Journal of Biogeography

WILEY

Journal of Biogeography

RESEARCH ARTICLE OPEN ACCESS

Community Analysis Reveals Biogeographical Patterns and Biodiversity Shortfalls in Antarctic Tardigrades

Matteo Vecchi[1] | Sara Brandoli[2,3] | Vladlen Mykolayovych Trokhymets[4]

[1]Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, Poland | [2]Department of Life Sciences, University of Modena and Reggio Emilia, Modena, Italy | [3]Department of Environmental Sciences, Informatics and Statistics, Ca'Foscari University of Venice, Venice Mestre, Italy | [4]Department of Ecology and Zoology, Taras Shevchenko National University of Kyiv, Kyiv, Ukraine

Correspondence: Sara Brandoli (sara.brandoli@unimore.it; sara.brandoli1@gmail.com)

Received: 8 August 2024 | **Revised:** 18 November 2024 | **Accepted:** 20 November 2024

Funding: The authors received no specific funding for this work.

Keywords: Antarctica | biodiversity | biogeography | community structure | Endemisms | Gressitt line | Linnean shortfall | Tardigrada | Wallacean shortfall

ABSTRACT

Aim: Tardigrades are important members of Antarctic metazoan communities with many endemic species. Major biogeographic patterns of Antarctic fauna have been identified, in particular regarding the zonation across the Gressitt line, dividing Continental and Peninsular Antarctica. Evidences suggest that Antarctic tardigrades follow this zonation too, but this has never been rigorously tested.
Location: Limnoterrestrial ecosystems of Antarctica.
Time Period: 1950 to Present.
Major Taxa Studied: Tardigrades.
Methods: Records of tardigrades from Antarctica were collected and their taxonomy and coordinates harmonised. Alpha and Beta diversity measures were calculated and compared across different Antarctica biogeographic areas, in particular across the Gressitt line. Analyses were repeated at different spatial scales to ensure their robustness.
Results: Tardigrades communities are different both in terms of alpha and beta diversity across the Gressitt line. Results were consistent across the analyses at different spatial scales. Taxa richness was higher in the Antarctic Peninsula compared to the Continental Antarctica. Sampling effort had a substantial effect on the measured richness. Despite having a significant effect, Gressitt line side and biogeographic areas explained a low amount of variance.
Main Conclusions: The presence of a different Tardigrade communities composition across the Gressitt line is supported, and a geographical structure is present also at smaller scales. This geographic structuring suggests local endemisms and calls for attention to eventual effects of climate change on tardigrades communities. Faunistic data on Antarctica is still far from being exhaustive and Linnean and Wallacean biodiversity shortfalls are the two most immediate issues to be solved to have a more reliable estimation of the true Antarctic tardigrades biodiversity.

1 | Introduction

Antarctica is the coldest, driest and windiest continent of the world, with less than 0.3% of its surface seasonally ice and snow free. The biodiversity of terrestrial Antarctica is constrained by specific environmental abiotic stressors. Among others, the scarcity of liquid water, the year-round constancy of extremely low temperatures, the high salinity and the reduced nutrient

---

Matteo Vecchi and Sara Brandoli contributed equally to this article.

Journal of Biogeography, 2025; 52:735–749
https://doi.org/10.1111/jbi.15063

availability act as strong filters for the biological communities (Convey et al. 2014). The taxa composing most of Antarctic terrestrial biodiversity are relatively few, yet showing an elevated biodiversity at the species level. Some of them (bacteria, algae and fungi) are found almost ubiquitously (Dragone et al. 2021), while others (micrometazoans, lichens and bryophytes) are rather confined to the sparse ice-free areas (Phillips, Leihy, and Chown 2022). Focusing on the latter group of organisms, it is known that isolation and fragmentation play a key role in shaping their evolutionary histories, resulting in a high level of endemism (Pugh and Convey 2008; Velasco-Castrillón, Gibson, and Stevens 2014). As a result of biotic, abiotic and historical features, a major biogeographic discontinuity named Gressitt line was identified by Chown and Convey (2007) between the Antarctic Peninsula and Continental Antarctica, underlining the ancient and different evolutionary history of their biological communities. More recent studies revealed that the Antarctic terrestrial ecosystems are highly spatially structured and can be further divided into a series of ecoregions, known as the Antarctic Conservation Biogeographic Regions (ACBRs; Terauds et al. 2012; Terauds and Lee 2016).

Many studies focused on specific taxa have demonstrated the existence of biodiversity patterns consistent with the biogeographical barrier represented by the Gressitt line. Considering bryophytes, for instance, though the extent of ice-free areas seems to be a key factor influencing their diversity levels, it is not sufficient to explain the observed biodiversity trends at the continental scale. This difference was therefore attributed to different evolutionary origins of the bryophyte communities present on either side of the Gressitt line (Cannone, Convey, and Guglielmin 2013; Saługa, Ochyra, and Ronikier 2022). Similarly, nematodes and mites show no overlap at the species level across the Gressitt line (Andrássy 1998; Pugh 1993), while in springtails, only a single species, *Friesea grisea* (Greenslade 1995) is found to be 'pan-Antarctic' and therefore present on either side of the Gressitt line (Torricelli et al. 2010).

In this study, we focus on the cosmopolitan phylum Tardigrada. In spite of their small dimensions (<1 mm in length), these bilaterians have a complex morphology and anatomy and need to be surrounded by a film of water to be active (Møbjerg et al. 2018). Terrestrial tardigrades dwell in moist microhabitats such as mosses, lichens and temporary ponds (Schill 2019). Nonetheless, thanks to their cryptobiotic ability, tardigrades are particularly adapted to deal with the cold desertic polar ecosystems. The cryptobiotic form, called 'tun', together with their small size and lightweight, favours their passive dispersal through Antarctic winds (e.g., Nkem et al. 2006); additionally, the parthenogenetic reproduction, which characterises many tardigrade species, implies that a single specimen is potentially able to start a new population after being dispersed.

Similarly to other microfaunal metazoans, tardigrades taxonomy is a complex task constrained by the scarcity and small dimension of morphological characters. Before the implementation of an integrative approach to tardigrades taxonomy (Cesari et al. 2009), it was thought that many species also found in Antarctica were cosmopolitan and had a very wide distribution. Nonetheless, genotyping is revealing increasing evidence in the presence of very localised endemisms within the Antarctic continent (e.g., Guidetti et al. 2014, 2019b; Velasco-Castrillón et al. 2015; Vecchi et al. 2016a), but the dispersal vectors for these animals are still understudied and, therefore, their role in determining the current biogeographical patterns of tardigrade species is hardly predictable (Gąsiorek 2023). Currently, 12 families and 31 genera of tardigrades have been reported for Antarctica (Register of Antarctic Species, accessed on 05/02/2024; RAS 2024).

Studies on the biogeographic pattern of tardigrades in Antarctica are scarce, with only McInnes and Pugh (1998) providing a whole-phylum formal analysis of tardigrade faunas. The phylum Tardigrada was found to exhibit a marked Laurasian/Gondwana separation at familial and generic levels in their extant representatives (McInnes and Pugh 1998, 2007; Pugh and McInnes 1998; Guidetti et al. 2017), and in particular, three loose faunistic clusters were found in the Antarctic region (Continental Antarctica, Maritime Antarctica and sub-Antarctic islands), with about a 50% of species overlap between the Antarctic Peninsula and continental Antarctica (Chown and Convey 2007; Convey and McInnes 2005).

Here, we aim to study the biogeographic pattern of tardigrades in Antarctica at a finer scale than in previous studies, by assessing the similarity in communities across different spatial granularity. To perform this task, we collected and harmonised the primary records of tardigrades from Antarctica, evaluating how sampling effort and the geographic area (in terms of side of the Gressitt line and geographic region) influence the alpha and beta diversity. We also tested if the results were robust across different spatial scales by replicating the analyses at different spatial granularities.

2 | Materials and Methods

2.1 | Study Area

Antarctica is geographically divided into East Antarctica, West Antarctica, the Antarctic Peninsula, the maritime Antarctic and the sub-Antarctic islands, with most of these regions characterised by a polar climate (category ET as for the Köppen climate classification, i.e., with monthly average temperatures never exceeding 0°C; Köppen 1931), apart from some areas of the Peninsula and the islands, that show a tundra climate (category EF, i.e., at least a month with an average temperature above 0°C) (Gonzalez and Vasallo 2020).

The Antarctic continent with its biota underwent a process of increasing isolation from the other landmasses starting from the early Cretaceous and culminating with the opening of the Drake Passage at the Eocene–Oligocene transition (about 34 million years ago), once connecting the Antarctic Peninsula to South America (e.g., Bergstrom, Hodgson, and Convey 2006). As a result of both environmental and biogeographical conditions, the organisms dwelling Antarctic ecosystems are profoundly different if compared to that of other continents (Convey and Smith 2006), with Antarctic organisms presenting highly specialised adaptations, such as short life cycles, small body size and the ability to withstand protracted freezing and desiccation.

2.2 | Dataset Assembly

A database containing all the tardigrade records from Antarctica (i.e., all records southern than 60° S; in agreement with Terauds and Lee 2016) was assembled by screening all the tardigrade literature available in the personal collections of the authors, supplemented by a search on Google Scholar done on 01/12/2023 (Keyword: 'Tardigrad* Antarctica'). Only primary records below the family level (only genus and species levels) were retained (checklist and reviews were excluded). The extracted tardigrade taxa occurrence data were included in the database by, when available, single analysed sample. In the case of records in which data could not be disaggregated to single sample level, the number of total samples composing that record was noted. When the number of samples composing a record was not indicated, it was assumed to be a single sample. Coordinates were extracted and when not available they were derived by the locality names indicated in the references. ACBR (Terauds and Lee 2016) and the position in relation to the Gressitt line (Continental or Peninsular side of the line) of each record were also noted. When indicated, we also included in the dataset samples inspected for tardigrades but found empty (to have a more precise quantification of the sampling effort). Tardigrade taxa names were harmonised to be comparable across studies, following the taxonomic changes that happened during the records timespan. The compiled dataset is available in Data S1 and the related references are available in Appendix 1.

2.3 | Data Analysis

For the data analysis, community data (presence or absence of taxa) was binned into approximate equal-area hexagons. To test the robustness of the analyses, they were replicated by using 14 different-sized hexagons, spanning from about 12,000 to 231,000 km^2. Due to inherently distortions at different latitudes (as the latitude decreases, a greater span of the Earth's surface falls into a given grid cell) by the used Polar stereographic projection (https://spatialreference.org/ref/epsg/3031/), all hexagon cells in a given replicate do not exactly show the same area, thus only the approximate average area in square kilometres is indicated from now on. Additionally, all the analyses were repeated with the full dataset and for a subset of the dataset excluding the taxa records to genus level. As the sample size of individual ACBRs was too heterogeneous, seven geographic regions with comparable sample size were delimitated by merging contiguous ACBRs (Figure 1, left panel).

To test the effect of sampling bias and geographical region on the alpha diversity (number of taxa found per hexagon), a Poisson GLM (Generalised Lineal Model) with log link was implemented using the number of taxa found in each hexagon as dependent variable and the sampling effort (number of examined samples per hexagon) and locality (administrative region nested inside the side of Gressitt line) as predictors. The formula of this model is 'Number of taxa ~ Sampling effort + Side of Gressitt line/Geographic region' and is referred to hereon as Model 1.

To test if the Gressitt line influences beta diversity, a PERMANOVA was implemented. To obtain a community distance matrix to be used as the dependent variable, a zero-adjusted Sørensen dissimilarity (Clarke, Somerfield, and Chapman 2006) was calculated between hexagons. This adjusted dissimilarity measure was chosen due to its higher performance when samples with very few taxa are present in the dataset. As predictors in the PERMANOVA, geography (geographic region nested inside the side of the Gressitt line) was used, together with the alpha diversity (number of taxa found per hexagon) and the sampling effort (number of examined samples per hexagon) as covariates. The formula of this model is 'Community dissimilarity matrix ~ Side of Gressitt line/Geographic region + Sampling effort + Alpha diversity' and is referred to hereon as Model 2.

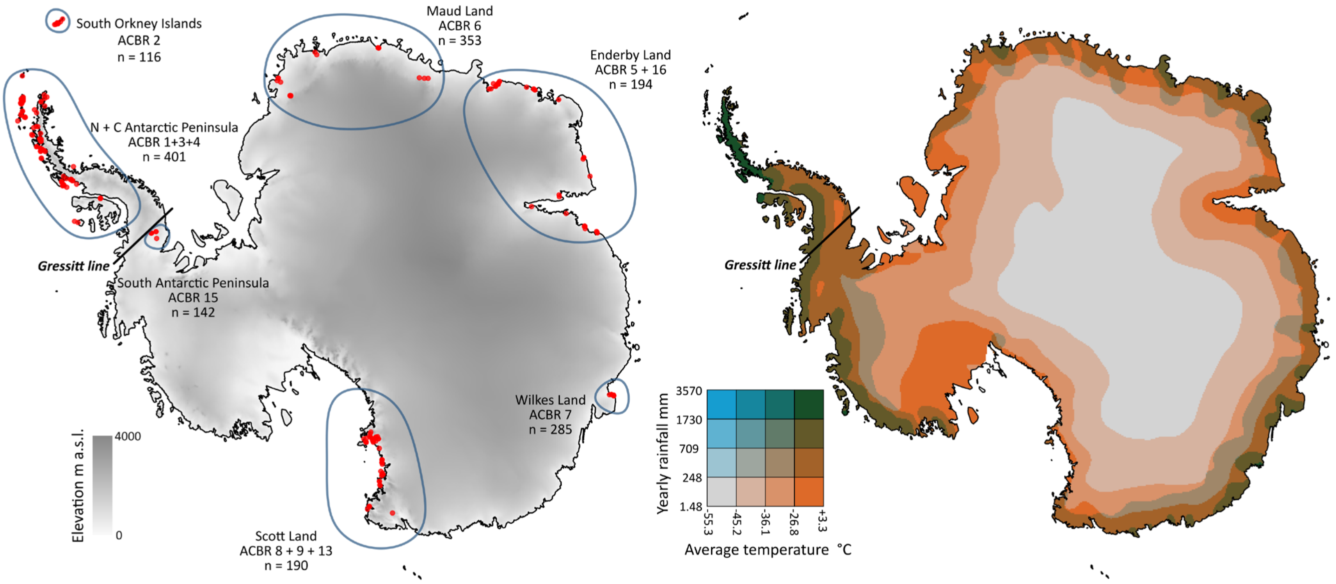

FIGURE 1 | Sampling points in Antarctica. Left panel: Antarctica landmass relief map showing sampling locations (in red) and the geographical regions used in this study, along with the ACBRs that compose them, and the number of samples collected and analysed. n = number of samples. Right panel: Antarctica bivariate map (Prener, Grossenbacher, and Zehr 2022) of yearly average temperature and total rainfall. Climatic data obtained from Wagner et al. (2018), temperature and rainfall breaks for visualisation were calculated with the Fisher's Natural Breaks Classification algorithm (Fisher 1958; Jenks 1977).

Climatic data was not included in the models as (except for the climatic difference between Continental and Antarctic Peninsula, which correlates to the Gressitt side variable) all the areas from where tardigrades have been recorded share similar temperature and precipitation patterns (Wang and Hou 2009; Souverijns 2019; Figure 1, right panel). Substrate type (moss, lichen, freshwater sediment, etc.) was not considered in this study (although reported in Data S1) due to the inconsistencies in how it was reported in different studies and the presence of many mixed-type samples in the dataset.

The consistency of the results across the different versions (hexagons areas and the presence or not of genus-level records) of the analyses was assessed by comparing the explained variance by each predictor in the two models. P-values were not used to evaluate the consistency between the different versions of the analyses, since the number of data points (number of hexagons) varies when different analyses with different hexagon areas are used, and p-values are sensitive to sample size (Thiese, Ronna, and Ott 2016).

All data analyses were performed in R (R Core Team 2024) with the packages 'targets' (Landau 2021), 'Rmarkdown' (Allaire et al. 2024), 'readxl' (Wickham and Bryan 2023), 'magrittr' (Bache and Wickham 2022), 'sp' (Pebesma and Bivand 2005), 'raster' (Hijmans 2023), 'vegan' (Oksanen et al. 2024), 'geosphere' (Hijmans 2022), 'data.table' (Barrett et al. 2024), 'graph4lg' (Savary et al. 2021), 'ecodist' (Goslee and Urban 2007), 'plotrix' (Lemon 2006), 'tidyr' (Wickham, Vaughan, and Girlich 2024), 'ggplot2' (Wickham 2016), 'ggbreak' (Xu et al. 2021), 'hexbin' (Carr et al. 2023), 'patchwork' (Pedersen 2024), 'dplyr' (Wickham et al. 2023), 'grDevices' (R Core Team 2024), 'scales' (Wickham, Pedersen, and Seidel 2023), 'cowplot' (Wilke 2024), 'sf' (Pebesma and Bivand 2023), 'factoextra' (Kassambara and Mundt 2020). The analysis script, along with the results, are available as html file rendered with Rmarkdown (Data S2).

3 | Results

3.1 | Dataset and Geographic Regions Delimitation

A total of 71 references published after 1950 with primary records, providing data for 511 sampling locations (Figure 1, left panel) for a total of 1681 samples were identified (Data S1). The number of recorded taxa is 94, of which 83 are classified below genus level (species or species group) and belong to a total of 16 families and 28 genera (Data S1). Sampling effort, alpha and beta diversity were found to vary, even between adjacent hexagons (Figure 2), and this heterogeneity is not influenced much by granularity (Figure 2) or by the removal of genus-only records (Data S2). Due to the similarity between the analyses with and without genus-only records, only the results on the full dataset are presented and discussed below (genus-only results are available in Data S2).

3.2 | Model 1 – Alpha Diversity

Sampling effort (number of samples) explained 9.26%–24.28% (average 13.66%) of variance in alpha diversity across the different granularities, whereas the side of the Gressitt line explained 7.96%–27.94% (average 18.97%) of variance and the geographic region explained 4.81%–14.12% (average 10.23%) of variance (Figure 3). The effect of the number of samples was significant only at lower hexagon sizes (Table 1; Data S3), whereas the Gressitt line size was significant through all the hexagon sizes (Table 1; Data S3), finally the effect of the Geographic region was not significant on alpha diversity (Table 1; Data S3). The model coefficients for the Number of samples (Data S4) are always positive, indicating a positive relationship between sampling effort and alpha diversity. The model coefficients for the side of the Gressitt line (with the continental side used as intercept) are also always positive (Data S4), indicating a higher alpha diversity in the Peninsular side of the Gressitt line.

3.3 | Model 2 – Beta Diversity

Sampling effort (number of samples) explained 2.37%–4.22% (average 2.97%) of variance in beta diversity across the different granularities, number of taxa explained 10.19%–16.96% (average 13.93%) of variance in beta diversity across the different granularities. The side of the Gressitt line explained 8.49%–18.23% (average 12.63%) of variance and the geographic region explained 14.05%–18.23% (average 18.99%) of variance (Figure 4).

The effect of the number of samples was never significant (Table 2; Data S3), whereas the number of taxa was significant across granularities (Data S3). The Gressitt line size was significant through all the hexagon sizes (Table 2; Data S3), finally the effect of the Geographic region was almost always significant (Table 2), except for some isolated cases with no evident pattern (Data S3).

4 | Discussion

Our data analysis points to a geographical structuring of tardigrades communities, both in terms of alpha and beta diversity, in agreement with previous studies. The observed patterns are also robust across the spatial scale of the analyses, providing additional support to our conclusions.

Our compiled dataset provides an updated checklist of limnoterrestrial Antarctic tardigrade species (Data S1). The total number of families (16) and genera (28) we report is not consistent with the data that can be derived from the Register of Antarctic Species (RAS 2024; accessed on 05/02/2024), where 12 families and 31 genera are reported. This incongruence can probably be explained by taxonomical changes occurred in the last few years (e.g., erection of new families, transfer of species from one genus to another) that have not yet been included in the Register.

Other than the sampling effort, the main driver of alpha diversity was found to be the localization compared to the Gressitt line (Figures 2 and 3): more taxa are generally found on the Peninsular side of the line compared to the continental side. Multiple factors could be hypothesized to explain this pattern:

i. In a palaeogeographical framework, the Antarctic Peninsula has a different geological and ice sheet formation history with respect to Continental Antarctica (McLoughlin 2001; Davies et al. 2012) that likely

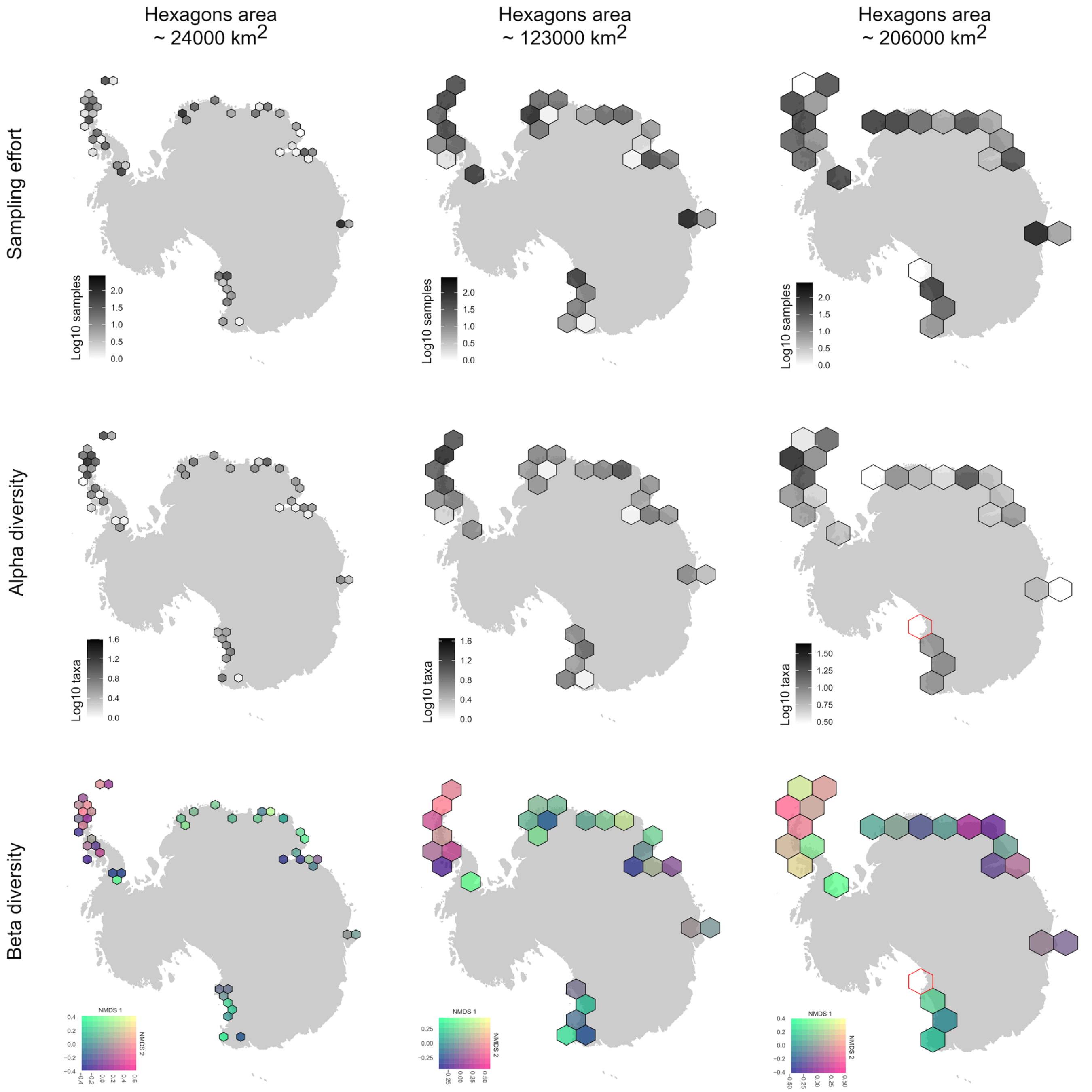

FIGURE 2 | Sampling effort, alpha and beta diversity. Number of examined samples (Sampling), alpha diversity (number of taxa) and beta diversity (NMDS of zero-adjusted Sørensen dissimilarity matrix) of tardigrade communities at three arbitrarily chosen granularities covering the range of tested hexagon sizes (approximate area in square Kilometres indicated above each column). One hexagon (red border) in the ~206,000 km^2 granularity plots contained only one sample in which no tardigrades were found.

influenced the biogeography of species, including tardigrades. The connection between the Antarctic Peninsula and South America was the last bridge allowing population interchange with Antarctica, since Continental Antarctica was already isolated during the breakup of Gondwana (about 100–60 million years ago; McLoughlin 2001). Even though the estimates for the opening of the Drake passage are still debated (e.g., Livermore et al. 2005; Evangelinos et al. 2024), this event marked the history of the Antarctic continent allowing the onset of the Antarctic Circumpolar Current, a deep-water circulation that established around the Antarctic continent enhancing its thermal isolation and leading to the inception of the continental ice sheet. After the last glacial maximum, the Antarctic Peninsula showed a generally warmer climate with respect to the areas on the Continental side of the Gressitt line. This may have helped species colonising the Antarctic Peninsula that survived the last glacial maximum to extensively recolonize the Peninsular side once the climate warmed, leaving more ice-free areas available for colonisation.

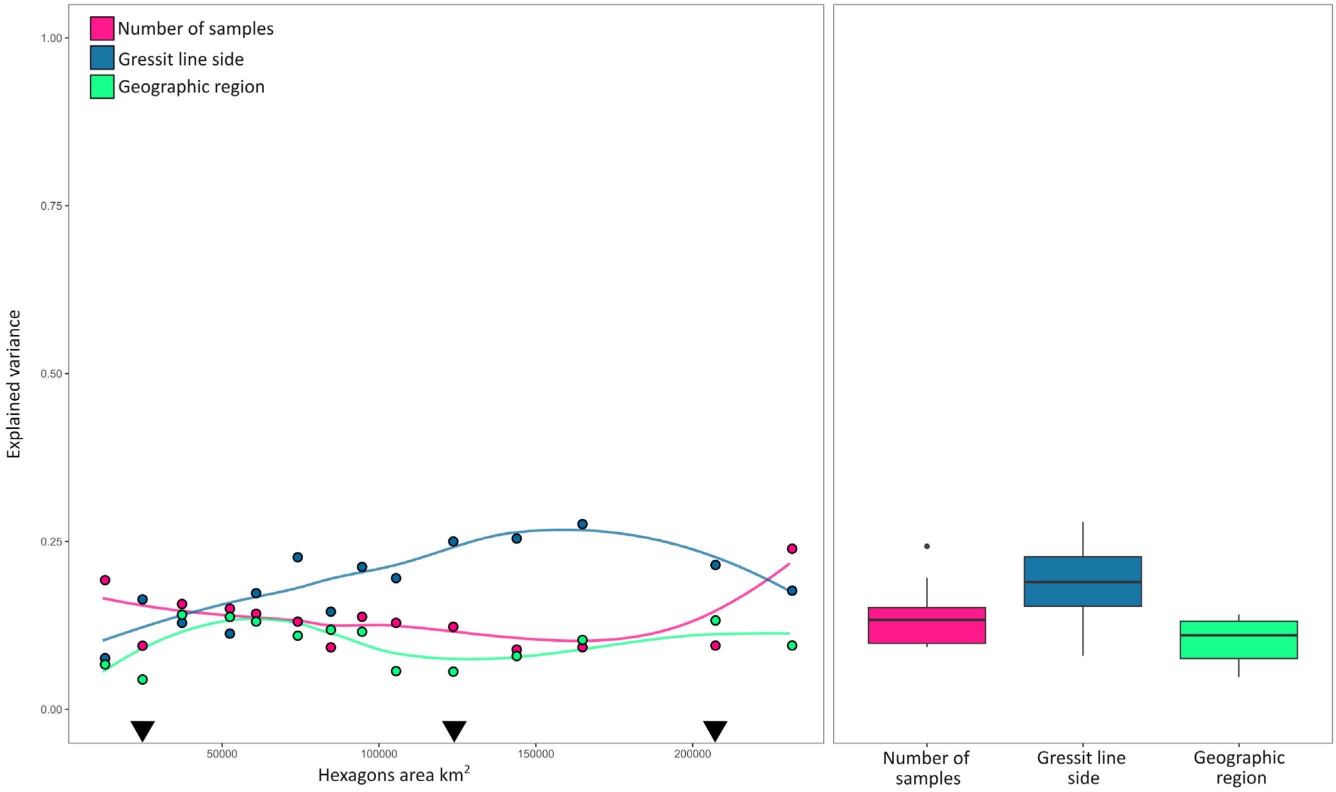

FIGURE 3 | Explained variance on alpha diversity across different granularities. Explained variance on alpha diversity across different granularities by number of samples, Gressitt line side and geographic region. Left panel: Explained variance for each examined hexagon side with LOESS regression lines, black triangles indicate the three arbitrarily hexagon sizes shown in Figure 2 and Table 1. Right panel: Boxplot of explained variance by each of the three predictors across different granularities.

ii. Climate is different between Continental Antarctica and Antarctic Peninsula (Gonzalez and Vasallo 2020), with the Peninsula experiencing higher average temperatures. The presence of a warmer climate in the Antarctica could provide either a more welcoming habitat for species colonising it from South America or by favouring in situ speciation thanks to more resources from primary producers.

iii. For the effect of climate change, the glacial retreat in the Antarctic Peninsula progressively exposes new terrestrial areas suitable for colonisation by non-native species (e.g., Chown et al. 2012; Znój et al. 2017). To date, the Drake passage separates South America and Antarctica for 1000 km. Notoriously, tardigrades undergo passive long distance dispersal events mediated by, for example, endozoochory (Mogle et al. 2018; Robertson et al. 2020). Recent, ongoing immigration of tardigrade species from South America to the Antarctic Peninsula is therefore not to exclude, and their establishment may be favoured by climate warming.

iv. The Antarctic Peninsula is subject to tourism, that may enhance the introduction of non-native species from elsewhere (e.g., Huiskes et al. 2014). This could also apply to tardigrades, whose cryptobiotic ability makes them certainly able to survive and be dispersed by footwear (Cukier, Fudala, and Bialik 2023).

The patterns of beta diversity we identified (effect of Gressitt line side and biogeographic area on tardigrades community composition) were robust across the different granularity analyses and provided clear evidence of a separation between the Peninsular and Continental Antarctica communities, confirming and reinforcing previous results (Chown and Convey 2007; Convey and McInnes 2005).

However, the variance explained by those factors was generally low (usually < 25%) than what was expected based on extreme bio-regionalization patterns found in other Antarctic taxa, in particular regarding the different sides of Gressitt line (Pugh 1993; Andrássy 1998; Peat, Clarke, and Convey 2007; Stevens, Greenslade, and D'Haese 2021; Torricelli et al. 2010).

Those results could have been generated by two non-mutually exclusive causes: a biological one and a technical one. The biological explanation relies on the coexistence of tardigrade species showing extremely localised distributions with cosmopolitan species (including all the variations in between). As reviewed by Gąsiorek (2023), tardigrades show variable distribution patterns: almost cosmopolitan (see for example *Paramacrobiotus fairbanksi*; Kayastha et al. 2023), continental endemic (*Acutuncus antarcticus*; Cesari et al. 2016) and regional endemic species (e.g., *Mesobiotus aradasi* found only in the Antarctic Peninsula; Vecchi et al. 2024) are known to exist. The coexistence of species with different distribution breadth could be a probable cause leading to the presence of a weak, but significant biogeographic signal in tardigrade communities. Previous studies (Chown and Convey 2007; Convey and McInnes 2005) identified approximately 50% of species overlap between the Antarctic Peninsula and continental Antarctica, supporting these conclusions.

TABLE 1 | Analysis of deviance results for Model 1 under three arbitrarily chosen granularities covering the range of tested hexagon sizes.

	Hexagons area ~24,000 km²						Hexagons area ~123,000 km²						Hexagons area ~206,000 km²					
	Df	**Sum Sq**	**Mean Sq**	**R^2**	**F**	**p**	**Df**	**Sum Sq**	**Mean Sq**	**R^2**	**F**	**p**	**Df**	**Sum Sq**	**Mean Sq**	**R^2**	**F**	**p**
Number of samples	1	248.8	248.8	0.335	5.443	**0.025**	1	280.6	280.6	0.301	4.517	**0.046**	1	204.3	204.3	0.26	2.883	0.109
Gressitt line side	1	423.4	423.4	0.57	9.262	**0.004**	1	562.5	562.5	0.604	9.054	**0.007**	1	453.2	453.2	0.577	6.394	**0.022**
Geographical region	5	121.5	24.3	0.033	0.532	0.751	5	132.5	26.5	0.028	0.426	0.825	5	281.9	56.4	0.072	0.795	0.569
Residuals	38	1737.2	45.7	0.062			20	1242.5	62.1	0.067			16	1134	70.9	0.09		

Note: p-values below 0.05 are bolded.

Abbreviations: Df = Degrees of freedom; F = F-statistic; Mean Sq = Mean of Squares; p = p-value; R^2 = Explained variance; Sum Sq = Sum of Squares. p-values below 0.05 are bolded.

A correct and unbiased estimation of the biogeographic patterns is however subordinate to the quality and quantity of data that we can gather, which is influenced by technical and methodological factors affecting our ability to recognise and detect species. Fonseca, Fontaneto, and Di Domenico (2018) listed seven shortfalls of biodiversity (Hortal et al. 2015) that affect our meiofauna biodiversity knowledge. Based on the data collected for this study, some insight can be gathered on the magnitude of effect and possible solutions on three of these shortfalls impacting specifically the study of Antarctic tardigrades communities:

- *Linnean shortfall* (large number of unknown species): world's tardigrade species are far from being all known (Bartels et al. 2016 estimated that only 44.5% of extant tardigrade species have been described). Antarctica is not an exception, and the high number of species described in the last decades (see Data S1) suggests that many species remain undiscovered. One particular reason behind the recent increase in species description rate is the relatively recent acknowledgement that cryptic and pseudocryptic species are common in tardigrades (e.g., Gąsiorek et al. 2019; Guidetti et al. 2019a; Stec et al. 2021), which was allowed by the adoption of an integrative taxonomy approach (Padial et al. 2010). The identified relationship between sampling effort and alpha diversity (Figure 3) coupled with an extremely heterogeneous sampling effort across Antarctica hints that a big fraction of diversity (including undescribed species) has not been sampled yet. Additional exploration, sampling, and faunistic studies coupled with increased use of integrative taxonomy and biogeographical considerations would significantly reduce the Linnean shortfall in our knowledge of Antarctic tardigrades (e.g., Guidetti et al. 2017, 2019b).
- *Wallacean shortfall* (unknown distribution for most of the species): obtaining reliable distribution maps requires the coordinated effort of many researchers in extracting and classifying many individuals. Despite being a trivial task on the paper, this is a complex and problematic issue in tardigrades research. The correct identification of many tardigrade species requires the analysis of both animals and eggs (as exemplified by the genera *Macrobiotus*, *Mesobiotus* and *Paramacrobiotus*: Kaczmarek and Michalczyk 2017; Kaczmarek et al. 2020; Guidetti et al. 2019a), which are not always found together. To further complicate the framework, rare cases are known in which the same tardigrade species lays markedly different egg morphotypes (e.g., Kihm et al. 2020; Brandoli et al. 2024), making genotyping even more important for species delimitation. In addition, the differentiation of many species relies on minute characters (often morphometrics), which can be influenced by the preparation method (Morek et al. 2016), thus making a positive species determination difficult. A misidentification stemming from those issues would lead to incorrect geographic ranges estimates, but the inability to provide a reliable positive identification could be equally problematic. This last issue seems to be common in our dataset (Data S1), as in particular (but not limited to) for some genera (*Milnesium* and *Macrobiotus*), most of the record could be assigned only to genus level. Other

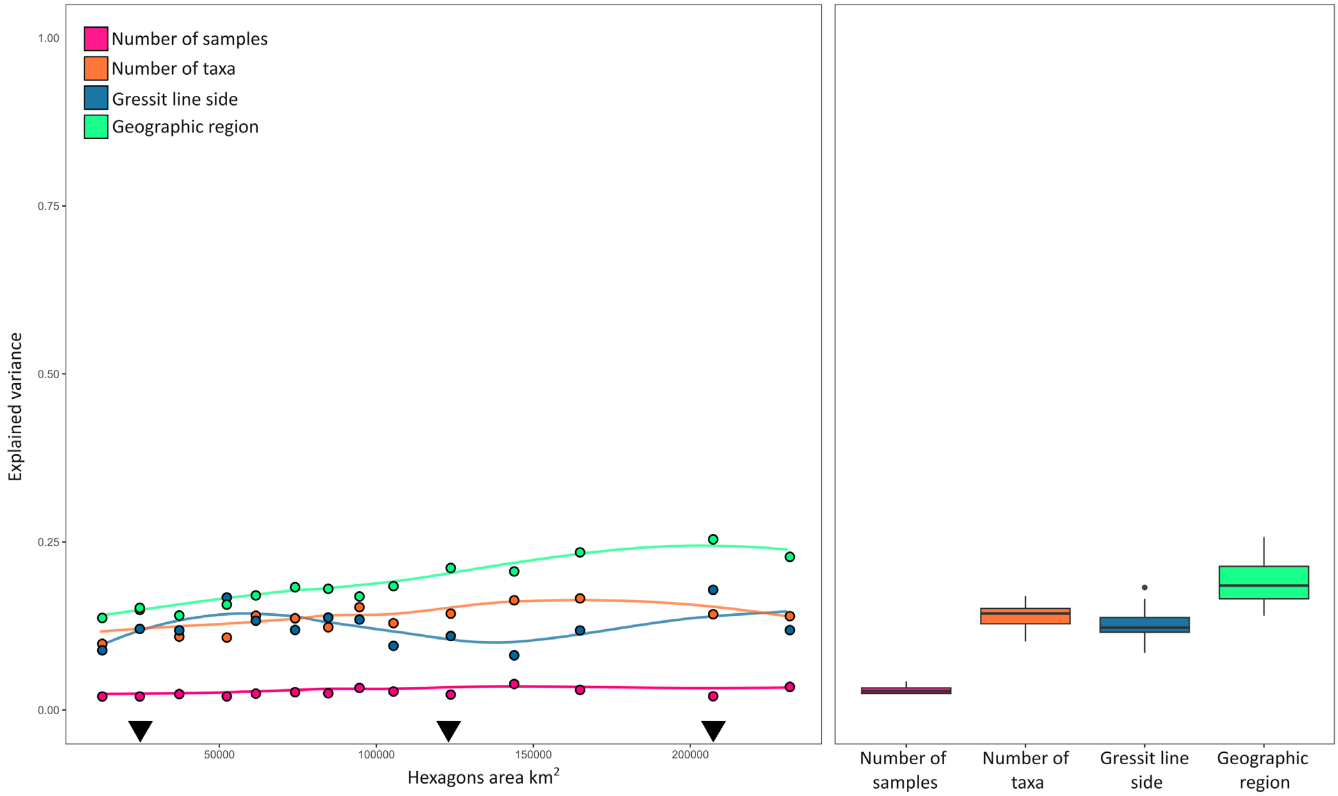

FIGURE 4 | Explained variance on beta diversity across different granularities. Explained variance on beta diversity across different granularities by number of samples, number of taxa, Gressitt line side and geographic region. Left panel: Explained variance for each examined hexagon side with LOESS regression lines, black triangles indicate the three arbitrarily hexagon sizes shown in Figure 2 and Table 2. Right panel: Boxplot of explained variance by each of the four predictors across different granularities.

> than the training of new taxonomists, an increment in the use of molecular techniques like DNA metabarcoding (which has been shown to be useful in tardigrades detection and identification: Topstad et al. 2021; Arakawa 2020; Pust et al. 2024; He et al. 2024), alongside with the use of integrative taxonomy to describe species and produce reliable DNA databases, would allow to alleviate this issue. Unknown distribution also refers to the habitat type: for example, despite tardigrades being usually found in cryptogams (Nelson, Bartels, and Guil 2018), they can also be present in unusual habitats like rock pools (Vecchi et al. 2022, 2023a, 2023b; Troell and Jönsson 2023), which were neglected by tardigradologists until a few years ago. Rock pools are present in Antarctica (Trokhymets, Zinkovskyi, and Dykyy 2024) and represent still an unexplored habitat from this point of view.

Linnean and Wallacean shortfalls are not independent, and species description and identification and determination of their distributions are interconnected. The presence and distribution of the genus *Barbaria* in Antarctica is an example of how these two aspects are linked to each other: *Barbaria jenningsi* (Dastych 1984) belong to a prevalently South American genus, which dispersed recently northward in North America [*B. danieli* (Meyer, Tsaliki, and Sorgee 2017)] and southward in the Antarctic Peninsula (*B. jenningsi*) (Gąsiorek et al. 2022), providing a clear example of Antarctic Peninsula colonisation by a South American taxon. However, Miller and Heatwole (1995) and Vecchi et al. (2016a) found individuals morphologically similar to *B. jenningsi* in continental Antarctica. Whether those individuals are conspecific of *B. jenningsi* found in the Antarctic Peninsula or a different species would lead to different conclusions regarding their biogeography (high dispersal capacity in the first case vs. low dispersal capacity and allopatric speciation in the second case, if not ever more complicated scenarios).

4.1 | Conservation Implications

Despite the noise in the dataset due to the different issues in tardigrade biodiversity data presented above, it is clear that the tardigrade fauna in Antarctica is regionalized and endemic taxa with restricted distribution exists. Antarctic taxa are also adapted to its peculiar climatic conditions, which makes them sensible to climate change (Convey 2006; Turner et al. 2009, 2014). While some widespread Antarctic taxa are known to tolerate higher temperatures (Giovannini et al. 2018, 2023), this does not mean that this will be true for all species. Climate change, as already happened for other cold-adapted groups (Felde, Kapfer, and Grytnes 2012; Hällfors et al. 2024) could mean range shift or, in the worst case, extinction. Introduction of alien species is also a concern as, despite we don't know almost anything about the trophic relationships between tardigrades and other taxa, the introduction of predators, competitors or even pathogens (Vecchi et al. 2016b) could be the nail on the coffin for some species already weakened by climate change.

TABLE 2 | PERMANOVA results for Model 2 under three arbitrarily chosen granularities covering the range of tested hexagon sizes.

	Hexagons area ~24,000 km^2						Hexagons area ~123,000 km^2						Hexagons area ~206,000 km^2					
	Df	Sum Sq	Mean Sq	R^2	*F*	*p*	Df	Sum Sq	Mean Sq	R^2	*F*	*p*	Df	Sum Sq	Mean Sq	R^2	*F*	*p*
Number of taxa	1	1.72	1.72	0.152	10.369	**0.001**	1	1.044	1.044	0.147	5.607	**0.001**	1	0.837	0.837	0.146	5.238	**0.001**
Number of samples	1	0.268	0.268	0.024	1.615	0.084	1	0.188	0.188	0.027	1.012	0.446	1	0.138	0.138	0.024	0.864	0.588
Gressitt line side	1	1.401	1.401	0.124	8.446	**0.001**	1	0.807	0.807	0.114	4.336	**0.001**	1	1.045	1.045	0.182	6.542	**0.001**
Geographical region	5	1.754	0.351	0.155	2.115	**0.001**	5	1.526	0.305	0.215	1.639	**0.002**	5	1.475	0.295	0.257	1.848	**0.002**
Residuals	37	6.137	0.166	0.544			19	3.537	0.186	0.498			14	2.236	0.16	0.39		

Note: p-values below 0.05 are bolded.
Abbreviations: Df = Degrees of freedom; *F* = F-statistic; Mean Sq = Mean of Squares; *p* = *p*-value; R^2 = Explained variance; Sum Sq = Sum of Squares.

5 | Conclusions

We presented an updated checklist of Antarctic limnoterrestrial tardigrades, and identified geographical structuring of tardigrade communities, with more taxa on the Antarctic Peninsula compared to Continental Antarctica. In other words, the presence of a different Tardigrade communities composition across the Gressitt line is supported, and a geographical structure is present also at smaller scales, influenced by historical biogeography and current climatic differences. However, the variance explained by these factors is low, likely due to a mix of endemic and more spread species. Addressing challenges through higher sampling effort, involvement of expert taxonomists and innovative molecular approaches will improve our understanding of Antarctic biodiversity.

Author Contributions

Matteo Vecchi: conceptualization, methodology, software, formal analysis, data curation, visualization, writing – original draft, writing – review and editing. **Sara Brandoli:** data curation, methodology, writing – original draft, writing – review and editing. **Vladlen Mykolayovych Trokhymets:** conceptualization, methodology, data curation, writing – review and editing.

Acknowledgements

The authors wish to thank Roberto Guidetti for his critical reading of the manuscript and precious suggestions. The authors declare that no permits for fieldwork were required for this research.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All the data and code used in this manuscript are available as Supporting Information.

References

Allaire, J., Y. Xie, C. Dervieux, et al. 2024. "rmarkdown: Dynamic Documents for R." R package version 2.27. https://github.com/rstudio/rmarkdown.

Andrássy, I. 1998. "Nematodes in the Sixth Continent." *Journal of Nematode Morphology and Systematics* 1: 107–186.

Arakawa, K. 2020. "Simultaneous Metabarcoding of Eukaryotes and Prokaryotes to Elucidate the Community Structures Within Tardigrade Microhabitats." *Diversity* 12: 110. https://doi.org/10.3390/d12030110.

Bache, S., and H. Wickham. 2022. "magrittr: A Forward-Pipe Operator for R." R package version 2.0.3. https://CRAN.R-project.org/package=magrittr.

Barrett, T., M. Dowle, A. Srinivasan, J. Gorecki, M. Chirico, and T. Hocking. 2024. "data.table: Extension of 'data.frame'." R package version 1.15.4. https://CRAN.R-project.org/package=data.table.

Bartels, P. J., J. J. Apodaca, C. Mora, and D. R. Nelson. 2016. "A Global Biodiversity Estimate of a Poorly Known Taxon: Phylum Tardigrada." *Zoological Journal of the Linnean Society* 178: 730–736. https://doi.org/10.1111/zoj.12441.

Bergstrom, D. M., D. A. Hodgson, and P. Convey. 2006. "The Physical Setting of the Antarctic." In *Trends in Antarctic Terrestrial and Limnetic Ecosystems*, edited by D. M. Bergstrom, P. Convey, and A. H. L. Huiskes, 15–33. Dordrecht: Springer.

Brandoli, S., M. Cesari, E. Massa, M. Vecchi, L. Rebecchi, and R. Guidetti. 2024. "Diverse Eggs, Diverse Species? Production of Two Egg Morphotypes in *Paramacrobiotus Bifrons*, a New Eutardigrade Species Within the *Areolatus* Group." *European Zoological Journal* 91: 274–297. https://doi.org/10.1080/24750263.2024.2317465.

Cannone, N., P. Convey, and M. Guglielmin. 2013. "Diversity Trends of Bryophytes in Continental Antarctica." *Polar Biology* 36: 259–271. https://doi.org/10.1007/s00300-012-1257-5.

Carr, D., N. Lewin-Koh, M. Maechler, and D. Sarkar. 2023. "hexbin: Hexagonal Binning Routines." R package version 1.28.3. https://CRAN.R-project.org/package=hexbin.

Cesari, M., R. Bertolani, L. Rebecchi, and R. Guidetti. 2009. "DNA Barcoding in Tardigrada: The First Case Study on *Macrobiotus macrocalix* Bertolani & Rebecchi 1993 (Eutardigrada, Macrobiotidae)." *Molecular Ecology Resources* 9: 699–706. https://doi.org/10.1111/j.1755-0998.2009.02538.x.

Cesari, M., S. J. McInnes, R. Bertolani, L. Rebecchi, and R. Guidetti. 2016. "Genetic Diversity and Biogeography of the South Polar Water Bear *Acutuncus antarcticus* (Eutardigrada: Hypsibiidae) - Evidence That It Is a Truly Pan-Antarctic Species." *Invertebrate Systematics* 30: 635–649. https://doi.org/10.1071/IS15045.

Chown, S. L., and P. Convey. 2007. "Spatial and Temporal Variability Across life's Hierarchies in the Terrestrial Antarctic." *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 362: 2307–2331. https://doi.org/10.1098/rstb.2006.1949.

Chown, S. L., A. H. Huiskes, N. J. Gremmen, et al. 2012. "Continent-Wide Risk Assessment for the Establishment of Nonindigenous Species in Antarctica." *Proceedings of the National Academy of Sciences* 109: 4938–4943. https://doi.org/10.1073/pnas.111978710.

Clarke, K. R., P. J. Somerfield, and M. G. Chapman. 2006. "On Resemblance Measures for Ecological Studies, Including Taxonomic Dissimilarities and a Zero-Adjusted Bray-Curtis Coefficient for Denuded Assemblages." *Journal of Experimental Marine Biology and Ecology* 330: 55–80. https://doi.org/10.1016/j.jembe.2005.12.017.

Convey, P. 2006. "Antarctic Climate Change and Its Influences on Terrestrial Ecosystems." In *Trends in Antarctic Terrestrial and Limnetic Ecosystems: Antarctica as a Global Indicator*, edited by D. M. Bergstrom, P. Convey, and A. H. L. Huiskes, 253–272. Dordrecht: Springer. https://doi.org/10.1007/1-4020-5277-4_12.

Convey, P., S. L. Chown, A. Clarke, et al. 2014. "The Spatial Structure of Antarctic Biodiversity." *Ecological Monographs* 84: 203–244. https://doi.org/10.1890/12-2216.1.

Convey, P., and S. J. McInnes. 2005. "Exceptional Tardigrade-Dominated Ecosystems in Ellsworth Land, Antarctica." *Ecology* 86: 519–527. https://doi.org/10.1890/04-0684.

Convey, P., and R. L. Smith. 2006. "Responses of Terrestrial Antarctic Ecosystems to Climate Change." In *Plants and Climate Change*, edited by J. Rozema, R. Aerts, and H. Cornelissen, 1–12. Dordrecht: Springer. https://doi.org/10.1007/978-1-4020-4443-4_1.

Cukier, S., K. Fudala, and R. J. Bialik. 2023. "Are Antarctic Aquatic Invertebrates Hitchhiking on Your Footwear?" *Journal for Nature Conservation* 72: 126354. https://doi.org/10.1016/j.jnc.2023.126354.

Dastych, H. 1984. "The Tardigrada From Antarctica With Descriptions of Several New Species." *Acta Zoologica Cracoviensia* 27: 377–436.

Davies, B. J., M. J. Hambrey, J. L. Smellie, J. L. Carrivick, and N. F. Glasser. 2012. "Antarctic Peninsula Ice Sheet Evolution During the Cenozoic Era." *Quaternary Science Reviews* 31: 30–66. https://doi.org/10.1016/j.quascirev.2011.10.012.

Dragone, N. B., M. A. Diaz, I. D. Hogg, et al. 2021. "Exploring the Boundaries of Microbial Habitability in Soil." *Journal of Geophysical Research: Biogeosciences* 126: e2020JG006052. https://doi.org/10.1029/2020JG006052.

Evangelinos, D., J. Etourneau, T. van de Flierdt, et al. 2024. "Late Miocene Onset of the Modern Antarctic Circumpolar Current." *Nature Geoscience* 17: 165–170. https://doi.org/10.1038/s41561-023-01356-3.

Felde, V. A., J. Kapfer, and J. A. Grytnes. 2012. "Upward Shift in Elevational Plant Species Ranges in Sikkilsdalen, Central Norway." *Ecography* 35: 922–932. https://doi.org/10.1111/j.1600-0587.2011.07057.x.

Fisher, W. D. 1958. "On Grouping for Maximum Homogeneity." *Journal of the American Statistical Association* 53: 789–798.

Fonseca, G., D. Fontaneto, and M. Di Domenico. 2018. "Addressing Biodiversity Shortfalls in Meiofauna." *Journal of Experimental Marine Biology and Ecology* 502: 26–38. https://doi.org/10.1016/j.jembe.2017.05.007.

Gąsiorek, P. 2023. "Catch Me if You Can, or How Paradigms of Tardigrade Biogeography Evolved From Cosmopolitism to 'Localism'." *Zoological Journal of the Linnean Society* 202: zlad191. https://doi.org/10.1093/zoolinnean/zlad191.

Gąsiorek, P., K. J. Jackson, H. A. Meyer, et al. 2019. "*Echiniscus virginicus* Complex: The First Case of Pseudocryptic Allopatry and Pantropical Distribution in Tardigrades." *Biological Journal of the Linnean Society* 128: 789–805. https://doi.org/10.1093/biolinnean/blz147.

Gąsiorek, P., A. Wilamowski, K. Vončina, and Ł. Michalczyk. 2022. "Neotropical Jewels in the Moss: Biodiversity, Distribution and Evolution of the Genus *Barbaria* (Heterotardigrada: Echiniscidae)." *Zoological Journal of the Linnean Society* 195: 1037–1066. https://doi.org/10.1093/zoolinnean/zlab087.

Giovannini, I., T. Altiero, R. Guidetti, and L. Rebecchi. 2018. "Will the Antarctic Tardigrade *Acutuncus antarcticus* Be Able to Withstand Environmental Stresses Related to Global Climate Change?" *Journal of Experimental Biology* 221: jeb160622. https://doi.org/10.1242/jeb.160622.

Giovannini, I., C. Manfrin, S. Greco, et al. 2023. "Increasing Temperature-Driven Changes in Life History Traits and Gene Expression of an Antarctic Tardigrade Species." *Frontiers in Physiology* 14: fphys1258932. https://doi.org/10.3389/fphys.2023.1258932.

Gonzalez, S., and F. Vasallo. 2020. "Antarctic Climates." In *Encyclopedia of the World's Biomes*, edited by M. I. Goldstein and D. A. Della Sala, 595–605. Amsterdam: Elsevier. https://doi.org/10.1016/B978-0-12-409548-9.11876-7.

Goslee, S. C., and D. L. Urban. 2007. "The Ecodist Package for Dissimilarity-Based Analysis of Ecological Data." *Journal of Statistical Software* 22: 1–19. https://doi.org/10.18637/jss.v022.i07.

Greenslade, P. 1995. "Collembola From the Scotia Arc and Antarctic Peninsula Including Descriptions of Two New Species and Notes on Biogeography." *Polish Journal of Entomology* 64: 305–319. https://doi.org/10.1007/s003000050383.

Guidetti, R., M. Cesari, R. Bertolani, T. Altiero, and L. Rebecchi. 2019a. "High Diversity in Species, Reproductive Modes and Distribution Within the *Paramacrobiotus Richtersi* Complex (Eutardigrada, Macrobiotidae)." *Zoological Letters* 5: 1–28. https://doi.org/10.1186/s40851-018-0113-z.

Guidetti, R., E. Massa, R. Bertolani, L. Rebecchi, and M. Cesari. 2019b. "Increasing Knowledge of Antarctic Biodiversity: New Endemic Taxa of Tardigrades (Eutardigrada; Ramazzottiidae) and Their Evolutionary Relationships." *Systematics and Biodiversity* 17: 573–593. https://doi.org/10.1080/14772000.2019.1649737.

Guidetti, R., S. J. McInnes, M. Cesari, L. Rebecchi, and O. Rota-Stabelli. 2017. "Evolutionary Scenarios for the Origin of an Antarctic Tardigrade Species Based on Molecular Clock Analyses and Biogeographic Data." *Contributions to Zoology* 86: 97–110. https://doi.org/10.1163/18759866-08602001.

Guidetti, R., L. Rebecchi, M. Cesari, and S. J. McInnes. 2014. "*Mopsechiniscus Franciscae*, a New Species of a Rare Genus of

Tardigrada From Continental Antarctica." *Polar Biology* 37: 1221–1233. https://doi.org/10.1007/s00300-014-1514-x.

Hällfors, M. H., R. K. Heikkinen, M. Kuussaari, et al. 2024. "Recent Range Shifts of Moths, Butterflies, and Birds Are Driven by the Breadth of Their Climatic Niche." *Evolution Letters* 8: 89–100. https://doi.org/10.1093/evlett/qrad004.

He, Z. Y., H. W. Hu, B. A. T. Nguyen, et al. 2024. "Distribution of Soil Tardigrades as Revealed by Molecular Identification Across a Large-Scale Area of Australia." *Soil Biology and Biochemistry* 196: 109506. https://doi.org/10.1016/j.soilbio.2024.109506.

Hijmans, R. 2022. "geosphere: Spherical Trigonometry." R package version 1.5-18. https://CRAN.R-project.org/package=geosphere.

Hijmans, R. 2023. "raster: Geographic Data Analysis and Modeling." R package version 3.6-26. https://CRAN.R-project.org/package=raster.

Hortal, J., F. de Bello, J. A. F. Diniz-Filho, T. M. Lewinsohn, J. M. Lobo, and R. J. Ladle. 2015. "Seven Shortfalls That Beset Large-Scale Knowledge of Biodiversity." *Annual Review of Ecology, Evolution, and Systematics* 46: 523–549. https://doi.org/10.1146/annurev-ecolsys-112414-054400.

Huiskes, A. H., N. J. Gremmen, D. M. Bergstrom, et al. 2014. "Aliens in Antarctica: Assessing Transfer of Plant Propagules by Human Visitors to Reduce Invasion Risk." *Biological Conservation* 171: 278–284. https://doi.org/10.1016/j.biocon.2014.01.038.

Jenks, G. F. 1977. *Optimal Data Classification for Choropleth Maps, Occasional Paper No. 2*. Lawrence, Kansas: University of Kansas, Department of Geography.

Kaczmarek, Ł., T. Bartylak, D. Stec, et al. 2020. "Revisiting the Genus *Mesobiotus* Vecchi Et al., 2016 (Eutardigrada, Macrobiotidae) - Remarks, Updated Dichotomous Key and an Integrative Description of New Species From Madagascar." *Zoologischer Anzeiger* 287: 121–146. https://doi.org/10.1016/j.jcz.2020.05.003.

Kaczmarek, Ł., and Ł. Michalczyk. 2017. "The *Macrobiotus hufelandi* Group (Tardigrada) Revisited." *Zootaxa* 4363: 101–123. https://doi.org/10.11646/ZOOTAXA.4363.1.4.

Kassambara, A., and F. Mundt. 2020. "Factoextra: Extract and Visualize the Results of Multivariate Data Analyses." R Package Version 1.0.7. https://CRAN.R-project.org/package=factoextra.

Kayastha, P., W. Szydło, M. Mioduchowska, and Ł. Kaczmarek. 2023. "Morphological and Genetic Variability in Cosmopolitan Tardigrade Species - *Paramacrobiotus Fairbanksi* Schill, Förster, Dandekar & Wolf, 2010." *Scientific Reports* 13: 17672. https://doi.org/10.1038/s41598-023-42653-6.

Kihm, J. H., S. Kim, S. J. McInnes, et al. 2020. "Integrative Description of a New *Dactylobiotus* (Eutardigrada: Parachela) From Antarctica That Reveals an Intraspecific Variation in Tardigrade Egg Morphology." *Scientific Reports* 10: 9122. https://doi.org/10.1038/s41598-020-65573-1.

Köppen, W. P. 1931. *Grundriss der Klimakunde*. Berlin: Walter de Gruyter Co.

Landau, W. M. 2021. "The Targets R Package: A Dynamic Make-Like Function-Oriented Pipeline Toolkit for Reproducibility and High-Performance Computing." *Journal of Open Source Software* 6: 2959. https://doi.org/10.21105/joss.02959.

Lemon, J. 2006. "Plotrix: A Package in the Red Light District of R." *R-News* 6: 8–12.

Livermore, R., A. Nankivell, G. Eagles, and P. Morris. 2005. "Paleogene opening of Drake passage." *Earth and Planetary Science Letters* 236: 459–470. https://doi.org/10.1016/j.epsl.2005.03.027.

McInnes, S. J., and P. J. A. Pugh. 1998. "Biogeography of Limno-Terrestrial Tardigrada, With Particular Reference to the Antarctic Fauna." *Journal of Biogeography* 25: 31–36. https://doi.org/10.1046/j.1365-2699.1998.251176.x.

McInnes, S. J., and P. J. A. Pugh. 2007. "An Attempt to Revisit the Global Biogeography of Limno-Terrestrial Tardigrada." *Journal of Limnology* 66: 90–96. https://doi.org/10.4081/jlimnol.2007.s1.90.

McLoughlin, S. 2001. "The Breakup History of Gondwana and Its Impact on Pre-Cenozoic Floristic Provincialism." *Australian Journal of Botany* 49: 271–300. https://doi.org/10.1071/BT00023.

Meyer, H. A., M. Tsaliki, and B. Sorgee. 2017. "New Water Bear Records (Phylum Tardigrada) From South Carolina, Southeastern USA, With the Description of *Echiniscus Danieli* Sp. Nov. (Heterotardigrada, Echiniscidae, *Bigranulatus* Group)." *Proceedings of the Biological Society of Washington* 130: 98–107.

Miller, W. R., and H. Heatwole. 1995. "Tardigrades of the Australian Antarctic Territories: The Mawson Coast, East Antarctic." *Invertebrate Biology* 114: 27–38.

Møbjerg, N., A. Jørgensen, R. M. Kristensen, and R. C. Neves. 2018. "Morphology and Functional Anatomy." In *Water Bears: The Biology of Tardigrades*, edited by R. O. Schill, 57–94. Cham: Springer. https://doi.org/10.1007/978-3-319-95702-9_2.

Mogle, M. J., S. A. Kimball, W. R. Miller, and R. D. McKown. 2018. "Evidence of Avian-Mediated Long Distance Dispersal in American Tardigrades." *PeerJ* 6: e5035. https://doi.org/10.7717/peerj.5035.

Morek, W., D. Stec, P. Gąsiorek, R. O. Schill, Ł. Kaczmarek, and Ł. Michalczyk. 2016. "An Experimental Test of Eutardigrade Preparation Methods for Light Microscopy." *Zoological Journal of the Linnean Society* 178: 785–793.

Nelson, D. R., P. J. Bartels, and N. Guil. 2018. "Tardigrade ecology." In *Water Bears: The Biology of Tardigrades*, edited by R. O. Schill, 163–210. Cham: Springer. https://doi.org/10.1007/978-3-319-95702-9_7.

Nkem, J. N., D. H. Wall, R. A. Virginia, et al. 2006. "Wind Dispersal of Soil Invertebrates in the McMurdo Dry Valleys, Antarctica." *Polar Biology* 29: 346–352. https://doi.org/10.1007/s00300-005-0061-x.

Oksanen, J., G. Simpson, F. Blanchet, et al. 2024. "vegan: Community Ecology Package." R package version 2.6-6.1. https://CRAN.R-project.org/package=vegan.

Padial, J. M., A. Miralles, I. De la Riva, and M. Vences. 2010. "The Integrative Future of Taxonomy." *Frontiers in Zoology* 7: 1–14. https://doi.org/10.1186/1742-9994-7-16.

Peat, H. J., A. Clarke, and P. Convey. 2007. "Diversity and Biogeography of the Antarctic Flora." *Journal of Biogeography* 34: 132–146. https://doi.org/10.1111/j.1365-2699.2006.01565.x.

Pebesma, E., and R. Bivand. 2005. "Classes and Methods for Spatial Data in R." *R News* 5: 9–13. https://CRAN.R-project.org/doc/Rnews/.

Pebesma, E., and R. Bivand. 2023. *Spatial Data Science: With Applications in R*. New York: Chapman and Hall/CRC. https://doi.org/10.1201/9780429459016.

Pedersen, T. 2024. "patchwork: The Composer of Plots." R package version 1.2.0. https://CRAN.R-project.org/package=patchwork.

Phillips, L. M., R. I. Leihy, and S. L. Chown. 2022. "Improving Species-Based Area Protection in Antarctica." *Conservation Biology* 36: e13885. https://doi.org/10.1111/cobi.13885.

Prener, C., T. Grossenbacher, and A. Zehr. 2022. "biscale: Tools and Palettes for Bivariate Thematic Mapping." R package version 1.0.0. https://CRAN.R-project.org/package=biscale.

Pugh, P. J. A. 1993. "A Synonymic Catalogue of the Acari From Antarctica, the Sub-Antarctic Islands and the Southern Ocean." *Journal of Natural History* 27: 323–421. https://doi.org/10.1080/00222939300770171.

Pugh, P. J. A., and P. Convey. 2008. “Surviving out in the Cold: Antarctic Endemic Invertebrates and Their Refugia.” *Journal of Biogeography* 35: 2176–2186. https://doi.org/10.1111/j.1365-2699.2008.01953.x.

Pugh, P. J. A., and S. J. McInnes. 1998. “The Origin of Arctic Terrestrial and Freshwater Tardigrades.” *Polar Biology* 19: 177–182. https://doi.org/10.1007/s003000050232.

Pust, F. L., T. G. Frøslev, R. M. Kristensen, and N. Møbjerg. 2024. “Environmental DNA Metabarcoding of Danish Soil Samples Reveals New Insight Into the Hidden Diversity of Eutardigrades in Denmark.” *Zoological Journal of the Linnean Society* 200: 20–33. https://doi.org/10.1093/zoolinnean/zlad059.

R Core Team. 2024. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

RAS. 2024. “Register of Antarctic Species.” Accessed 02-05-2024. https://ras.biodiversity.aq.

Robertson, M. W., N. J. Russo, S. J. McInnes, B. Goffinet, and J. E. Jiménez. 2020. “Potential Dispersal of Tardigrades by Birds Through Endozoochory: Evidence From Sub-Antarctic White-Bellied Seedsnipe (*Attagis malouinus*).” *Polar Biology* 43: 899–902. https://doi.org/10.1007/s00300-020-02680-9.

Saługa, M., R. Ochyra, and M. Ronikier. 2022. “Phylogeographical Breaks and Limited Connectivity Among Multiple Refugia in a Pan-Antarctic Moss Species.” *Journal of Biogeography* 49: 1991–2004. https://doi.org/10.1111/jbi.14476.

Savary, P., J. C. Foltête, H. Moal, G. Vuidel, and S. Garnier. 2021. “graph4lg: A Package for Constructing and Analysing Graphs for Landscape Genetics in R.” *Methods in Ecology and Evolution* 12: 539–547. https://doi.org/10.1111/2041-210X.13530.

Schill, R. O., ed. 2019. *Water Bears: The Biology of Tardigrades (Vol. 2)*. Cham: Springer.

Souverijns, N. 2019. “Precipitation and Clouds Over Antarctica From an Observational and Modelling Perspective.” PhD thesis, KU Leuven.

Stec, D., M. Vecchi, M. Dudziak, P. J. Bartels, S. Calhim, and Ł. Michalczyk. 2021. “Integrative Taxonomy Resolves Species Identities Within the *Macrobiotus pallarii* Complex (Eutardigrada: Macrobiotidae).” *Zoological Letters* 7: 9. https://doi.org/10.1186/s40851-021-00176-w.

Stevens, M. I., P. Greenslade, and C. A. D'Haese. 2021. “Species Diversity in *Friesea* (Neanuridae) Reveals Similar Biogeographic Patterns Among Antarctic Collembola.” *Zoologica Scripta* 50: 647–657. https://doi.org/10.1111/zsc.12490.

Terauds, A., S. L. Chown, F. Morgan, et al. 2012. “Conservation Biogeography of the Antarctic.” *Diversity and Distributions* 18: 726–741. https://doi.org/10.1111/j.1472-4642.2012.00925.x.

Terauds, A., and J. R. Lee. 2016. “Antarctic Biogeography Revisited: Updating the Antarctic Conservation Biogeographic Regions.” *Diversity and Distributions* 22: 836–840. https://doi.org/10.1111/ddi.12453.

Thiese, M. S., B. Ronna, and U. Ott. 2016. “P Value Interpretations and Considerations.” *Journal of Thoracic Disease* 8: E928–E931. https://doi.org/10.21037/jtd.2016.08.16.

Topstad, L., R. Guidetti, M. Majaneva, and T. Ekrem. 2021. “Multi-Marker DNA Metabarcoding Reflects Tardigrade Diversity in Different Habitats.” *Genome* 64: 217–231. https://doi.org/10.1139/gen-2019-0218.

Torricelli, G., A. Carapelli, P. Convey, F. Nardi, J. L. Boore, and F. Frati. 2010. “High Divergence Across the Whole Mitochondrial Genome in the “Pan-Antarctic” Springtail *Friesea grisea*: Evidence for Cryptic Species?” *Gene* 449: 30–40. https://doi.org/10.1016/j.gene.2009.09.006.

Troell, S., and K. I. Jönsson. 2023. “Occurrence of Tardigrades and Morphometric and Chemical Conditions in Rock Pools by the Baltic Sea.” *Scientific Reports* 13: 19776. https://doi.org/10.1038/s41598-023-46697-6.

Trokhymets, V., A. Zinkovskyi, and I. Dykyy. 2024. “Distribution of *Boeckella poppei* (Copepoda: Centropagidae) in the Region of the Wilhelm Archipelago (Kyiv Peninsula, Maritime Antarctica).” *Polar Biology* 47: 349–365. https://doi.org/10.1007/s00300-024-03238-9.

Turner, J., N. E. Barrand, T. J. Bracegirdle, et al. 2014. “Antarctic Climate Change and the Environment: An Update.” *Polar Record* 50: 237–259. https://doi.org/10.1017/S0032247413000296.

Turner, J., R. Bindschadler, P. Convey, et al. 2009. “Scientific Committee on Antarctic Research.” Cambridge.

Vecchi, M., M. Cesari, R. Bertolani, K. I. Jönsson, L. Rebecchi, and R. Guidetti. 2016a. “Corrigendum to: Integrative Systematic Studies on Tardigrades From Antarctica Identify New Genera and New Species Within Macrobiotoidea and Echiniscoidea.” *Invertebrate Systematics* 30: 521.

Vecchi, M., I. Dykyy, P. Khoyetskyy, T. Vuori, S. Calhim, and V. Trokhymets. 2024. “The Tardigrade *Mesobiotus aradasi* (Binda, Pilato & Lisi, 2005) is Widely Distributed Along the Antarctic Peninsula.” *Polar Biology* 47: 227–238. https://doi.org/10.1007/s00300-023-03222-9.

Vecchi, M., C. Ferrari, D. Stec, and S. Calhim. 2022. “Desiccation Risk Favours Prevalence and Diversity of Tardigrade Communities and Influences Their Trophic Structure in Alpine Ephemeral Rock Pools.” *Hydrobiologia* 849: 1995–2007. https://doi.org/10.1007/s10750-022-04820-0.

Vecchi, M., J. L. McDaniel, J. Chartrain, T. Vuori, E. J. Walsh, and S. Calhim. 2023a. “Morphology, Phylogenetic Position, and Mating Behaviour of a New *Mesobiotus* (Tardigrada) Species From a Rock Pool in the Socorro Box Canyon (New Mexico, USA).” *European Zoological Journal* 90: 708–725. https://doi.org/10.1080/24750263.2023.2263033.

Vecchi, M., A. Tsvetkova, D. Stec, C. Ferrari, S. Calhim, and D. Tumanov. 2023b. “Expanding *Acutuncus*: Phylogenetics and Morphological Analyses Reveal a Considerably Wider Distribution for This Tardigrade Genus.” *Molecular Phylogenetics and Evolution* 180: 107707. https://doi.org/10.1016/j.ympev.2023.107707.

Vecchi, M., F. Vicente, R. Guidetti, R. Bertolani, L. Rebecchi, and M. Cesari. 2016b. “Interspecific Relationships of Tardigrades With Bacteria, Fungi and Protozoans, With a Focus on the Phylogenetic Position of *Pyxidium tardigradum* (Ciliophora).” *Zoological Journal of the Linnean Society* 178: 846–855. https://doi.org/10.1111/zoj.12446.

Velasco-Castrillón, A., J. A. E. Gibson, and M. I. Stevens. 2014. “A Review of Current Antarctic Limno-Terrestrial Microfauna.” *Polar Biology* 37: 1517–1531. https://doi.org/10.1007/s00300-014-1544-4.

Velasco-Castrillón, A., S. J. McInnes, M. B. Schultz, et al. 2015. “Mitochondrial DNA Analyses Reveal Widespread Tardigrade Diversity in Antarctica.” *Invertebrate Systematics* 29: 578–590. https://doi.org/10.1071/IS14019.

Wagner, M., W. Trutschnig, A. C. Bathke, and U. Ruprecht. 2018. “A First Approach to Calculate BIOCLIM Variables and Climate Zones for Antarctica.” *Theoretical and Applied Climatology* 131: 1397–1415.

Wang, Y., and S. Hou. 2009. “A New Interpolation Method for Antarctic Surface Temperature.” *Progress in Natural Science* 19: 1843–1849. https://doi.org/10.1016/j.pnsc.2009.07.012.

Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. New York: Springer-Verlag.

Wickham, H., and J. Bryan. 2023. “readxl: Read Excel Files.” R package version 1.4.3. https://CRAN.R-project.org/package=readxl.

Wickham, H., R. François, L. Henry, K. Müller, and D. Vaughan. 2023. “dplyr: A Grammar of Data Manipulation.” R package version 1.1.4. https://CRAN.R-project.org/package=dplyr.

Wickham, H., T. Pedersen, and D. Seidel. 2023. “scales: Scale Functions for Visualization.” R package version 1.3.0. https://CRAN.R-project.org/package=scales.

Wickham, H., D. Vaughan, and M. Girlich. 2024. “tidyr: Tidy Messy Data.” R package version 1.3.1. https://CRAN.R-project.org/package=tidyr.

Wilke, C. 2024. “cowplot: Streamlined Plot Theme and Plot Annotations for ‘ggplot2’.” R package version 1.1.3. https://CRAN.R-project.org/package=cowplot.

Xu, S., M. Chen, T. Feng, L. Zhan, L. Zhou, and G. Yu. 2021. “Use Ggbreak to Effectively Utilize Plotting Space to Deal With Large Datasets and Outliers.” *Frontiers in Genetics* 12: 774846. https://doi.org/10.3389/fgene.2021.774846.

Znój, A., K. J. Chwedorzewska, P. Androsiuk, et al. 2017. “Rapid Environmental Changes in the Western Antarctic Peninsula Region due to Climate Change and Human Activity.” *Applied Ecology and Environmental Research* 15: 525–539. https://doi.org/10.15666/aeer/1504_525539.

Supporting Information

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

Appendix 1

Data Sources: Reference List of the Antarctic Tardigrades Dataset

Altiero, T., Giovannini, I., Guidetti, R., & Rebecchi, L. (2015). Life history traits and reproductive mode of the tardigrade *Acutuncus antarcticus* under laboratory conditions: strategies to colonize the Antarctic environment. *Hydrobiol*., 761, 277–291.

Binda, M. G., & Pilato, G. (1992). *Minibiotus furcatus*, nuova posizione sistematica per *Macrobiotus furciger* Ehrenberg, 1859, e descrizione di due nuove specie (Eutardigrada). *Animalia*, 19, 111–120.

Binda, M. G., & Pilato, G. (1994). *Macrobiotus mottai*, nuova specie di eutardigrado dell’Antartide. *Animalia*, 21, 53–56.

Binda, M. G., & Pilato, G. (2000). *Diphascon* (Adropion) *tricuspidatum*, a new species of eutardigrade from Antarctica. *Polar Biol*., 23, 75–76.

Cathey, D. D., Parker, B. C., Simmons Jr., G. M., Yongue Jr., W. H., & Van Brunt, M. R. (1981). The microfauna of algal mats and artificial substrates in Southern Victoria Land Lakes of Antarctica. *Hydrobiol*., 85, 3–15.

Convey, P., & McInnes, S. J. (2005). Exceptional tardigrade-dominated ecosystems in Ellsworth Land, Antarctica. *Ecology*, 86, 519–527.

Czechowski, P., Sands, C. J., Adams, B. J., D’Haese, C. A., Gibson, J. A. E., McInnes, S. J., & Stevens, M. I. (2012). Antarctic Tardigrada: a first step in understanding molecular operational taxonomic units (MOTUs) and biogeography of cryptic meiofauna. *Invertebr. Syst*., 26, 526–538.

Dastych, H. (1984). The Tardigrada from Antarctic with descriptions of several new species. *Acta Zool. Cracov*., 27, 377–436.

Dastych, H. (1989). An annotated list of Tardigrada from the Antarctic. *Entomol. Mitt. Zool. Mus. Hambg*., 9, 249–257.

Dastych, H. (1998). Description of eggs in the Antarctic tardigrade *Minibiotus stuckenbergi* (Dastych et al., 1990) (Tardigrada, Macrobiotidae). *Entomol. Mitt. Zool. Mus. Hambg*., 12, 289–294.

Dastych, H., & Drummond, A. E. (1996). Notes on limnic water-bears (Tradigrada) from the Robertskollen nunataks, Dronning Maud Land, Antarctica. *Entomol. Mitt. Zool. Mus. Hambg*., 12, 111–117.

Dastych, H., & Harris, J. M. (1994). A new species of the genus *Hebesuncus* from the Antarctic nunataks, Dronning Maud Land (Tardigrada). *Entomol. Mitt. Zool. Mus. Hambg*., 11, 139–145.

Dastych, H., & Harris, J. M. (1995). A new species of the genus *Macrobiotus* from inland nunataks in western Dronning Maud Land, continental Antarctica (Tardigrada). *Entomol. Mitt. Zool. Mus. Hambg*., 11, 175–182.

Dastych, H., & McInnes, S. J. (1994). *Hexapodibius boothi* sp. n., a new species of semi-terrestrial tardigrade from the Maritime Antarctic. *Entomol. Mitt. Zool. Mus. Hambg*., 11, 111–117.

Dastych, H., & McInnes, S. J. (1996). A new species of the genus *Diphascon* (Tardigrada) from the Maritime Antarctic. *Entomol. Mitt. Zool. Mus. Hambg*., 12, 35–41.

Dastych, H., Ryan, P. G., & Watkins, B. P. (1990). Notes on Tardigrada from western Dronning Maud Land (Antarctica) with a description of two new species. *Entomol. Mitt. Zool. Mus. Hambg*., 10, 57–66.

Dougherty, C. E. (1964). Cultivation and nutrition of micrometazoa. II. An Antarctic strain of the tardigrade *Hypsibius arcticus* (Murray, 1907) Marcus, 1928. *Trans. Am. Microsc. Soc*., 83, 7–11.

Dougherty, C. E., & Harris, L. G., (1963). Antarctic micrometazoa: freshwater species in McMurdo Sound area. *Science*, 140, 497–498.

Everitt, D. A. (1981). An ecological study of an Antarctic freshwater pool with particular reference to Tardigrada and Rotifera. *Hydrobiol*., 83, 225–237.

Gąsiorek, P., Wilamowski, A., Vončina, K., & Michalczyk, Ł. (2022). Neotropical jewels in the moss: biodiversity, distribution and evolution of the genus Barbaria (Heterotardigrada: Echiniscidae). *Zool. J. Linn. Soc*., 195, 1037–1066.

Gąsiorek, P. (2023). Eventually tested: Phylogenetic position of “*Testechiniscus*” *meridionalis* (Murray, 1906) (Heterotardigrada) revealed. *Zool. Anz*., 304, 49–60.

Gibson, J. A. E., Cromer, L., Agius, J. T., McInnes, S.J ., & Marley, N. J. (2007). Tardigrade eggs and exuviae in Antarctic lake sediments: insights into Holocene dynamics and origins of the fauna. *J. Limnol*., 66, 65–71.

Guidetti, R., Massa, E., Bertolani, R., Rebecchi, L., & Cesari, M. (2019). Increasing knowledge of Antarctic biodiversity: new endemic taxa of tardigrades (Eutardigrada; Ramazzottiidae) and their evolutionary relationships. *Syst. Biodivers*., 17, 573–593.

Guidetti, R., Rebecchi, L., Cesari, M., & McInnes, S. J. (2014). *Mopsechiniscus franciscae*, a new species of a rare genus of Tardigrada from continental Antarctica. *Polar Biol*., 37, 1221–1233.

Heatwole, H., & Miller, W. R. (2019). Structure of micrometazoan assemblages in the Larsemann Hills, Antarctica. *Polar Biol*., 42, 1837–1848.

Heywood, R. B. (1977). A limnological Survey of the Ablation Point area, Alexander Island, Antarctica. *Phil. Trans. R. Soc. Lond. B*, 279, 34–54.

Janiec, K. (1996). The comparison of freshwater invertebrates of Spitsbergen (Arctic) and King George Island (Antarctic). *Pol. Polar. Res*., 17, 173–202.

Jennings, P. G. (1975). The Signy Island terrestrial reference sites: V. Oxygen uptake of *Macrobiotus furciger* J. Murray (tardigrada). *Br. Antarct. Surv. Bull*., 41, 161–168.

Jennings, P. G. (1976a). The Tardigrada of Signy Island, South Orkney Islands, with a note on the Rotifera. *Br. Antarct. Surv. Bull*., 44, 1–25.

Jennings, P. G. (1976b). Tardigrada from the Antarctic Peninsula and Scotia Ridge region. *Br. Antarct. Surv. Bull*., 44, 77–95.

Jennings, P. G. (1979). The Signy Island terrestrial reference sites. X: Population dynamics of Tardigrada and Rotifera. *Br. Antarct. Surv. Bull.*, 47, 89–105.

Kaczmarek, Ł., Janko, K., Smykla, J., & Michalczyk, Ł. (2014). Soil tardigrades from the Antarctic Peninsula with a description of a new species and some remarks on the genus *Ramajendas* (Eutardigrada, Isohypsibiidae). *Polar Rec.*, 50, 176–182.

Kaczmarek, Ł., Mioduchowska, M., Kačarević, U., Kubska, K., Parnikoza, I., Gołdyn, B., & Roszkowska, M. (2020). New Records of Antarctic Tardigrada with Comments on Interpopulation Variability of the *Paramacrobiotus fairbanksi* Schill, Förster, Dandekar and Wolf, 2010. *Diversity*, 12, 108.

Kaczmarek, L., Parnikoza, I., Gawlak, M., Esefeld, J., Peter, H. U., Kozeretska, I., & Roszkowska, M. (2018). Tardigrades from Larus dominicanus Lichtenstein, 1823 nests on the Argentine Islands (maritime Antarctic). *Polar Biol.*, 41, 283–301.

Kagoshima, H., Imura, S., & Suzuki, A. C. (2013). Molecular and morphological analysis of an Antarctic tardigrade, *Acutuncus antarcticus*. *J. Limnol.*, 72, 15–23.

Kihm, J. H., Kim, S., McInnes, S. J., Zawierucha, K., Rho, H. S., Kang, P., & Park, T. Y. S. (2020). Integrative description of a new *Dactylobiotus* (Eutardigrada: Parachela) from Antarctica that reveals an intraspecific variation in tardigrade egg morphology. *Sci. Rep.*, 10, 9122.

Lukashanets, D. A., Convey, P., Borodin, O. I., Miamin, V. Y., Hihiniak, Y. H., Gaydashov, A. A., Yatsyna A. P., Vezhnavets, V. V., Maysak., N. N., & Shendrik, T. V. (2021). Eukarya biodiversity in the Thala Hills, East Antarctica. *Antarct. Sci.*, 33, 605–623.

McInnes, S. J. (1995). Tardigrades from Signy Island, South Orkney Islands, with particular reference to freshwater species. *J. Nat. Hist.*, 29, 1419–1445.

McInnes, S. J. (2010). *Echiniscus corrugicaudatus* (Heterotardigrada; Echiniscidae) a new species from Ellsworth Land, Antarctica. *Polar Biol.*, 33, 59–70.

McInnes, S. J., & Ellis-Evans, J. C. (1990). Micro-invertebrate structure within a Maritime Antarctic lake. *Proc. NIPR Symp. Polar Biol.*, 3, 179–189.

McInnes, S. J., & Pugh, P. J. A. (2013). The impact of tourists on Antarctic tardigrades: an ordination-based model. *J. Limnol.*, 72, 128–135.

Miller, J. D., Horne, P., Heatwole, H., Miller, W. R., & Bridges, L. (1988). A survey of the terrestrial Tardigrada of the Vestfold Hills, Antarctica. *Hydrobiol.*, 165, 197–208.

Miller, W. R., & Heatwole, H. (1995). Tardigrades of the Australian Antarctic Territories: the Mawson Coast, East Antarctic. *Invertebr. Biol.*, 114, 27–38.

Miller, W. R., Heatwole, H., Pidgeon, R. W. J., & Gardiner, G. R. (1994). Tardigrades of the Australian Antarctic Territories: the Larsemann Hills, East Antarctica. *Trans. Am. Microsc. Soc.*, 113, 142–160.

Miller, W. R., Miller, J. D., & Heatwole, H. F. (1996). Tardigrades of the Australian Antarctic Territories: the Windmill Islands, East Antarctica. *Zool. J. Linn. Soc.*, 116, 175–184.

Mioduchowska, M., Kacarevic, U., Miamin, V., Giginiak, Y., Parnikoza, I., Roszkowska, M., & Kaczmarek, Ł. (2021). Redescription of Antarctic eutardigrade *Dastychius improvisus* (Dastych, 1984) and some remarks on phylogenetic relationships within Isohypsibioidea. *Eur. Zool. J.*, 88, 117–131.

Morikawa, K. (1962). Notes on some Tardigrada from the Antarctic region. *Biol. Res. Jpn. Ant. Res. Exp.*, 17, 3–6.

Murray, J. (1906). Scottish National Antarctic Expedition; Tardigrada of the South Orkneys. *Trans. R. Soc. Edinb.*, 45, 323–339.

Murray, J. (1910). Tardigrada. British Antarctic Expedition 1907–1909. Reports of the Scientific Investigation. Biology. Vol. 1. London, William Heinemann, 83–185.

Pilato, G., & Binda, M. G. (1990). Tardigradi dell'Antartide. I. *Ramajendas*, nuovo genere di eutardigrado. Nuova posizione sistematica di *Hypsibius renaudi* Ramazzotti, 1972 e descrizione di *Ramajendas frigidus* n. sp. *Animalia*, 17, 61–71.

Pilato, G., & Binda, M. G. (1999). Three new species of *Diphascon* of the *pingue* group (Eutardigrada, Hypsibiidae) from Antarctica. *Polar Biol.*, 21, 335–342.

Pilato, G., McInnes, S. J., & Lisi, O. (2012). *Hebesuncus mollispinus* (Eutardigrada, Hypsibiidae), a new species from maritime Antarctica. *Zootaxa*, 3446, 60–68.

Pilato, G., Sabella, G., D'Urso, V., & Lisi, O. (2017). Two new species of Eutardigrada from Victoria Land, Antarctica. *Zootaxa*, 4317, 541–558.

Polishchuk, A., Kayastha, P., Kovalenko, P., Parnikoza, I., & Kaczmarek, Ł. (2023). New Records of Tardigrades from the Danco and Graham Coasts, the Maritime Antarctic. *Ann. Zool.*, 73, 17–28.

Porazinska, D., Fountain, A. G., Nylen, T., Tranter, M., Virginia, R. A., & Wall, D. H. (2004). The biodiversity and biogeochemistry of cryoconite holes from McMurdo dry valley glaciers, Antarctica. *Arct. Antarct. Alp. Res.*, 36, 84–91.

Richters, F. (1904). Vorläufiger Bericht über die antarktische Moosfauna. *Verh. Dtsch. Zool. Ges.*, 14, 236–239.

Richters, F. (1908). Antarktische Tardigraden. *Zool. Anz.*, 34, 915–916.

Richters, F. (1909). Tardigrada unter 77º Südpol. *Zool. Anz.*, 36, 604–606.

Ryan, P. G., Watkins, B. P., Lewis Smith, R. I., Dastych, H., Eicker, A., Foissner, W., Heatwole, H., Miller, W. R., & Thompson, G. (1989). Biological survey of Robertskollen, western Dronning Maud Land: area description and preliminary species list. *S. Afr. J. Antarct. Res.*, 19, 10–20.

Short, K. A., Sands, C. J., McInnes, S. J., Pisani, D., Stevens, M. I., & Convey, P. (2022). An ancient, Antarctic-specific species complex: large divergences between multiple Antarctic lineages of the tardigrade genus *Mesobiotus*. *Mol. Phylogenet. Evol.*, 170, 107429.

Smykla, J., Iakovenko, N., Devetter, M., & Kaczmarek, Ł. (2012). Diversity and distribution of tardigrades in soils of Edmonson Point (Northern Victoria Land, continental Antarctica). *Czech Polar Rep.*, 2, 61–70.

Sohlenius, B., Boström, S., & Hirschfelder, A. (1995). Nematodes, rotifers and tardigrades from nunataks in Dronning Maud Land, East Antarctica. *Polar Biol.*, 15, 51–56.

Sohlenius, B., Boström, S., & Jönsson, K. I. (2004). Occurrence of nematodes, tardigrades and rotifers on ice-free areas in East Antarctica. *Pedobiologia*, 48, 395–408.

Sudzuki, M. (1964). On the microfauna of the Antarctic region. 1. Moss-water community at Langhovde. *JARE Sci. Rep.*, 19, 1–41.

Suzuki, A. C., Sugiura, K., Tsujimoto, M., Nakai, R., McInnes, S. J., Kagoshima, H., & Imura, S. (2023). A New Species of Bisexual Milnesium (Eutardigrada: Apochela) Having Aberrant Claws from Innhovde, Dronning Maud Land, East Antarctica. *Zool. Sci.*, 40, 246–261.

Tsujimoto, M., Imura, S., & Kanda, H. (2016). Recovery and reproduction of an Antarctic tardigrade retrieved from a moss sample frozen for over 30 years. *Cryobiology*, 72, 78–81.

Tsujimoto, M., McInnes, S. J., Convey, P., & Imura, S. (2014). Preliminary description of tardigrade species diversity and distribution pattern around coastal Syowa Station and inland Sør Rondane Mountains, Dronning Maud Land, East Antarctica. *Polar Biol.*, 37, 1361–1367.

Tumanov, D. V. (2006). Five new species of the genus Milnesium (Tardigrada, Eutardigrada, Milnesiidae). *Zootaxa*, 1122, 1–23.

Tumanov, D. V. (2022). End of a mystery: Integrative approach reveals the phylogenetic position of an enigmatic Antarctic tardigrade genus *Ramajendas* (Tardigrada, Eutardigrada). *Zool. Scr.*, 51, 217–231.

Usher, M. B., & Dastych, H. (1987). Tardigrada from the maritime Antarctic. *Br. Antarct. Surv. Bull.*, 77, 163–166.

Utsugi, K., & Ohyama, Y. (1989). Antarctic Tardigrada. *Polar Biol.*, 2, 190–197.

Utsugi, K., & Ohyama, Y. (1991). Antarctic Tardigrada II. Molodezhnaya and Mt. Riiser-Larsen areas. *Proc. NIPR Symp. Polar. Biol.*, 4, 161–170

Utsugi, K., & Ohyama, Y. (1993). Antarctic Tardigrada III. Fildes Peninsula of King George Island. *Proc. NIPR Symp. Polar. Biol.*, 6, 139–151.

Vecchi, M., Cesari, M., Bertolani, R., Jönsson, K. I., Rebecchi, L., & Guidetti, R. (2016). Corrigendum to: Integrative systematic studies on tardigrades from Antarctica identify new genera and new species within Macrobiotoidea and Echiniscoidea. *Invertebr. Syst.*, 30, 521–521.

Vecchi, M., Dykyy, I., Khoyetskyy, P., Vuori, T., Calhim, S., & Trokhymets, V. (2024). The tardigrade *Mesobiotus aradasi* (Binda, Pilato & Lisi, 2005) is widely distributed along the Antarctic Peninsula. *Polar Biol.*

Venkataraman, K. (1998). Studies on Phylum Tardigrada and Other Associated Fauna, South Polar Skua and Bird and Mammal Logging During 1994–1995 Expedition/Fourteenth Indian Expedition to Antarctica, Scientific Report. Department of Ocean Development, Technical Publication, 12, 221–243.