessing local environmental conditions and guiding the development of targeted conservation strategies.

Materials and methods

Data extraction

Occurrence records of the Leptocheliidae family were compiled from four primary sources: (1) the Ocean Biodiversity Information System (OBIS), (2) the Global Biodiversity Information Facility (GBIF), (3) published literature, and (4) new data obtained from material collected during Census of Coral Reefs Ecosystems (Creefs) (Plaisance et al. 2009, 2011a; Stępień et al. 2019). Datasets were merged and quality-checked using R tools like "robis" (Provoost 2018), following Saeedi et al. (2022a, b). Records lacking coordinates, duplicates, or those with ambiguous localities were excluded from the analysis.

Taxonomic identity was validated against the World Register of Marine Species (WoRMS) to correct synonyms and ensure taxonomic consistency, yielded reliable data for 71 species.

Literature distribution data were retrieved from papers by Anderson (2023) (Online resource 1), and quality was checked in similar manner. Literature sources added records for 32 species not listed in the online databases. To ensure comprehensive distribution coverage, Google Maps coordinates were calculated for species whose localities were described without precise coordinates. Only records with exact locality descriptions (e.g. named marina/beach/island sectors) were used. Coordinates were determined for 24 species.

Moreover, distribution data for 21 undescribed species from coral reefs near Lizard Island (Great Barrier Reef, GBR), Heron Island (GBR), and Ningaloo Reef (NW Australia) were added. Species were collected during the CReefs. The final dataset included 3,891 occurrence records, covering 148 species across 36 genera. Depth ranges were available for 2,349 records (60%).

Environmental data

Environmental variables were obtained from BIO-ORACLE (Tyberghein et al. 2012; Assis et al. 2024) as raster layers with a spatial resolution of 5 arc-minutes (~10 km). Benthic variables included average temperature (°C), dissolved oxygen (%), salinity, primary productivity ($g \cdot m^{-3} \cdot d^{-1}$), chlorophyll concentration ($mg \cdot m^{-3}$), and phytoplankton biomass (as a proxy for productivity), and nutrients: silicate, nitrate, and phosphate ($mol \cdot m^{-3}$), which are considered factors influencing primary productivity. Environmental data were extracted for each record using the Point Sampling Tool in QGIS (qgis.org, version 3.35). The average value of environmental data was calculated for hexagons and latitude bands (see Data Analysis).

Data analysis

To capture spatial patterns of species diversity at different scales and resolutions ocean area was divided into 5° latitudinal bands and hexagonal cells of 800,000 km^2. In each hexagon/band, sampling effort (number of records), species richness (number of species), and expected species richness (ES15) were calculated. Expected species richness was used to minimize the sampling bias using the rarefaction method (ES15), in which 15 records were randomly chosen from all available records to calculate the average species number per 15 records. Data importing, plotting, and manipulation were performed using the following R packages: "tidyverse" (Wickham et al. 2019), "ggplot2" (Wickham 2016), and "sf" (Pebesma 2018). ES15 was computed using the "vegan" package (Oksanen et al. 2017). Additionally, hierarchical cluster analysis was performed using Jaccard distance (binary method) and complete linkage to assess assemblage composition, based on a presence-absence matrix of species per marine provinces (Spalding et al. 2007). Approximately Unbiased (AU) and Bootstrap Probability (BP) p-values were used to assess the robustness and reliability of the clusters identified in hierarchical clustering analysis (Shimodaira 2004). The AU value indicates the confidence level of the cluster existence based on multiscale bootstrap resampling; the BP value represents the bootstrap probability for the cluster, calculated from normal bootstrap resampling. Cluster analysis was performed using the "vegan" package, and bootstrap support was calculated with "Pvclust" (Suzuki and Shimodaira 2006). Graphics were prepared with Adobe Illustrator CS6.

Pearson correlation coefficient was calculated to check the correlation between environmental variables. Generalized additive models (GAMs) were used to examine the impact of environmental predictors on species richness and ES15 within hexagon, while generalized linear models (GLMs) were used to predict species richness and ES15 along the latitudinal gradient. Both models were built using the negative binomial error distribution and were fitted via restricted maximum likelihood. Automatic predictor selection, implemented in the "mgcv" package (Wood 2013), was used to control the complexity of smooth terms. For each analysis we fitted an intercept-only model that represents a null hypothesis with the assumption that richness is not explained by environment, spatial sampling bias, or spatial autocorrelation. For models with species richness as the response variable, the number of records for each locality was used to control for sampling effort. For models where ES15 was the response variable, the number of records was not used as an explanatory variable, as ES15 calculations are themselves intended to control for sampling effort. To model the

effects of spatial autocorrelation on predictor and response variables, a two-dimensional spherical spline on the latitude and longitude of sampling sites was used.

To assess model support, Akaike's Information Criterion (AIC) and Akaike weights were calculated (Burnham et al. 2011). Akaike weights estimate the probability that a model is the best among those considered, based on the data and model set. Derived from ΔAIC values, they offer a normalized metric of model likelihood, enabling direct comparisons. Models with higher weights indicate stronger empirical support, with $\Delta AIC \leq 2$ denoting substantial support and inclusion among plausible models (Burnham et al. 2011). To evaluate predictor contributions within top-performing models ($\Delta AIC < 2$), model-averaged importance scores were calculated using summed Akaike weights. Analyses incorporated the following R packages: "mgcv" for GLMs/GAMs, "ggcorrplot" for correlation analysis, and "ggplot2" for visualization.

Results

General overview of species richness and sampling effort

Members of the family Leptocheliidae were recorded across a broad latitudinal range, from 75° N to 75° S, and at depths from 0 to 2,351 m (Online resource 2). However, the majority of species (88%) occurred in waters shallower than 200 m. Species richness increased towards lower latitudes but declined in equatorial regions (Fig. 1a). Mean species richness and ES15 (expected species richness) were 10.53 and 4.72, respectively, in the Southern Hemisphere and 8.4 and 4.71 in the Northern Hemisphere. The latitudinal bands with the highest richness were 20° S (34 species), 25° N (21 species) and 40° N (20 species), while the highest ES15 values were observed at 5° N (10.2 species) and 20° S (9.8 species), respectively (Fig. 1a, b).

Hexagons with the highest species richness were concentrated in the Indo–Australian region, particularly near Heron Island/Moreton Bay, Lizard Island (NE Australia), the Celebes Sea, and Ningaloo Reef (W Australia), with values ranging from 10 to 18 species per hexagon (Fig. 2a). Additional, hexagons of high species richness were found around the Gulf of Mexico, specifically near Cuba and Florida, with up to 10 species per hexagon. The highest value of ES15 per hexagon was observed in the Celebes Sea (eight species), followed by Heron Island/Moreton Bay, and the eastern Bass Strait (seven species each). High ES15 values (six species) were also noted near Lizard Island, Ningaloo, the Gulf of Mexico (near Panama, Florida and Atlantic adjacent to Mediterranean (Fig. 2b).

Sampling effort was considerably greater in the Northern Hemisphere, with a mean of 202.9 records compared to 56.6 records in the Southern Hemisphere. The highest number of records was reported at 40°N (554 records), 30°N (474 records), and 55°N (439 records) (Fig. 1c). Hexagons with the greatest sampling effort were located along the US coastline, with maxima near California (211 records) and the Florida coast (192 records). Other well-sampled regions included the southern coast of Great Britain, with up to 132 records per hexagon (Fig. 2c).

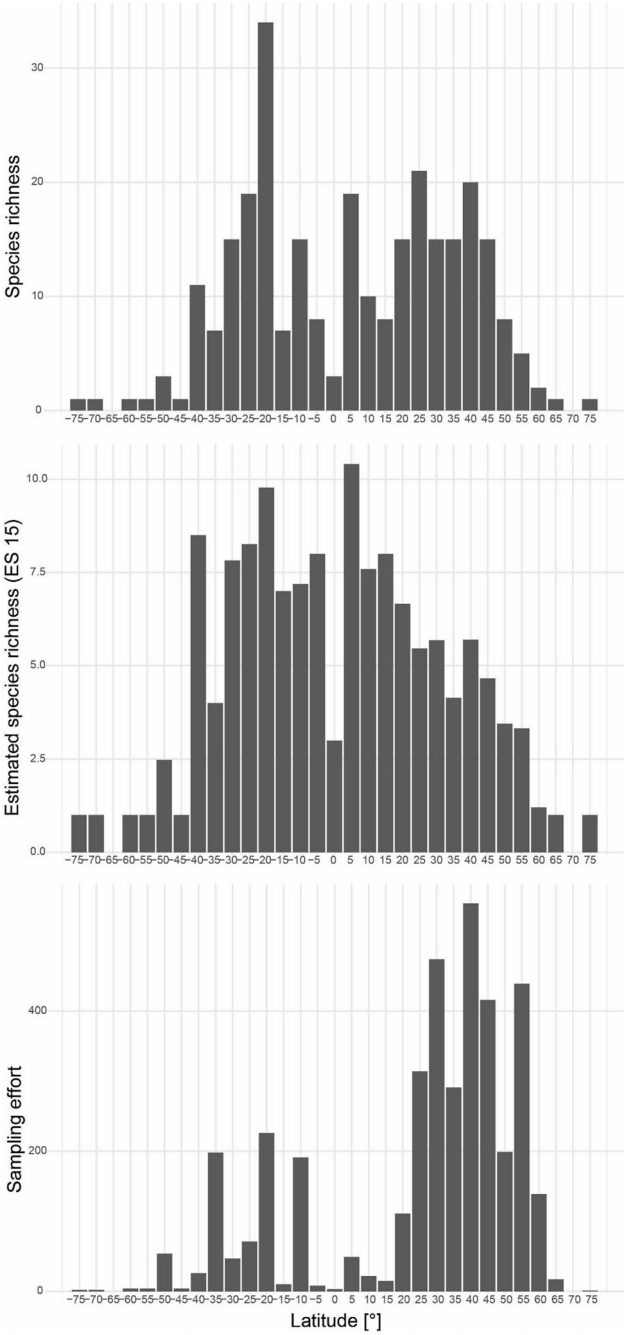

Fig. 1 Species richness (**a**), estimated species richness (**b**) and sampling effort (**c**) of Leptocheliidae calculated for 5° latitudinal band; negative values indicate Southern Hemisphere, positive values Northern Hemisphere

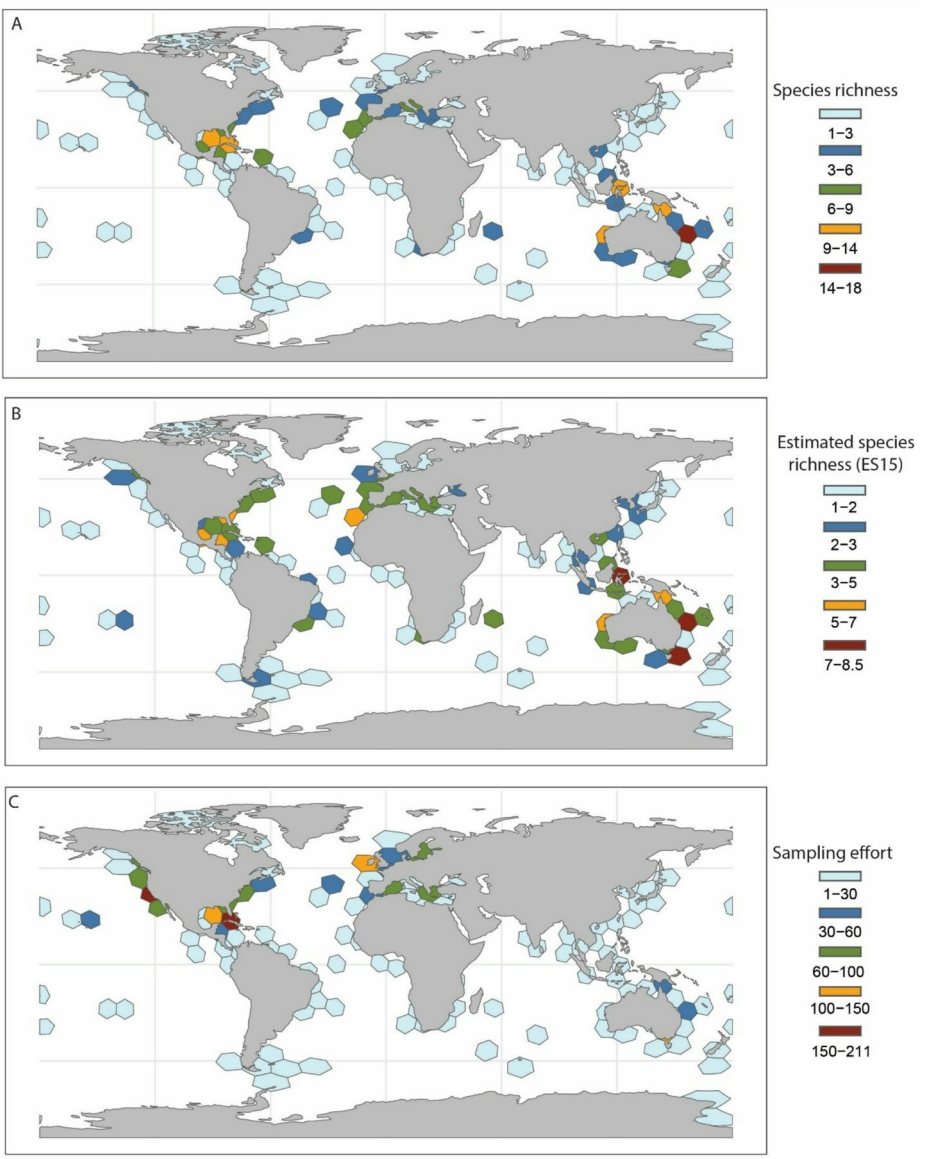

Fig. 2 Leptocheliidae species richness (**a**), estimated species richness (**b**) and sampling effort (**c**) calculated for 800,000 km^2 hexagonal cell

Assemblage composition

The following groups were distinguished based on the cluster analysis (Fig. 3):

Group 1 (clade 11) consisted of two temperate Australian provinces, clustered at ~0.6. This group exhibited high species richness, including 13 endemic species (e.g., *Allolep-*

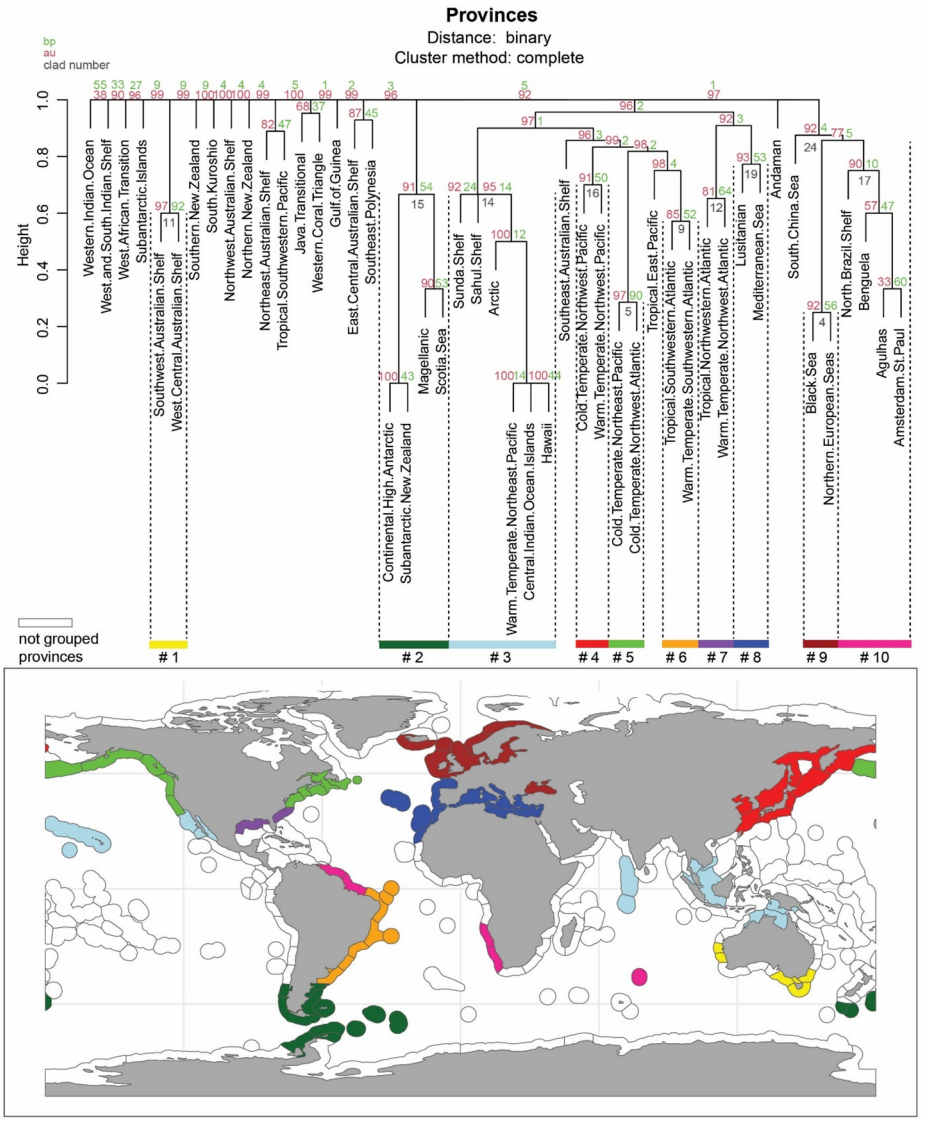

Fig. 3 Cluster analysis of Leptocheliidae assemblages, highlighting distinct groups and their spatial patterns across the study area

tochelia evansi, *Araleptochelia macrostonyx*, *Bassoleptochelia verro*, *Chondrochelia billambi*, *C. ignota*, *C. occiporta*, *Parakonarus corrigendum*, *P. robertsoni*, *Poorea johannesi*, *P. wrighti*), although none occurred in both provinces. Support values were high: AU = 97 and BP = 92.

Group 2 (clade 15) comprised four Subantarctic provinces, clustered at ~0.7, with moderate support (AU = 91, BP = 54). The stability of this group was largely maintained by *Pseudonototanais bransfieldensis*, found in all four provinces. Two other endemic species (*Leptochelia antarctica*, *P. werthi*) occurred less frequently.

Clade 30 included 14 provinces worldwide, clustered at ~0.9, dominated by widespread species *Chondrochelia dubia* and *C. savignyi*. Though overall support for this clade was low, it was subdivided into six smaller groups. Only one of these (**Group 3**, clade 14 at ~0.7) was directly associated with *C. dubia*, the remaining groups contained endemic species.

Group 4 (clade 16) included two temperate NW Pacific provinces, clustered at ~0.7 (AU = 91, BP = 50). It was supported by endemic *Makassaritanais itoi* (present in both provinces) and supplemented by occasional records of *M. grandidentatus*, *M. modestus*, *Chondrochelia sublitoralis*, *C. taitungensis*, *Mesotanais birdi*, and *Paraleptochelia setosa*.

Group 5 (clade 5) included two cold provinces in the North Atlantic and Pacific, clustered at 0.3 with strong support (AU = 97, BP = 90), characterized by endemic species: *Heterotanais groenlandicus* and *Pseudonototanais filum*.

Group 6 (clade 9) encompasses four SW Atlantic provinces clustered at ~0.6 (AU = 85, BP = 52), defined by *Intermedichelia gracilis* (present in both provinces), alongside less frequent *I. jesseri*, *Leptochelia brasiliensis*, and *Makraleptochelia potiguara*.

Group 7 (clade 12) included two NW Atlantic provinces, clustered at ~0.6 (AU = 81, BP = 64), dominated by *Cacoheterotanais rogerbamberi*, *Mesotanais longisetosus*, and *M. vadicola*, with additional occurrences of *Bathyleptochelia oculata*, *Chondrochelia caribensis*, *C. ortizi*, *C. winfieldi*, *Grallatotanais antipai*, *Hargeria chetumalensis*, *Kalloleptochelia tenuicula*, *Leptochelia longichelipes*, *L. mortenseni*, *Ogleus pilarae*, *Parakonarus juliae*, *P. sozo*, and *Poorea tartanensis*.

Group 8 (clade 19) comprised two provinces in the Mediterranean and adjacent Atlantic, clustered at ~0.8 (AU = 93, BP = 53), including endemic species such as: *Azobacescus longidactylus*, *A. mosteiros*, *Bathyleptochelia selvagema*, *Chondrochelia caldera*, *C. corsica*, *Leptochelia tanykeraia*, *Mesotanais dubius*, *M. elongatus*, *M. pinguiculus*, *M. styxis*, and *Pseudoleptochelia anomala*.

Clade 24 clustered at ~0.9 due to *C. savignyi*, with weak support (AU = 92, BP = 4) and was split into:

Group 9 (clade 4) associated with *Heterotanais oerstedii* and *C. savignyi*.

Group 10 (clade 17) comprising four provinces clustered at ~0.7 (AU = 90, BP = 10), including *Leptochelia barnardi*, *L. columbina*, and *L. timida*.

Additionally, three poorly supported clusters (AU ~ 80, BP ~ 40) were found at: NE Australia and Melanesia, central Indo-Pacific, and SE Australia and Polynesia.

Environmental predictor

The model using oxygen as the sole environmental predictor for species richness along latitude had the lowest AIC value (182.378) and the highest Akaike weight (0.998). For ES15, the model using oxygen had the lowest AIC (114.070) and the highest Akaike weight (0.661); however, it was followed by the model with temperature, with a difference of 1.342 (Table 1). High collinearity of those two factors needs to be mentioned.

In case of species richness organized in hexagons, the model using salinity as a predictor exhibited the lowest AIC value (429.103), and the highest Akaike weight (0.301), indicating it had the strongest support among the candidate models. The model was closely followed by the model using all factors and oxygen only (ΔAIC equal 0.58 and 1.332, respectively). The model-averaged importance scores revealed that among the environmental variables, salinity showed high importance (sum of weight = 0.87), oxygen presented low influence

Table 1 Models selection calculated for species richness and estimated species richness organized in latitudinal band

	Model	AIC	ΔAIC	rel.LL	weights	Cumulative.Weight
Species richness	GLM.oxygen	182.378	0	1	0.994	0.994
	GLM.temperatue	192.704	10.325	0.005	0.005	0.999
	GLM.salinity	239.721	57.342	3.533	0.000	0.999
	GLM.nitrate	247.805	65.426	6.206	0.000	0.999
	GLM.phosphate	249.651	67.272	2.465	0.000	1
	GLM.productivity	259.343	76.964	1.937	0.000	1
	GLM.records	268.280	85.901	2.221	0.000	1
	GLM.latitude	268.353	85.974	2.142	0.000	1
	GLM.chlorophyll	270.197	87.818	8.519	0.000	1
	GLM.intercept	309.081	126.702	3.068	0.000	1
Estimated species richness	GLM.oxygen	114.070	0	1	0.661	0.661
	GLM.temperature	115.412	1.342	0.511	0.338	0.999
	GLM.nitrate	135.462	21.391	2.263	1.497	0.999
	GLM.phosphate	137.338	23.268	8.858	5.861	0.999
	GLM.salinity	142.452	28.381	6.869	4.545	0.999
	GLM.productivity	144.322	30.252	2.696	1.784	0.999
	GLM.intercept	151.017	36.946	9.485	6.276	0.999
	GLM.chlorophyll	153.247	39.177	3.109	2.057	0.999
	GLM.latitude	153.328	39.258	2.986	1.976	1

(0.14), and other factors were almost insignificant (<0.01). For ES15, the most supported model was the one including all environmental factors, which had the lowest AIC (411.002) and the highest model weight (0.445). However, the model using temperature with an ΔAIC of 0.40 also seems to be a good model. The model-averaged importance scores showed that among environmental variables, temperature showed the highest importance (1). In contrast, other predictors: oxygen, salinity, primary productivity, phosphate, nitrate, and chlorophyll had low scores (0.2), indicating weaker and less consistent contributions (Table 2) (Online resource 2).

Discussion

Our study presents the first global-scale assessment of distribution patterns within the family Leptocheliidae, highlighting their potential as effective bioindicators. We identified a clear latitudinal gradient in species richness and pinpointed specific regions of high biodiversity and endemism. This knowledge, combined with an understanding of the key factors influencing their diversity, may contribute to the early detection of environmental stress and ecosystem change.

An overview of biodiversity and its global hotspots

Recent research has confirmed a bimodal latitudinal diversity pattern in marine invertebrates across various taxonomic and ecological groups, including benthic and pelagic amphipods, pelagic foraminiferans, and benthic clams (Fautin et al. 2013; Chaudhary et

Table 2 Models selection calculated for species richness and estimated species richness organized in hexagons

	Model	AIC	ΔAIC	rel.LL	weights	Cumulative.Weight
Species richness	GAM.salinity	429.103	0	1	0.301	0.301
	GAM. all_factor	429.685	0.582	0.747	0.225	0.526
	GAM.oxygen	430.435	1.332	0.513	0.154	0.681
	GAM.productivity	432.424	3.321	0.190	0.057	0.739
	GAM.chlorophyll	432.424	3.321	0.189	0.057	0.796
	GAM.latlong	432.425	3.322	0.189	0.057	0.853
	GAM.nitrate	432.426	3.322	0.189	0.057	0.910
	GAM.phosphate	432.668	3.564	0.168	0.050	0.961
	GAM.temperature	433.225	4.122	0.127	0.038	0.999
	GAM.records	463.363	34.260	3.634	0.000	1
	GAM.intercept	517.744	88.641	5.645	0.000	1
Estimated species richness	GAM.all_factor	411.002	0	1	0.445	0.445
	GAM.temperature	411.411	0.4093	0.814	0.362	0.808
	GAM.oxygen	415.008	4.006	0.134	0.060	0.868
	GAM.salinity	416.248	5.246	0.072	0.032	0.900
	GAM.phosphate	416.360	5.358	0.068	0.030	0.930
	GAM.nitrate	417.238	6.235	0.044	0.019	0.950
	GAM.chlorophyll	417.598	6.596	0.036	0.016	0.967
	GAM.productivity	417.598	6.596	0.036	0.016	0.983
	GAM.latlong	417.598	6.596	0.036	0.016	0.999
	GAM.intercept	436.249	25.247	3.293	0.000	1

al. 2016; Saeedi et al. 2017a, b; Momtazi and Saeedi 2024). Our findings in Leptocheliidae align with this general pattern, with diversity increasing toward lower latitudes and declining near the equator. Peak estimated species richness occurred at 5° N for Leptocheliidae, compared with maxima for clams and pelagic and benthic amphipods occurred at 10°S, 30°N, and 45°N, respectively. Anemones peaked between 30º and 10° in both hemispheres (Fautin et al. 2013). These intertaxon differences likely reflect varying tolerances to environmental factors across taxa, although methodological inconsistencies may also influence the observed global diversity and distribution patterns (Núñez–Flores et al. 2019; Saeedi et al. 2019).

The Indo-Australian region and central Indo-Pacific exhibited the highest species richness and estimated richness of Leptocheliidae, particularly among reef-associated taxa, confirming previous findings of exceptional biodiversity in these areas (Reaka et al. 2008; Veron 2011; Arfianti and Costello 2021). High topographic complexity, a history of geological dynamics and presence of deep basins acting as refugia during Pleistocene glaciations likely underpin this diversity (Paulay 1990; Reaka et al. 2008). In addition, the region's position at the confluence of Indian and Pacific currents further facilitates faunal exchange (VeronThon'sregi po 1996; Bowen et al. 2013). Notably, 21 undescribed coral-associated Leptocheliidae species were discovered—12 from the Great Barrier Reef and nine from Ningaloo Reef.

Beyond the Indo-Pacific, the Gulf of Mexico and the Caribbean Sea constitute the second most diverse region in terms of marine species richness. This biodiversity is rooted in geological events such as the Cretaceous formation of the Yucatan and Florida Peninsulas, which isolated water masses and shaped a distinct hydrological regime in the Gulf

of Mexico (Vázquez-Domínguez and Arita 2010; Turner and Rabalais 2019). Pleistocene glaciations and sea-levels fluctuations further modified shallow margins (Davis et al. 2017; Mendelssohn et al. 2017), creating a mosaic of habitats including seagrass beds, tidal flats, mangroves, salt marshes, and deep-water habitats. Presently, the Gulf of Mexico is influenced by both temperate and tropical conditions (McKinney et al. 2021).

Leptocheliidae diversity in the Gulf reflects its ecological heterogeneity. Deep-water taxa such as *Mesotanais longisetosus* and *M. vadicola* inhabit bathyal zones (Sieg and Heard 1989), while *Chondrochelia winfieldi* is associated with macroalgae and soft-bottom substrates (Jarquín-González and Carrera-Parra 2022). Coral reef systems host warm-water species, including *Alloleptochelia longimana* and *Leptochelia forresti* (Cházaro-Olvera et al. 2018).

In the Caribbean, biodiversity expanded following the closure of the Isthmus of Panama ~ 3 Ma, which altered regional marine connectivity and isolated fauna from the Indo-Pacific (Jaramillo et al. 2018). This event contributed to the diversification of specific faunal groups associated with coral reefs, seagrass beds, and mangroves (Miloslavich et al. 2010). Most Caribbean Leptocheliidae are predominantly coral-associated, such as *Chondrochelia ortizi* (Jarquin-Gonzales 2016) and *Leptochelia longichelipes* (Lang 1973), or inhabit algae-rich environments, including *Hargeria chetumalensis* and *C. caribensis* (Jarquin-Gonzales and Carrera-Parra 2019; 2022).

Outside tropical hotspots, regions of moderate biodiversity, such as the Mediterranean, adjacent Atlantic, and temperate Australia, exhibit distinct ecological traits and notable faunal richness. Although the overall number of species is lower, biodiversity levels may rival those of the Caribbean, Gulf of Mexico, or central Indo-Pacific, when considering endemism and ecological distinctiveness. The Mediterranean's intricate geological history, including isolation from the Atlantic during the Messinian Crisis and Pleistocene glacial impacts, produced a faunal comprising boreal, tropical, subtropical, and endemic species (Blondel 2010; Bianchi et al. 2012). This legacy includes the boreal *Heterotanais oerstedi*, the warm-water Atlantic *C. savignyi*, and endemic *L. tanykeraia* from the Israeli coast. The presence of deep-water *Mesotanais* species (*M. dubius*, *M. elongatus*, and *M. pinguiculus*), shared with the Gulf of Mexico (Sieg and Bird 1989), highlights biogeographic connections. Volcanic Macaronesia islands, also contribute unique taxa such as *C. caldera* and *Azobacescus mosterios* (Bamber and Costa 2009; Bamber 2014).

In the southern hemisphere, temperate Australian ecosystems illustrates how geological history shapes marine biodiversity. Following its separation from Antarctica in the late Cretaceous, Australian fauna evolved largely in isolation, punctuated by occasional influxes of tropical and temperate species (Poore and O'Hara 2007). This evolutionary trajectory has produced highly specialized benthic communities, with endemism rates reaching 95% (Poore and O'Hara 2007; Butler et al. 2010; Waters et al. 2010). Characteristic Leptocheliidae taxa from this region include *C. billambi*, *C. occiporta*, *Bassoleptochelia verro*, and *Araleptochelia macrostonyx* (Błażewicz-Paszkowycz and Bamber 2012).

Environmental factors influencing species richness

Oxygen was the most important factor influencing on diversity of Leptocheliidae at global scale – across latitude gradient. Temperature was identified as a supporting driver, affecting diversity both locally (in hexagons) and across latitudes. Due to the correlation between

oxygen and temperature, their importance likely reflects a shared ecological signal rather than entirely independent effects.

The highest diversity of leptocheliids was observed at intermediate oxygen levels, typical of lower and warmer latitudes. In contrast, the oxygen-rich subpolar regions are inhabited by relatively few species. It is hypothesized that respiratory costs increase in cold, viscous water, requiring aquatic ectotherms to evolve specific physiological adaptations (Spicer et al. 2019). However, developing such adaptations may be too challenging for organisms that evolved in tropical environments, where their respiratory systems were shaped by warm-water conditions—such as in the case of Leptocheliidae. This phylogenetically ancient family originated and diversified in shallow, warm seas during the Cretaceous period (Vonk and Schram 2007). As a result, their physiology may limit their ability to colonize and diversify in the cold, and highly oxygenated ecosystems of subpolar and polar waters (Błażewicz-Paszkowycz, 2014). Similar pattern is observed within other typically shallow-water and phylogenetically old tanaidacean families like Tanaididae, or Paratanaidae as well as some crustacean including decapods (Sieg 1992; Legeżyńska et al. 2020).

Leptocheliidae diversity reaches its maximum in tropical waters but declines toward the equator where temperatures are highest. This pattern, commonly observed in many marine species is likely driven by thermal stress (Chaudhary et al. 2016; Saeedi et al. 2019; Arfianti and Costello 2020). Fossil evidence indicates that similar trends occurred during postglacial warming events in the Quaternary (Chaudhary et al. 2016, 2021; Yasuhara et al. 2020).

A third factor, moderately influencing Leptocheliidae diversity across hexagonal grids was salinity. Most species in the Leptocheliidae thrive in fully marine conditions, where the species richness is the highest. However, *Heterotanais oerstedii* exhibit remarkable tolerance for low-salinity environments at 2 to 25 PSU, well below the threshold tolerated by most other Leptocheliidae (Bonifazi et al. 2017; Bałazy et al. 2019; Brzana et al. 2019). This broad salinity tolerance was clearly reflected in models assessing salinity as predictor of species distribution.

Conservation implications for species and habitats

Most Leptocheliidae species exhibit narrow distribution ranges. Cluster analysis revealed ten assemblages, five of which (temperate Australia, temperate NW Pacific, Mediterranean, cold NW Atlantic – Pacific, and Subantarctic) comprised predominantly endemic taxa and were strongly supported. The remaining five groups (temperate SW and NW Atlantic, NE Australian coast and Melanesia, central Indo-Pacific, and SE Australia and Polynesia) had weaker support and should be interpreted with caution. High endemism in Tanaidacea is linked to their absence of planktonic larval stage and low adult mobility (Larsen 2005; Błażewicz–Paszkowycz et al. 2012; Bamber 2013), a pattern also observed in other peracarids (Arfianti and Costello 2020; Quintanar–Retma et al. 2024; Viera et al. 2022).

Many endemic or species-rich assemblages occur in habitats increasingly threatened by climate change and anthropogenic pressures, such as coral reefs in the Caribbean and tropical Australia (Knowlton 2001; Spalding and Brown 2015; Hoegh-Guldberg et al. 2017, 2018). Reef degradation from rising temperatures and ocean acidification poses the most serious risk as the three-dimensional coral reefs structure underpins diverse microhabitats critical to sustaining species richness (Nelson et al. 2016; González-Gómez et al. 2018). While dead coral may provide short-term refuge, structural declines reduce long-term suit-

ability (Fabricius et al. 2014; Idjadi and Edmunds 2006) and rapid degradation often outpaces reef recovery, leading to invertebrate community collapse (Nelson et al. 2016).

High-diverse and endemic Leptocheliidae assemblages were also recorded in temperate Australian waters and colder regions such as the Subantarctic, NW Atlantic, and Pacific, where climate change is expected to reshape community composition and distribution (Johnson et al. 2011; Hughes 2011; Ingels 2012). In southern Australia and Tasmania, warming may alter macroalgal communities and lead to local extinctions of species near northern range limits (Wernberg et al. 2011). Temperature rise can impar vital biological functions such as feeding and locomotion in small, low-mobility invertebrates (Ingels et al. 2012). Studies on the Antarctic peracarid, *Serolis polita*, showed righting and burying behaviors were more sensitive to warming than swimming (Janecki et al. 2010), suggesting that cold-water Leptocheliidae may also be vulnerable to climate-driven disruptions in functional traits.

In the Mediterranean narrow ecological tolerances render endemic Leptocheliidae highly susceptible to biological invasions and pollution. Invasive peracarid crustaceans with overlapping niches, such as amphipods (*Caprella scaura*), isopods (*Paranthura japonica*, *Sphaeroma walkeri*), and tanaidaceans *Zeuxo turkensis* (Molina et al. 2017; Martinez-Laiz et al. 2018; Stępień et al. 2023), pose major threats due to their competitive advantage for food and habitat. Although *Chondrochelia savignyi* may colonizes new habitats rapidly, long-term observations suggest ultimately outcompeted by the opportunistic *Z. turkensis* (pers. obs).

Given the broad geographic span of endemic leptocheliid assemblages—from tropical coral reefs to temperate and subantarctic zones—a regionally adapted but unified conservation strategy is essential. Priorities include:

(1) Habitat protection and management of critical habitats (e.g., coral reefs, macroalgal beds): establish or expand Marine Protected Areas (MPAs) in biodiversity hotspots and climate-vulnerable regions or in areas facing environmental shifts.
(2) Monitoring of environmental and biological indicators: Implement long-term ecological monitoring targeting small benthic invertebrates, such as Leptocheliidae across key regions.
(3) Integrative taxonomic and functional studies: Many species of Leptocheliidae remain undescribed, especially in tropical and deep-sea environments. Invest in taxonomic research to understand species identities, ranges, and ecological roles, particularly in tropics where vulnerability to climate driven stressors remains high.

Methodological limitations

Global patterns in Leptocheliidae diversity are shaped by both ecological and sampling biases. While diversity general increases toward lower latitudes, a pronounced peak at 20° S—nearly double the richness observed at other latitudes—was identified. This peak is largely attributed to intensive coral reef surveys along the Australian coastline (10–20° S) conducted under the Census of Coral Reef Ecosystems (CReefs) as part of the Census of Marine Life (Plaisance et al. 2009, 2011a, b). By targeting small, often-overlooked invertebrates, these surveys markedly inflated recorded Leptocheliidae richness (Knowlton et al.

2010). Given the absence of equally intensive surveys elsewhere suggests, this peak likely reflects sampling bias rather than genuine global diversity maxima.

Expected species richness provides a more balanced perspective, correcting for over-representation and revealing underappreciated diversity at latitudes such as 40° S and 5° S (Fig. 1a, b). Nevertheless, even with ES15 adjustments, under-sampling remains evident, particularly in the Southern Hemisphere. Records from this region are dominated by Australian coast, while extensive gaps along the African and South American coasts. This mirrors the broader pattern of limited sampling in developing regions. Likewise, the Indian coastline in the Northern Hemisphere remains inadequately surveyed. This lack of correlation between observed or estimated richness and sampling effort (Fig. 1a–c) further underlines these spatial gaps.

Spatial autocorrelation also influenced diversity patterns. For observed species richness per hexagons, the difference between the best-fitting model including salinity and the spatial-only model was minor ($\Delta AIC = 3$), suggesting spatial structure plays a substantial role, while salinity contributes only modestly. In ES15 models per hexagon, spatial autocorrelation had a weaker effect, with the environmental model notably outperforming the spatial-only model ($\Delta AIC = 6.5$), indicating a stronger influence of the environmental factor.

In models evaluating environmental effects on species richness and ES15 across latitudinal bands, the best-fitting models including oxygen or temperature yielded much better fits than the spatial-only models ($\Delta AIC > 40$), clearly demonstrating that environmental factors substantially shape spatial diversity patterns.

Finally, the accuracy of our data may be influenced by potential mistakes in taxonomical identification in source databases. Widely recorded species such as *Chondrochelia dubia*, *C. savignyi*, and *Heterotanais oerstedii* present identification challenges due to pronounced polymorphism and sexual dimorphism, especially in females (Lang 1973; Bamber 2010; Iwasa-Arai et al. 2024). The distribution of *C. savignyi* has been revised to the Mediterranean and adjacent Atlantic regions (Bamber 2010), while cosmopolitan status of *C. dubia* is disputed, with some records—e.g. from the Mexican Caribbean and Gulf of Mexico—reassessed (Jarquín-González and Carrera-Parra 2022). The distribution of *H. oerstedii* remains unrevised. Until these species are critically reassessed, interpretations of their global distributions should be approached with caution. Consequently, clades supported solely by the occurrences of these three species were not taken into consideration.

Conclusion

Our analysis reveals high diversity within the Leptocheliidae family and underscores their potential as indicators of environmental changes across different regions. We identify specific biodiversity hotspots, each with endemic assemblages and relatively high statistical support, that are at risk of population decline, structural changes, or even extinction. Key regions include:

- temperate Australia with endemic *Alloleptochelia evansi*, *Araleptochelia macrostonyx*, *Bassoleptochelia verro*, *Chondrochelia billambi*, *C. ignota*, *C. occiporta*, *Parakonarus corrigendum*, *P. robertsoni*, *Poorea johannesi*, and *P. wrighti*.
- Subantarctic region with *Pseudonototanais bransfieldensis*, *Leptochelia antarctica,* and

P. werthi,

- temperate NW Pacific, with endemic *Makassaritanais itoi*, *M. grandidentatus*, *M. modestus*, *Chondrochelia sublitoralis*, *C. taitungensis*, *Mesotanais birdi*, and *Paraleptochelia setosa*.
- cold North Atlantic and Pacific, with endemic *Heterotanais groenlandicus* and *Pseudonototanais filum*.
- Mediterranean and adjacent Atlantic, with *Azobacescus longidactylus*, *A. mosteiros*, *Bathyleptochelia selvagema*, *Chondrochelia caldera*, *C. corsica*, *Leptochelia tanykeraia*, *Mesotanais dubius*, *M. elongatus*, *M. pinguiculus*, *M. styxis*, and *Pseudoleptochelia anomala*.

We found that the species richness of Leptocheliidae is influenced by factors such as oxygen levels, temperature, and moderately by salinity. Consequently, the ongoing increase in ocean temperatures, local pollution, eutrophication, and the associated reduction in oxygen levels will negatively impact the diversity of Leptocheliidae.

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Data availability The datasets generated during and analyzed during the current study are available in the Mendeley repository [https://data.mendeley.com/datasets/82sy86s859/1](https:/data.mendeley.com/datasets/82sy86s859/1).

Declarations

Competing interests The authors declare no competing interests.

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