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# Bipolarity and Antitropicality in Marine Taxa: Understanding the Complexities of Latitudinal Distribution

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**ABSTRACT**

**Aim:** This systematic review aims to analyse the current status of research on marine bipolar and antitropical distribution patterns by exploring temporal trends, studied taxa, inconsistencies in definitions and the extent of molecular evidence in bipolar and antitropical species.

**Location:** Global marine environments, with a special focus on Polar Regions.

**Time Period:** 1800s to 2024.

**Major Taxa Studied:** Marine taxa across all phyla, ranging from algae and zooplankton groups to fish and cetaceans.

**Methods:** A systematic literature search was conducted using Scopus, PubMed and Google Scholar databases. Studies were screened for relevant publications of marine taxa displaying bipolar or antitropical distributions, and data were extracted in order to perform a numerical summary of aspects including temporal trends, taxa representation and agreement with this article's standardised definitions. Additional data were gathered from The Arctic Register of Marine Species (ARMS) and The Register of Antarctic Marine Species (RAMS) databases. Distribution data were then extracted to verify the potential bipolarity of species present in both databases.

**Results:** From 221 articles, 665 marine taxa records were extracted, of which 517 records were categorised as antitropical and 148 as bipolar. Molecular evidence existed for 25% of non-paleontological records. A considerable amount of records (44%) did not match the definitions used in this review. The data taken from ARMS and RAMS revealed 408 shared species, of which 41 species were listed as bipolar by the literature collected in this study.

**Main Conclusions:** Marine bipolarity and antitropicality have been topics of interest since the 1800s, especially between 2008 and 2017. However, the discrepancy between the number of potentially bipolar species in publicly available species databases and literature-based estimates underscores the need for further research of neglected taxa. Future research should prioritise including molecular evidence, transparent terminology and interdisciplinary approaches to address the complexities of marine disjunct distributions.

## 1 | Introduction

Intriguing researchers for decades, disjunct distributions of marine fauna have been documented at all taxonomic levels, from species to families. One of the most distinctive disjunct patterns is called 'bipolarity'—when identical or closely related taxa naturally occur in polar environments of both hemispheres without connecting populations in the tropics (Briggs 1987a; Crame 1993; Lindberg 1991). While bipolarity is rarer, as it refers to populations or closely related species

restricted only to the poles, antitropicality, introduced by Hubbs (1952), is a more common latitudinal distribution pattern, as it refers to temperate species that are present on both sides of the tropics. Recognised in both the fossil record and living populations, the presence of these disjunct distributions, especially strict bipolarity, has remained a classic topic of debate as far back as the 1800s (Herdman 1898; Murray 1898; Ortmann 1898).

As the field of biogeography advanced, hypotheses for latitudinal disjunct distributions were proposed under the two broad mechanisms: vicariance or dispersal (Allcock and Griffiths 2015; Lindberg 1991; Ludt 2021; Stepanjants et al. 2006). While there have been other hypotheses suggested from convergent origin (Stepanjants et al. 2006) to anthropogenic transport (Hudson, McQuaid, and Rius 2020), vicariance and dispersal are the most commonly suggested origins of these distributions. Vicariance-based hypotheses suggest that species with a widespread, cosmopolitan distribution were wiped out by the emergence of a biogeographical barrier (Briggs 1987b; Crame 1993). Within this framework, potential explanations include mid-Miocene warming that limited distribution ranges to the organisms' physiological tolerances (White 1986), biotic exclusion from competition with tropical species that spread into temperate zones (Ekman 1953) and island integration from tectonic plate movements (Rotondo et al. 1981; Springer 1982). Meanwhile, dispersal-based disjunct distributions can be explained by cooler temperatures during glacial maxima in the tropics being sufficient to facilitate trans-tropical migration for a species previously present in only one hemisphere (Ekman 1953). The prevailing evidence that supports this dispersal process is a descent of polar species into deeper, colder waters at the tropics assisted by cold-water currents that join both polar systems, which is a more prevalent hypotheses for taxa in more recent evolutionary timescales (Crame 1993; Ekman 1953; Poortvliet et al. 2013).

Despite varying hypotheses, these mechanisms are not discrete but represent points on a continuum of distributional possibilities that could be influenced by similar or even identical evolutionary processes (Jurado-Rivera et al. 2017; Sanmartín 2012). The plasticity of these patterns suggests that they are dynamic and can shift over time depending on environmental conditions and species' adaptive responses. For example, both patterns could be influenced by similar evolutionary pressures such as climate fluctuations, species dispersal capabilities and ecological interactions. The potential fluidity and interconnectivity of these distribution patterns needs to be recognised, since historically recorded bipolar taxa may have shifted to an antitropical distribution in the past, and these same taxa could now be moving back towards the poles due to a warming ocean (Grant and Leslie 2001; Lindberg 1991). In addition, these mechanisms leading to bipolarity and antitropicality are not exclusive by taxonomic group, with different hypotheses potentially explaining the distribution of species/genera in the same phylum; for example, Grant and Leslie (2001) suggested that a bony fish genus, *Merluccius*, dispersed back and forth across equatorial waters depending on climate oscillations, while Francisco et al. (2011) proposed that the distribution of another bony fish genus, *Atherina*, was triggered by glacial events in the Pleistocene. It is widely accepted that bipolarity

is not just purely a distribution pattern but that it is a plastic phenomenon, so the ecology and oceanic processes need to be considered when discussing biogeography. This is why, despite various points of view, equatorial submergence, where species with disjunct distributions occur in deep waters in the tropics, should also be considered a valid form of bipolarity (Stepanjants et al. 2006).

Concerning bipolar distributions, it is important to note that both polar marine systems share several fundamental similarities, such as high latitude positioning and extensive ice coverage, but there are also key differences in their physical environments that impact the distribution of marine taxa, from megafauna to zooplankton communities. The Arctic receives freshwater input from surrounding continental land masses and experiences intensifying levels of warm, salty water from the Atlantic Ocean (Polyakov et al. 2017). The resulting borealization of the Arctic not only pushes polar marine life to their environmental tolerance thresholds but also causes an inflow of Atlantic species with different functional roles than traditional polar species (Basedow et al. 2018; Mańko, Gluchowska, and Weydmann-Zwolicka 2020). On the other side of the globe, the Antarctic is less vulnerable to the introduction of subantarctic/notalian species, in part due to the Antarctic Circumpolar Current acting as a natural barrier, preventing easy movement of species between latitudes (Dueñas et al. 2016; McBride et al. 2014). However, in the future, Antarctic polar species may shift their distribution in search of cooler habitats, contracting their range to higher latitudes, as described for the Arctic. This shift, together with the southward migration of the Antarctic Polar Front and changes in oceanic eddies or mesoscale circulation patterns, leaves an opportunity for the penetration of notalian species further south. These small-scale processes can act as transport mechanisms, particularly benefiting species with high dispersal potential by creating temporary pathways across current barriers (Azarian et al. 2024; Murphy et al. 2021; Wilson et al. 2016). These processes at both poles can have far-reaching consequences because true polar species, including those that are bipolar, are sensitive to environmental stressors due to specialised adaptations to polar regions such as build-up of energy stores for overwintering, slower growth rates and antifreeze proteins (Johnston 1990; Morley, Barnes, and Dunn 2019; Murphy et al. 2021). This means that while it may be difficult for true polar species to adapt to warmer conditions, the expansion of suitable habitats for boreal/notalian species into higher latitudes could blur the connectivity and traditional boundaries between polar and temperate ecosystems. As climate change intensifies, the mechanisms and consequences of climate-induced shifts on the latitudinal distribution of marine taxa are essential for predicting and managing ecosystemic impacts in the Polar Regions (Alabia et al. 2023; Seabra et al. 2015).

The development of new technology has allowed researchers to investigate species with greater morphological detail and use molecular techniques to help determine if a species is truly bipolar. With the shift in recent years from standard barcoding of specimens using universal primers and Sanger sequencing to the design of group or species-specific primers and using high-throughput techniques, researchers

are now able to resolve taxonomic uncertainties and population structure with better accuracy (Andrews et al. 2016; Santiago et al. 2023). This molecular evidence is necessary to verify the status of currently considered bipolar taxa (Angel and Błachowiak-Samołyk 2006), since morphological similarity alone is not sufficient (Allcock and Griffiths 2015; Ludt 2021; Sul et al. 2013). There have already been cases of bipolarity that were accepted based on morphological characteristics, as seen in the example of *Limacina helicina* (Lalli and Gilmer 1989), which was later molecularly proven to be false (Hunt et al. 2010). In addition to cryptic diversity biasing biogeographic patterns, conflicting identifications from changing taxonomy are a challenge when recognising species distribution ranges (Burridge and White 2000; Crame 1993; Kulagin and Neretina 2017). In general, bipolarity is thought to be rare on a species level and more common for genera or families (Briggs 1987b; Menegotto and Rangel 2018; Ronowicz et al. 2019). While taxonomic resolution is important, even at a higher taxonomic level, establishing baseline distribution patterns of specific taxa in Polar Regions will be helpful in monitoring changes in population ranges under climate change. For smaller taxa such as ostracods and copepods, understanding the extent of bipolarity will allow for modelling more accurate ecosystemic impacts, while for larger species such as fish and cetaceans, this could lead to more targeted conservation efforts if vulnerable species are confirmed to have diverging populations in another hemisphere.

However, our recognition of the existence and range of bipolarity is greatly limited due to high levels of inconsistency of the language used in the literature due to a current lack of universally accepted definitions, from using 'bipolar' when the northern hemisphere species range includes Mexico (Santelices 1980; Zaneveld and Sanford 1980) to using 'cosmopolitan', 'antitropical' and 'bipolar' interchangeably (Damborenea 1993; Rocka 2006). Antitropicality is even more difficult to define, as researchers report various latitudinal coordinate restrictions or temperature-based limitations in their definitions. 'Amphitropical' appears occasionally in the literature, but it is not as prevalent as the other terms, and since the Latin meaning is 'both tropics', Cox (1990) recommended against using this term to define disjunct distribution. This systematic review was initially conceptualised to focus on bipolarity, but the term and concept were so intertwined with antitropicality that a more holistic approach was determined to make a better contribution to the field of biogeography.

The main purpose of this review is to analyse the current status of research on marine bipolar and antitropical distributions to provide the first compiled list of studies that have researched these complex latitudinal distributions. This included investigating the temporal trends of research in this field, exploring the list of studied taxa, identifying common inconsistencies in terminology and their implications on ecological interpretation, and determining the extent of taxa that have molecular evidence suggesting bipolarity or antitropicality. By synthesising extracted information from previous studies in this field, it can help drive future research questions such as how shifts in distribution patterns (e.g. antitropical species becoming bipolar) impact ecosystem function in polar marine systems. This review comes at a relevant point in time as the threat of warming waters continues to accelerate at an unprecedented rate.

## 2 | Methods

### 2.1 | Definition

For the purpose of this study, bipolarity was defined as the area above the Arctic Circle (66°33′N) and below the Antarctic Circle (66°33′S) (Figure 1). Records that specifically stated deep equatorial submergence (Type II bipolarity by Stepanjants et al. 2006) were grouped together in the bipolar sheet. The Hubbs (1952) definition of antitropicality was modified to be inclusive of species present in polar and/or temperate regions but still absent in the tropics. In this study, antitropicality referred to the area above the Tropic of Cancer (23°26′N) in the northern hemisphere and the area below the Tropic of Capricorn (23°26′S) in the southern hemisphere (Figure 1). There were various definitions of disjunct distributions present in the literature, with some using thermal boundaries or ecoregions, which are better suited for specific regions, but the latitudinal boundary defined here was used for higher generality and greater comparability between studies.
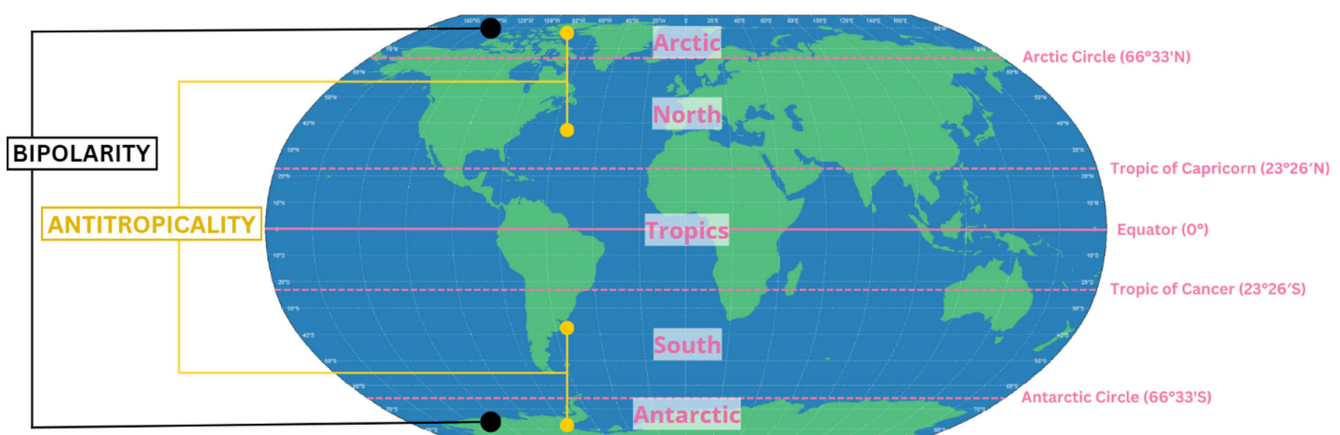


**FIGURE 1** | Graphic showing latitudinal ranges of the determined definition of bipolarity and antitropicality used in this study. This graphic was created in the design program Canva in January 2024.

## 2.2 | Literature Search Strategy

Using standard systematic review protocols following the Preferred Reporting Items for Systematic reviews and Meta-Analyses PRISMA guidelines (Page et al. 2021), keyword searches were conducted on the following databases: Scopus, PubMed and Google Scholar (Figure 2). The search string ('bipolar' OR 'bipolarity' OR 'antitropical' OR 'antitropicality' OR 'anti-tropical' OR 'antiequatorial' OR 'anti-equatorial') AND ('marine species' OR 'marine') was used to broadly identify articles with these terms in the title, abstract, or keywords (literature accessed: 1 April 2024). Any instances of 'anti-equatorial' and 'amphitropical' were merged as 'antitropical' for clarity. There was no cut-off date in the search strategy because fundamental research on disjunct distributions has

been published since the 1800s. The nature of the phrase 'bipolar' resulted in irrelevant articles in health sciences (e.g. bipolar disorder), biological sciences (e.g. bipolar cells) and morphological terminology (e.g. bipolar flagella), requiring manual screening of each article. Reviews were not included, as they provided redundant information, but references to each review were checked for additional relevant articles that may have been missed during the methodological literature search. Full-text publications retained in the final analyses met the following four criteria:

1. Publications were about research on disjunct distributions, studying either bipolarity or antitropicality of marine taxa. Publications proving, disproving, or discovering these distributions were included.
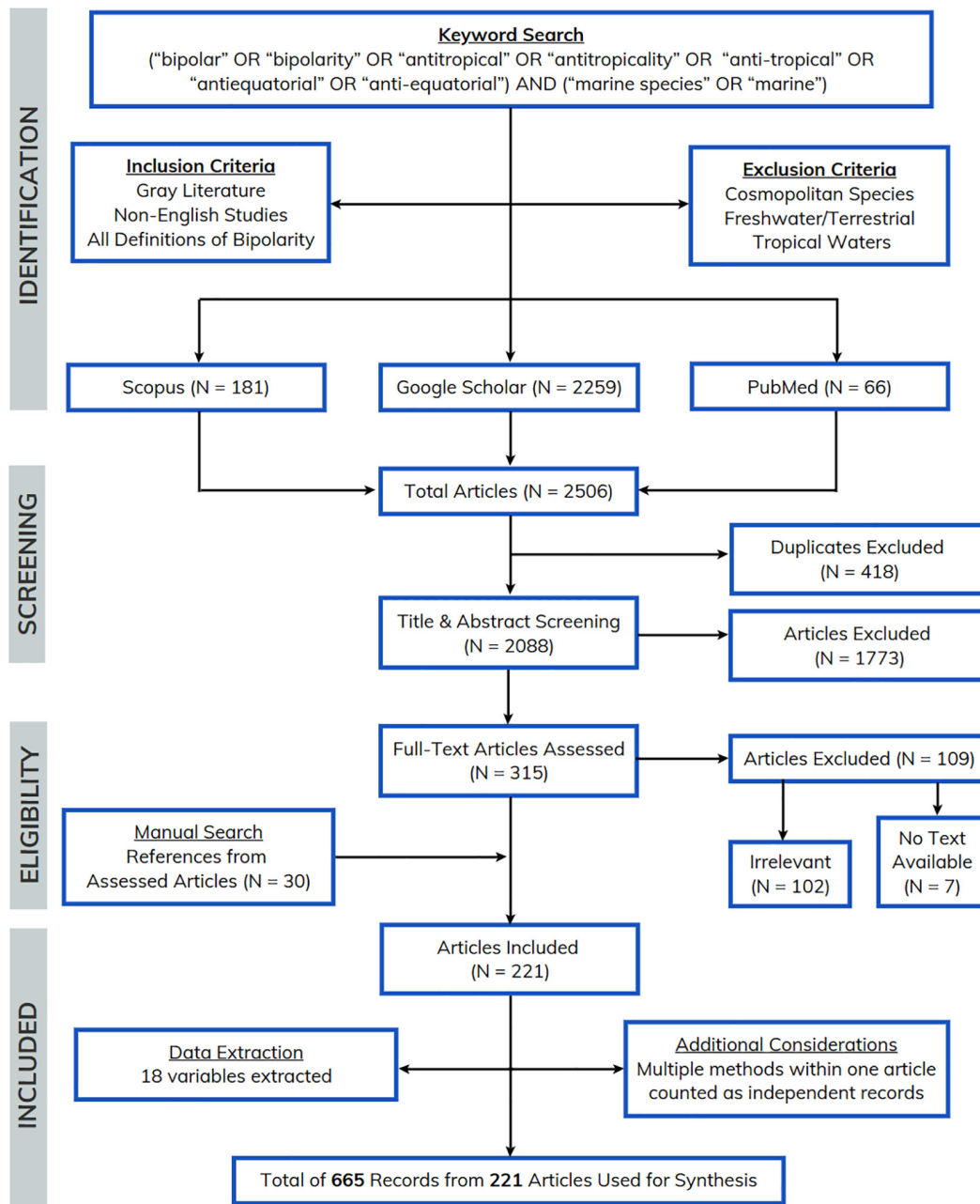


**FIGURE 2** | Flowchart following the Preferred Reporting Items for Systematic Review and Meta-analysis Protocols (PRISMA-P) PRISMA guidelines.

2. Publications were focusing on fully aquatic marine species. Publications on terrestrial or semi-aquatic species were excluded.

3. Publications were targeting non-cosmopolitan species. Publications focusing on historical biogeography and the fossil record were included.

4. Grey literature and non-English publications were included to reduce bias (Paez 2017). Grey literature included government reports, unpublished dissertations and research organisation reports.

## 2.3 | Article Screening and Data Collection

After compiling the list of articles outputted by the browsers, the reference lists of retained articles were scanned to gather additional literature. Because many of the articles from the early 1900s were digitally scanned from the original paper version, their outputs by automatic browsers were limited. Since a database search often does not match key words of scanned papers, older articles' reference lists needed to be manually checked for additional relevant literature. If articles stated examples of bipolarity or antitropicality in the text without either conducting the research or providing references for the examples, these articles were not included.

Following standard systematic review methodology, an article that studied multiple taxa was processed as separate records (e.g. a paper stating three species were bipolar would be inputted as three distinct records originating from the same reference). Data extracted included general article characteristics (i.e. authors, year published and journal name) and methodology (i.e. target taxa, location and molecular evidence). A comprehensive list of source references and data extracted from each study can be found in Table S1. For standardisation in analyses, all of the records were assigned to be bipolar or antitropical following the definitions set in this article regardless of the term the authors used. Deviations between the definitions of this study and the terms used by the authors were noted for subsequent analyses.

## 2.4 | Comparison of Species in Polar Databases

In a parallel analysis with the literature review, the concept of bipolarity was also tested by exploring lists of taxa from the Arctic Register of Marine Species (ARMS) and the Register of Antarctic Marine Species (RAMS) databases, which contain a comprehensive list of species present in both Polar Regions. Species lists from ARMS (https://www.marinespecies.org/arms/) and RAMS (https://www.marinespecies.org/rams/) were accessed and downloaded directly from the portals. The currently valid names were extracted from the World Register of Marine Species (WoRMS) to identify shared species in both databases, which acted as a proxy for potentially bipolar species. These databases included all species present in these Polar Regions, not necessarily restricted to either pole, so the Ocean Biodiversity Information System (OBIS) occurrence records were used to confirm bipolar distribution from the list of shared species in both ARMS and RAMS. The OBIS occurrence data were separated into Arctic,

North, Tropic, South and Antarctic according to the latitudinal definitions provided in this study. All of the data extracted from these databases can be found in Table S2.

## 3 | Results

### 3.1 | Record-Level Trends

A total of 665 records of marine taxa were extracted from 221 articles. From these 665 records, there were a total of 551 unique (i.e. unrepeated) taxa represented. There were 544 non-paleontological records, and 378 of these non-paleontological records had barcodes available in the National Center for Biotechnology Information (https://www.ncbi.nlm.nih.gov/). Although 378 records had deposited barcodes, only 137 of the 544 non-paleontological records, or 25% of records, had molecular evidence suggesting they belong to the same species or genus. Of the 544 non-paleontological records, there were 205 records of planktonic or pelagic taxa and 124 benthic or demersal taxa. The other records contained taxa spread over other habitats, such as epizoic and parasitic species, reef-associated species and ice-associated species.

From the total 665 records, according to this study's definitions, 517 records (449 unique taxa) were categorised as antitropical and 148 records (135 unique taxa) were categorised as bipolar across all taxonomic levels (Figure 3). Authors of 347 records, making up 52% of all records, matched this study's definitions of antitropicality and bipolarity, while 44% misclassified distributions as bipolar when they were antitropical or vice versa. The majority of disagreements were antitropical according to this study's definition but were classified as bipolar by the authors. A greater number of disjunct distribution records were found to be on the species level ($N = 389$) compared to the genus level ($N = 246$). On a higher taxonomic level (e.g. family), there were 30 records.

There were a total of 23 taxonomic groups researched across the 665 total records that represented the 551 unique taxa (Figure 4). In general, the trend of the number of valid species/genera followed the pattern of records, with some groups having each record representing an unrepeated valid species/genus (e.g. Brachiopoda, Bryozoa and Echinodermata). The phylum with the most antitropical records was Chordata, and the phylum with the most bipolar records was Retaria (e.g. foraminiferans), followed by Cnidaria and Arthropoda. There were numerically less bipolar records than antitropical records, but both bipolar and antitropical research exhibited comparable taxonomic diversity, each spanning 19 phyla, of which 15 phyla were represented in both categories. Chordata were individually the most studied group with 160 records, but the combined number of records for all marine invertebrates exceeded those for chordates, with 300 records. This reflected the vast species diversity among invertebrates, even though individual invertebrate groups had less records than chordates.

### 3.2 | Study-Level Trends

Research that fit this study's definition of antitropicality was dominant, but overall, studies featuring disjunct distributions
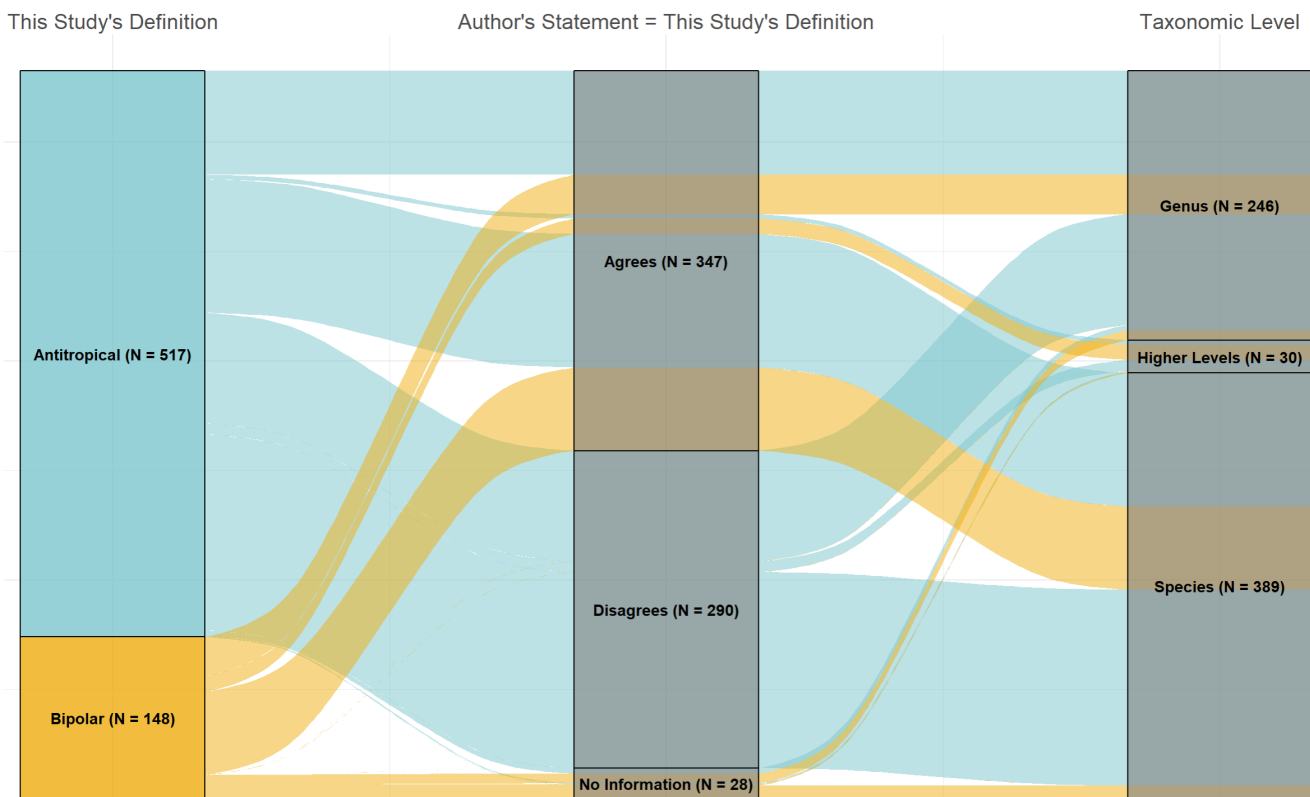
**FIGURE 3** | Alluvial plot of the record categorisation of the two distribution patterns: Antitropical and bipolar. The first column shows whether a record is bipolar or antitropical based on this study's definition. The second column shows if the authors' statement of bipolarity or antitropicality agrees with this study's definition. The last column shows if the record was on the genus or species level.

have increased since the early 1980s (Figure 5). Both antitropical and bipolar studies peaked in the 10-year period of 2008–2017, with 86 studies published within that timeframe. As seen in Figure 6, there were 221 studies published in 16 grey literature sources (i.e. reports, theses, book chapters) and 119 different academic journals, with journal scopes ranging from genetics (e.g. Molecular Ecology) to palaeontology (e.g. Journal of Vertebrate Palaeontology). The journal Molecular Phylogenetics and Evolution published 13 studies, which was the most for any single journal. A little over half of the studies were published in journals that each had less than four studies on marine disjunct distributions. 37 studies were from journals with regional or national names rather than a broad topic scope (e.g. Journal of Asia-Pacific Biodiversity).

## 3.3 | Register of Marine Species Databases

There were 408 valid species present in both the Arctic Register of Marine Species (ARMS) and the Register of Antarctic Marine Species (RAMS) databases. 41 of these shared species were also species recorded as bipolar in this study (Figure 7). OBIS occurrence data compiled for each species showed that there were 134 species with a cosmopolitan distribution, 31 with an antitropical distribution and only 2 species that displayed a truly bipolar distribution (i.e. *Rhabdoon reesi* and *Spinocalanus antarcticus*). The 241 remaining species exhibited a distribution in OBIS that did not match the definition of cosmopolitan, antitropical, or bipolar.

## 4 | Discussion

With science constantly advancing, we now have new methods that can answer, verify, or dispute old questions and concepts. For example, the age-old concept of bipolarity can now be tested and confirmed with molecular tools. Because of high levels of cryptic diversity in marine taxa and microscopic organisms like plankton being small and difficult to identify, especially during early life stages, molecular confirmation with traditional taxonomy is the only way to determine if a species that is identical at both poles is truly the same species (Ludt 2021; Sromek et al. 2015; Sul et al. 2013). It is therefore striking that, not counting paleontological records, only 135 out of 543 records had molecular evidence pointing out bipolarity or antitropicality. While morphological tools such as micro-CT or electron microscopy are helpful in taxonomy, some recent studies did not complement these analyses with any molecular tools; for example, using only morphology, the *Doridunculus* genus was suggested to display bipolarity based on a single specimen captured in the Southern Ocean (Moles et al. 2017). This is most likely because of significant gaps in public DNA barcode reference databases. The lack of reference barcodes for polar species impacts understanding of bipolar distributions because without robust genetic data, the ability to accurately identify geographically distinct species is limited and may lead to underestimations of species richness and biodiversity patterns (Bucklin et al. 2021; Fišer, Robinson, and Malard 2018; Weigand et al. 2019). This then has ecological consequences on accurate assessments of ecosystem functions (e.g. nutrient cycling), predictions of species response
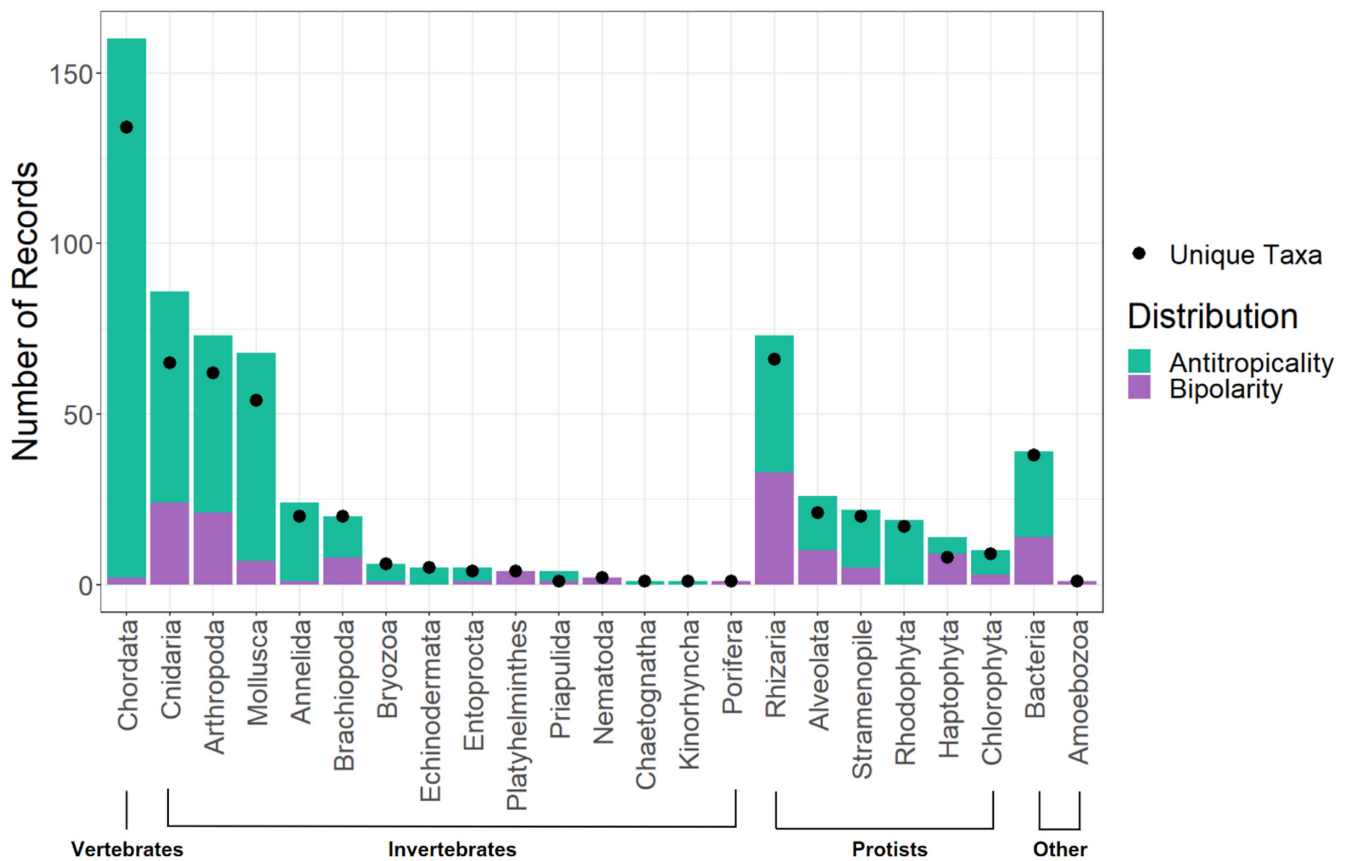
**FIGURE 4** | Stacked bar chart of the taxa records and whether they are antitropical or bipolar. The brackets on the bottom categorise the phyla into broader groups. The dots show the number of unique and unrepeated species/genera that were present in each taxonomic group.

to climate change (e.g. plasticity of life history traits) and conservation management strategies (e.g. informing Marine Protected Areas).

To combat this, there are many country-specific barcode campaigns to more efficiently target taxonomic identifications, such as the Norwegian Barcode of Life and the German Barcode of Life (Weigand et al. 2019). It would be beneficial to establish a similar campaign for the Polar Regions with the support of large networks such as ARMS/RAMS, perhaps by incorporating a molecular parameter into their database. In addition, incorporating molecular data into those cases of potential bipolar taxa solely based on morphological grounds will help to increase the resolution on the distribution of organisms potentially restricted to high latitudes at the poles and evaluate if bipolar distribution is as rare as currently assumed (Shi and Grunt 2000). However, despite the progress made with molecular tools, particularly in DNA barcoding efforts and increased phylogenomic studies, one of the limitations is that the frequent use of only a single molecular marker (e.g. COI), which while sufficient for basic species delimitation, cannot fully reveal the evolutionary links and population structure for those with a species complex (Serite et al. 2021). This approach can underestimate diversity or fail to detect hybridisation events, especially in taxa with rapid radiations or recent divergences, leading to inaccurate conclusions about disjunct distributions. With metabarcoding becoming the norm in oceanic sampling efforts, there has been a push to integrate multiple lines of evidence, including nuclear and mitochondrial markers, with traditional morphological and

ecological data for better interpretation. This, together with high-throughput techniques such as metagenomics, RAD-seq and multi-locus approaches, means that more sophisticated approaches will play a key role in advancing the understanding of distributional patterns, including bipolarity (Andrews et al. 2016; Santiago et al. 2023; Serite et al. 2021).

The word 'bipolarity' has become a buzzword since it is an attractive term to describe an extremely disjunct distribution, especially in today's context of climate change. Using buzzwords in the title or text gains higher levels of support and positive evaluations for research funding (Vinkenburg, Ossenkop, and Schiffbaenker 2021). This could be one of the reasons why the authors of nearly 200 records determined a taxa's distribution as bipolar when it fit this study's latitudinal definition of antitropicality (Figure 3). However, researchers may have been following a historical definition of bipolarity in which 'bipolar' was used to describe any latitudinally disjunct marine taxa (Crame 1993; Ludt 2021). Terminology usage fluctuates in any scientific field, but it will be beneficial for the biogeographical community if researchers define how they determine bipolar or antitropical distribution in order to enable comparability between studies, whether it be a temperature- or latitude-based definition. As the polar regions continue to rapidly warm and marine life responds to intensifying environmental stressors, climate-driven shifts in species distribution patterns and ecosystem services may be disrupted (Sul et al. 2013; Weber and Deutsch 2010). However, the changes in the Arctic and Antarctic are not uniform, so the responses of polar organisms may differ even for species within
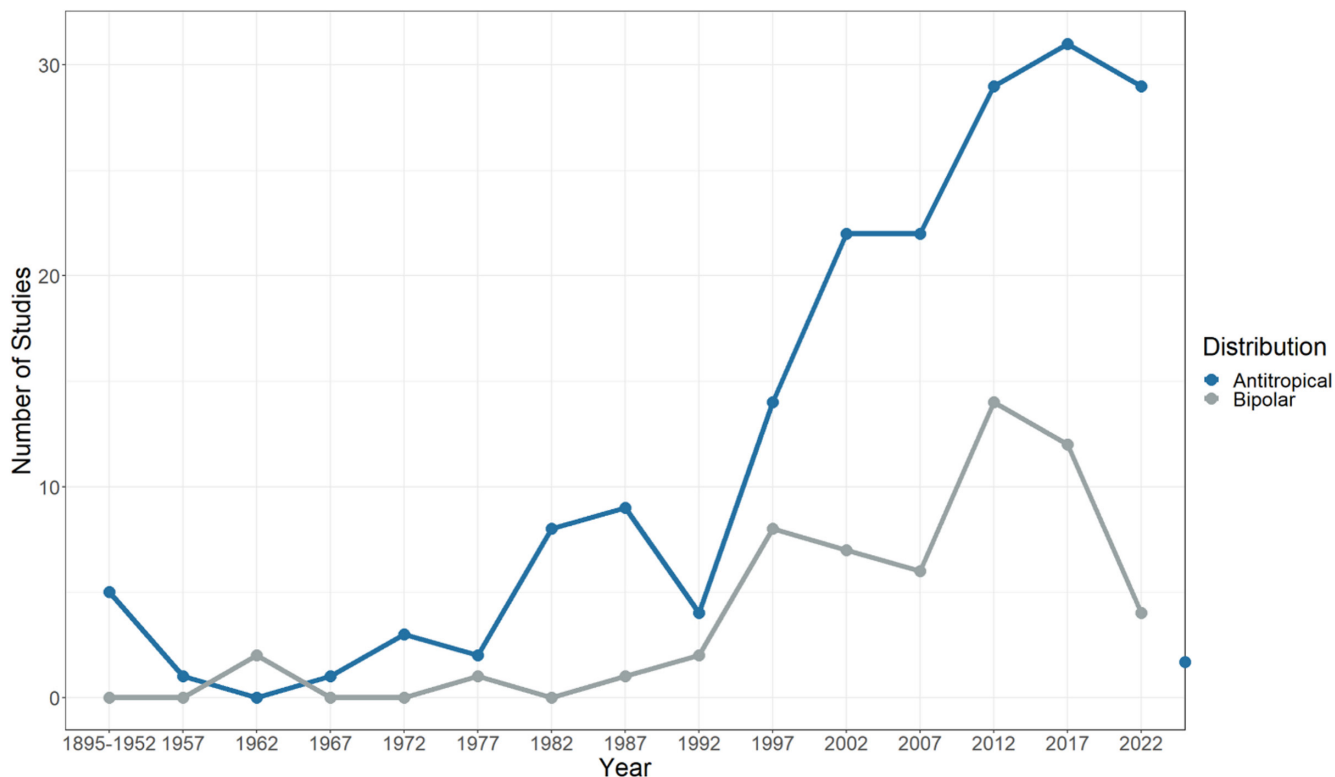
**FIGURE 5** | Temporal trend of number of studies on antitropicality and bipolarity, using this study's definition, summed over 5-year intervals. All years prior to 1952 were compiled together. The single dots at the end of the graph represent the years 2023 to the date that the literature search was conducted on April 1, 2024.
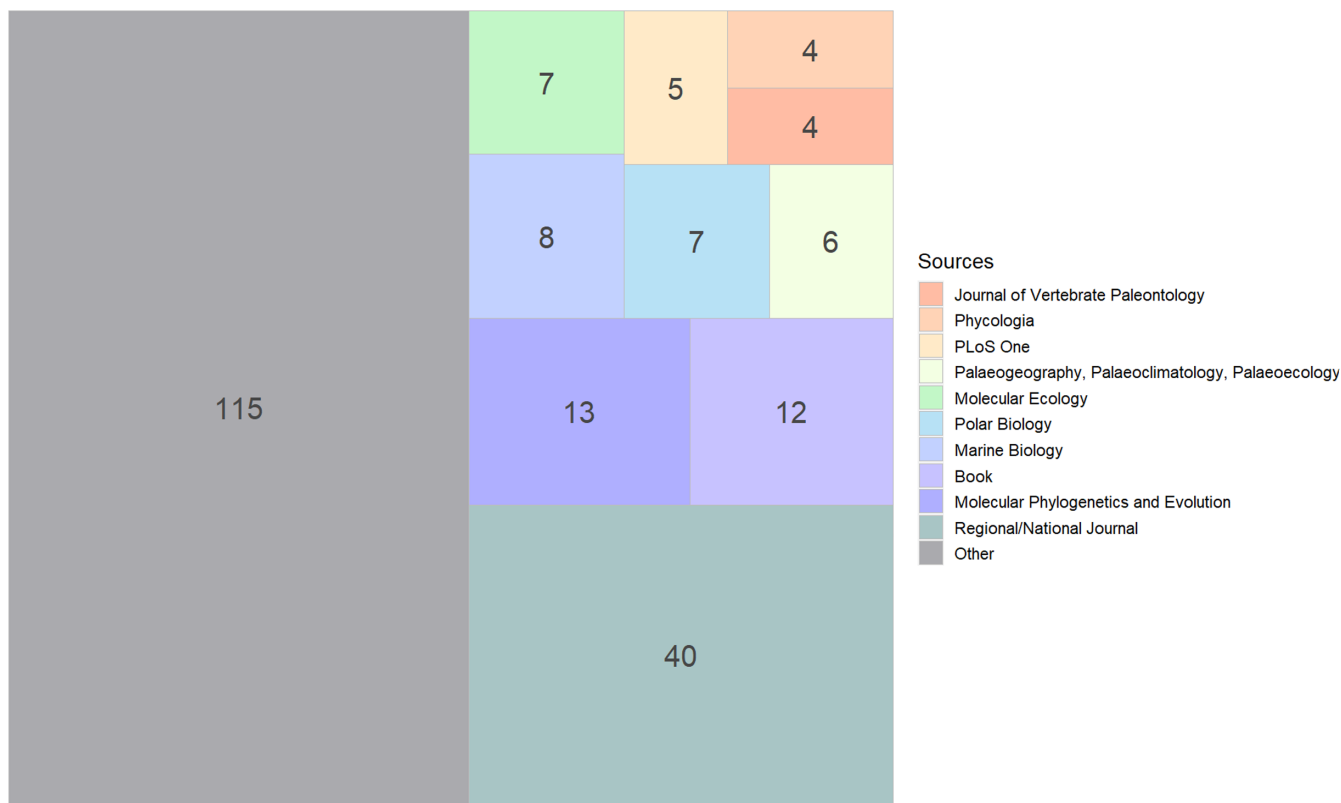


**FIGURE 6** | Treemap of numbers of studies per journal that published the 221 articles analysed in this review. The area rectangles are proportional to the number of articles published by each journal category. If there were four or more studies published in a single journal, the full name was included; otherwise, it was placed in 'Other'.
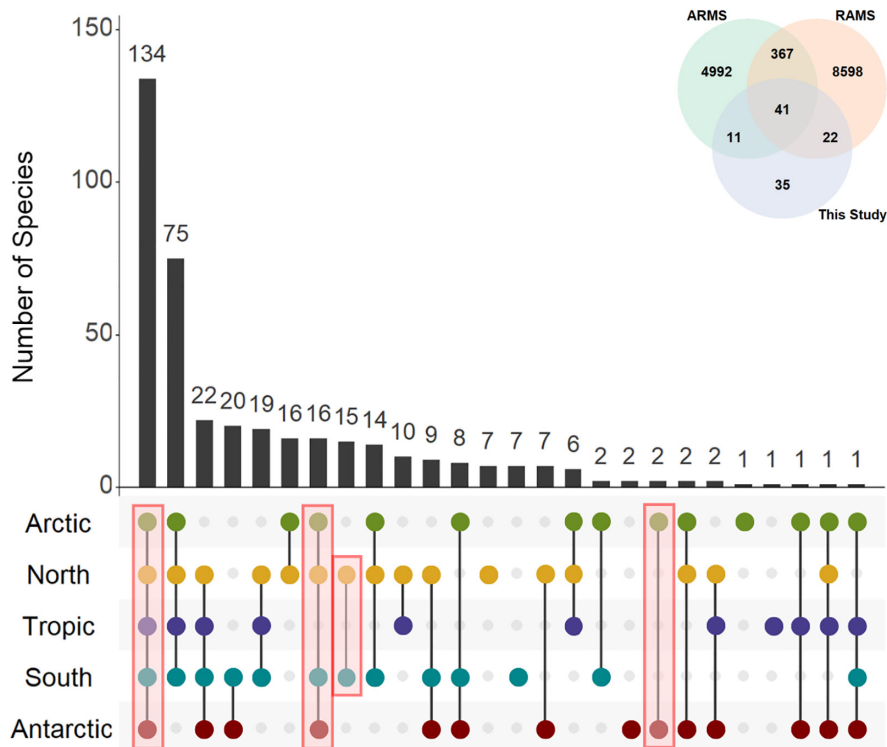
**FIGURE 7** | Upset plot of the distribution of 408 species shared in both the ARMS and RAMS databases. The coloured dots represent the presence of species in different biogeographic regions based on OBIS: Arctic, North, Tropic, South and Antarctic, with vertical lines connecting regions where species co-occur. The bars show the number of species with a particular distribution pattern. The highlighted red boxes indicate cosmopolitan (left), antitropical (two middle) and bipolar (right) distribution for reference. The inset Venn diagram shows shared overlap on the species level across ARMS, RAMS and this study's dataset.

the same genus (Convey and Peck 2019; Hunt et al. 2010). To accurately quantify ecosystem impacts, correct taxonomic data of whether a species really displays a bipolar range distribution will be key. If the word 'bipolar' is used to describe antitropical distributions, especially when the study area is not specified (e.g. North Atlantic), it may skew the biogeographical data.

With only 30 out of the total 665 records representing a higher taxonomic level than the genus level, the focus for bipolarity and antitropicality was primarily on species and genera. Based on the sources analysed in this study, more research effort was put into recognising these patterns at the species level compared to the genus level (Figure 3). A contributing factor for this could have been a greater interest in determining latitudinal disjunct distribution on the species level, since it is more specific and has greater ecological meaning than assessing distribution patterns at the genus or family level. There were also 34 total records of bipolar or antitropical distribution being disproved, often because of observations in temperate or tropical waters. This could be the result of multiple sampling efforts like Grohmann, Absalão, and da Silva (2013), which disproved bipolarity in the cnidarian *Monobrachium parasitum* based on three colonies found in Brazil, to even single specimen observations such as in Motomura and Peristiwady (2010), which disproved antitropicality in the scorpionfish *Scorpaena onaria* in Indonesia. Some records also refuted these distributions once they found that species displayed convergent evolution upon more detailed morphological analyses (Lee et al. 2015; Grey, Haggart, and Smith 2008). Therefore, discontinuity of species range along lower latitudes may be

explained by a lack or scarcity of sampling data in distant polar locations, which is an issue for all marine taxa (Menegotto and Rangel 2018; Park and Ferrari 2009). Knowledge of polar biodiversity is limited because of restricted sampling area, frequency of sampling efforts and seasonality. It is then expected that with increased time and sampling in understudied regions, there will be more species, particularly those in deep-water habitats, which will have disjunct distributions proven false. Some of these species might still be considered valid examples of bipolarity with equatorial submergence as described in Stepanjants et al. (2006), so bipolarity and antitropicality should only be dismissed when there is evidence that species are present in shallow waters in tropical regions. On the other hand, with progressive warming, the lower latitudes might be too warm for temperate species, and they might be pushed to higher latitudes and become primarily polar. Therefore, in addition to any biogeographical shifts, it will be important to monitor the ecological consequences and physiological changes in all vulnerable marine taxa, including those that display antitropicality and bipolarity.

Overall, there were some repeated species/genera present in different studies, but for all groups, the majority of records represented unique taxa (Figure 4). There were 20 total records on Brachiopoda, and all 20 were different valid taxa, while the greatest disparity was in Cnidaria, with 86 total records representing 62 unique taxa. The majority of antitropical records were focused on chordates, primarily fish. This may be explained by the fact that fish are commercially important, so it is necessary for multiple sectors to gather knowledge about their distribution patterns

and predict their biogeographical response to climate change. They can also be easily collected by taking directly from fish markets or anglers compared to pelagic invertebrates that need to be collected through dedicated sampling (Grant 1998; Stepien and Rosenblatt 1996). However, marine invertebrates were the main group of interest in bipolar records, potentially due to a recent push in understanding Arctic and Antarctic biodiversity (Alabia et al. 2023; Convey and Peck 2019) and the extent of latitudinal range shifts induced by a changing environment (Seabra et al. 2015). New monitoring efforts using environmental DNA and underwater video profilers may help inform where to conduct targeted sampling of proposed bipolar species for morphological and molecular analyses. As polar research advances, a broader exploration of different phyla and a better understanding of the evolutionary mechanisms that lead to bipolar isolation is expected.

Before antitropicality was introduced by Hubbs (1952), bipolarity was the primary representation of disjunct distributions. The reason why the time interval up to 1952 was solely antitropical was because these consisted of historical studies that used bipolarity for any instance of disjunct distribution, which did not match with this study's definition of bipolarity (Figure 5). Gradually, more research was conducted on non-polar species, as antitropicality became accepted as a different form of distribution and routinely used. On a study level, it cannot be confirmed if the rise in research on bipolarity and antitropicality since the 1980s was attributed to a growing interest in the biogeography of marine taxa or just to an overall increase in the number of papers published. With an exponential surge in academic papers being published annually from approximately 1 million papers in 1980 to over 7 million papers in 2014 (Fire and Guestrin 2019), the rise in disjunct distribution studies may be explained in part by a temporal increase in scientific publications. However, this field has increasingly become more interdisciplinary because the processes that shape modern, restrictive bipolar distributions are explained by integrating phylogeography, taxonomy, ecology and genomic data (Dawson, Correia, and Ladle 2022; Jenkins and Ricklefs 2011). This means that research which includes a biogeographical aspect may continue to increase and be published in a wide range of journals. This trend can already be seen in Figure 6, with 221 studies originating from 135 literature sources, ranging from topic-specific (e.g. Journal of Biogeography) to broad-scope journals (e.g. PLoS One). It is interesting to note that nearly a quarter of the studies were published in journals containing a regional or national name, such as the Italian Journal of Zoology and the Latin American Journal of Aquatic Mammals. In addition, the focus of many of these studies was not disjunct distributions, so these assignments may have just been a side note, which could explain the numerous publications in taxon-specific journals such as the Journal of Fish Biology instead of those more specific to the biogeographical field.

Both ARMS and RAMS databases are works in progress and curated by research experts on each taxonomic group. They are also constantly updated (e.g. Medusozoa was only added to ARMS on 2024-02-29), meaning that if the registers are incomplete, they may not be representative of potentially bipolar species. While it was expected that very few of the 408 shared species present in both databases would be proven to have bipolar distribution, it was surprising that only *R. reesi* and *S. antarcticus* matched the occurrence data while 134 displayed

a cosmopolitan distribution. However, this could be evidence of errors in OBIS since they have a disclaimer that states they rely on 'user feedback to identify technical, geographic, and taxonomic errors in data served' (OBIS 2024). For the rarer taxa present in the polar regions of this study's interest, taxonomic confirmation is more difficult. In addition, 56% of species in OBIS have less than 10 records, revealing not only a bias towards well-known species that are regularly monitored but also of the type of study that would deposit occurrence records in OBIS (Klein et al. 2019). For large-scale monitoring campaigns or those targeting a specific taxonomic group, the process of putting occurrence data into global data systems like OBIS may be required as standard procedures. However, many of the sources in this study did not have a biogeographical focus, so it may not be the top priority to share into OBIS, especially for those that documented new species records or early spread into new habitats. For example, Moles et al. (2017) determined bipolarity for a single occurrence of *Doridunculus* in the Antarctic, which was a genus previously only present in the Arctic, but this record was not uploaded to OBIS. These observations are important to fill in the gaps in understanding true range distributions so that more accurate estimates can be made about potential bipolar species.

Many different hypotheses were proposed to explain bipolarity or antitropicality from these 221 articles, but with such a wide variety of taxa and even conflicting results on the cause of distribution for different species in the same genus, making it difficult or near impossible to determine a pattern. From relict theory (Stepanjants et al. 2006) and transgressions during glacial periods (Angel and Błachowiak-Samołyk 2006) to deep-sea dispersal (Reid and James 2010) and modern anthropogenic transport (Hudson, McQuaid, and Rius 2020), a single reason is rarely considered the cause of these distributions but rather a combination of factors influenced by different geological and climatic events over time. However, depending on the nature of the taxa, hypotheses may fit better, such as dispersal for species that have high dispersion potential like planktonics or are mobile swimmers, which can allow extensive gene flow. In this study, most of the non-paleontological records were planktonic or pelagic taxa, but there were also many benthic or demersal taxa. There is still much unknown about the extent of true bipolarity; more research on these understudied taxa and distribution patterns, including the way they originate, is recommended in the near future. It is also important to note that this study was focused on the marine system and was not representative of disjunct distribution research as a whole because our inclusion criteria did not include freshwater or terrestrial flora and fauna (Figure 2). Moreover, only relying on the outputs from the three literature databases was insufficient to capture the full existing knowledge/records on disjunct distributions. The additional scanning of reference lists from found literature pointed out additional articles to build a more comprehensive dataset. However, such a step could have introduced a slight taxonomic bias depending on the target group of the considered article (e.g. a review article on cnidaria may have more relevant citations on other disjunct cnidaria but not necessarily on copepods).

Biogeography plays a critical role in understanding evolution and how environmental factors affect distribution patterns and what can be expected in the future. However, while the biogeographical aspect is important in determining bipolar

distributions, ecological information also needs to be gathered to realistically predict impacts on polar marine systems. As part of marine science turns from pure taxonomy to more functional and trait-based approaches, it will be interesting to check if the same taxa share the same functional and ecological roles in ecosystems at both poles, if their life histories and biological responses are identical, and if these traits and roles will shift with climate change. For example, Chen, Trudnowska, and Blachowiak-Samolyk (2023) found a stable and conserved sex ratio of pelagic ostracods across both polar systems, while shifts to smaller body sizes are expected in polar microcrustaceans such as Arctic *Calanus* copepods (Balazy et al. 2023; Campbell et al. 2021) and Antarctic *Serolis* isopods (Janecki, Kidawa, and Potocka 2010). These changes in life history traits could further shift species distribution, with warming causing true polar and bipolar species to migrate more polewards to survive and antitropical species expanding into the Arctic and Antarctic Circles to potentially become latitudinally bipolar. The continued borealization in the Arctic and the movement of the Antarctic Polar Front will likely facilitate more species dispersal across previously impassable barriers. Cheung et al. (2009) even modelled that marine invasion intensity in 2040–2060 will be nearly 5.5 and 2 times the global average in the Arctic Ocean and Southern Ocean, respectively. Looking forward, to make connections on an ecosystem level with higher confidence, a step in the right direction would be to designate disjunct distributions using ecoregions or oceanographic boundaries such as polar fronts that are characterised by shifts in water temperature and salinity. This will allow for better incorporation of ecological data for more accurate interpretations and predictions of the marine system. An interdisciplinary approach will be required to see how biogeographic shifts of polar, bipolar and antitropical marine taxa can inform predictions regarding the response of Polar Regions to climate change.

## Author Contributions

E.Y.-S.C. compiled and analyzed the data, and prepared the original manuscript draft. K.B.-S. acquired the funding and E.T. supervised data analyses. All authors conceptualized the study, contributed to manuscript preparation, and approved the submitted version.

## Conflicts of Interest

The authors declare no conflicts of interest.

## Data Availability Statement

The datasets compiled and used for analyses are available in Tables S1 and S2.

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## Supporting Information

Additional supporting information can be found online in the Supporting Information section.