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Review

Catch me if you can, or how paradigms of tardigrade biogeography evolved from cosmopolitism to 'localism'

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ABSTRACT

This review synthesizes recent developments in the field of tardigrade biogeography, tracing back to the origins of Baas Becking's hypothesis that 'everything is everywhere but the environment selects' to the latest empirical studies that favour biogeographic structuring of these microinvertebrates. I recapitulate evidence for diverse means of meiofauna dispersal, focusing on the two principal mechanisms suggested for tardigrades: wind (aeolian dispersal/anemochory) and animals (zoochory). I argue that tardigrade species with relatively well-documented geographic distributions display climatic regionalization. The literature treating purportedly cosmopolitan tardigrades is critically scrutinized and evidence for strict cosmopolitanism is deemed insufficient. Due to the presence of numerous endemics restricted to mountains, elevational diversity gradients can be recognized at a local scale (for example, within a single biogeographic region). Finally, the tardigrade faunas of a given region should be likely regarded as part of a regionalized macrometazoan fauna containing a small fraction of widespread, ubiquitous species (called 'biogeographic noise' herein).

Keywords: cosmopolitism; crypsis; dispersal; diversity gradients; endemism; postglacial refugia

INTRODUCTION

The extent of our understanding regarding the distribution of organisms is intrinsically linked to the sampling effort invested on a particular taxonomic group (Oliveira *et al.* 2017). Consequently, taxonomic groups characterized by a prolonged history of extensive collecting are more frequently utilized in biogeography to explain current distribution patterns, see e.g. Cracraft (1974) for vertebrates and Večeřa *et al.* (2019) for vascular plants. Conversely, enigmatic and poorly studied taxa are especially susceptible to sampling biases (Fontaneto *et al.* 2012) and inadequate systematics (Aksenova *et al.* 2018) when chosen as models to address specific biogeographic questions. The majority of microscopic animals, broadly termed as meiofauna (or microfauna in the case of terrestrial microinvertebrates) and comprising species no longer than 1 mm in body length, are inadequately researched and consequently infrequently used in biogeography (Giere and Schratzberger 2023). One such meiofaunal component, although admittedly usually scarce in numbers relative to nematodes or arthropods (see a comprehensive survey on marine communities in Leasi *et al.* 2018), are tardigrades, a charismatic animal phylum recognized for their cryptobiotic abilities (Møbjerg *et al.* 2011). Their simplified anatomy and miniaturization evolved in tandem with major genome rearrangements (Gross *et al.* 2019), including the emergence of genes linked with cryptobiosis. Tardigrades dwell in a broad range of habitats, both marine and terrestrial, but require a microfilm of water to thrive (Nelson and Marley 2000).

This contribution expounds on the progress in tardigrade biogeography that has been made in the past two decades and provides a novel perspective based on current literature. I begin with the first hypotheses relating to the global distribution of microscopic life (Beijerinck 1913, Baas Becking 1934) that consolidated the view that microinvertebrates lacked distinct biogeographic distributions. I discuss the main mechanisms of short- and long-distance dispersal in both meiofauna and tardigrades, and in doing so evaluate the validity of data gathered so

far. The relationship between tardigrade α-diversity and elevation above sea level is summarized and suggested as pertinent within the context of global biodiversity assessment. Moreover, I summarize the available information on regionalization of tardigrade assemblages. Finally, I assert that establishing the cosmopolitan distribution of a limno-terrestrial tardigrade species is intrinsically connected with providing DNA barcoding data to eliminate the possibility of crypsis, a phenomenon frequently encountered in these animals (Morek et al. 2021). Ultimately, I conclude that the currently unfolding picture of limno-terrestrial tardigrade distribution reflects a range of biogeographic patterns, from cosmopolitism to 'localism', the latter likely being prevalent in tardigrades. Such a variety of biogeographies, or types of geographic distributions, has already been indicated for other meiofaunal groups including rotifers and flatworms (Segers and De Smet 2008, Artois et al. 2011, Tessens et al. 2021).

COSMOPOLITISM

There is no underlying and precise definition of cosmopolitism. For the sake of clarity, a cosmopolitan species is defined as present in all or almost all (e.g. 9–10 out of 11) zoogeographic regions (Holt et al. 2013); the pan-Antarctic region is usually excluded from this definition due to the harshness of environmental conditions that make it unsuitable for most living organisms. In the first half of the 20th century, microbiologists formulated the authoritative hypothesis 'everything is everywhere but the environment selects' (abbreviated EiE herein) based on multiple observations of individual bacterial species across different regions of the globe exhibiting similar climatic and habitat conditions (Beijerinck 1913, Baas Becking 1934). It soon became a paradigm in the biogeography of other microorganisms, such as protists (Finlay 2002) and meiofauna (Artois et al. 2011, Guil 2011). Taxonomists specializing in these groups reported species, which were typically regarded as morphologically variable, from a plethora of localities worldwide [see e.g. a global summary of limno-terrestrial tardigrade records in McInnes (1994) and records of such species as *Bryodelphax parvulus* Thulin, 1928; *Echiniscus quadrispinosus* Richters, 1902; *Hypsibius dujardini* (Doyère, 1840); *Macrobiotus hufelandi* C.A.S. Schultze, 1834; *Milnesium tardigradum* (Doyère, 1840); *Paramacrobiotus richtersi* (Murray, 1911); or *Pseudechiniscus suillus* (Ehrenberg, 1853)]. With the advent of molecular techniques, what was deemed to be a single species often turned out to be a conglomerate of related taxa structured biogeographically [see e.g. Faurby et al. 2012 and the global cytochrome oxidase I subunit (*COI*) gene fragment dataset of the intertidal tardigrade genus *Echiniscoides* Plate, 1888; or Heger et al. 2013 and the Holarctic *COI* dataset of the testate amoeba *Hyalosphenia papilio* Leidy, 1874]. As a result, both morphological and molecular support for many purportedly cosmopolitan species started to crumble [e.g. Petrusek et al. 2004 questioning cosmopolitism of the cladoceran *Moina micrura* Kurz, 1875; Faurby et al. 2011 challenging the wide geographic distribution of *Echiniscoides sigismundi* (M. Schultze, 1865) in the North Atlantic Ocean]. However, the ecological rationales behind claiming microorganisms as cosmopolitan are not empirically corroborated. For example, the assumption of a virtually infinite population size for cosmopolitan elements (Fenchel and Finlay 2004) appears unrealistic in the case of tardigrades, which in comparison with other meiofaunal organisms are typically recorded in small population densities. While sampling the beaches of Panama, Leasi et al. (2018) found that tardigrades were, alongside gnathostomulids, the least numerous meiofaunal component among the 15 phyla represented in the meiofaunal communities. Hohberg (2006) and Hohberg et al. (2011), despite encountering population peaks under certain conditions in post-industrial sites, recorded an overall low population density among soil tardigrades in Germany. In parallel, molecular evidence augmented the hypothetically assumed cosmopolitan distributions for many rotifers [Mills et al. 2007 and the global *COI* dataset of *Brachionus plicatilis* (Müller, 1786); Fontaneto et al. 2008 and the global *COI* dataset for the genera *Adineta* Hudson, 1886 and *Rotaria* Scopoli, 1777].

In the case of meiofauna, the theory assumes that cosmopolitan species are more common among parthenogenetic (asexually reproducing) than bisexual taxa (Artois et al. 2011). The asexual mode of reproduction is widely considered advantageous in newly inhabited environments and marginal habitats, as it allows for faster population growth and thus successful colonization (Fontaneto et al. 2008 addressed rotifers; Tilquin and Kokko 2016 provided a general review; Ptatscheck and Traunspurger 2020 addressed nematodes). In fact, all limno-terrestrial tardigrade species that have been reliably reported from at least two zoogeographic regions were found to be parthenogenetic [Jørgensen et al. 2007: *Echiniscus testudo* (Doyère, 1840); Gąsiorek et al. 2019a, b, 2021a, 2022a: *Echiniscus lineatus* Pilato et al., 2008, *E. perarmatus* Murray, 1907, *E. testudo*, *Nebularmis cirinoi* (Binda & Pilato, 1993); Kaczmarek et al. 2020: *Paramacrobiotus fairbanksi* Schill et al., 2010; Kiosya et al. 2021: *Echiniscus tropicalis* Binda & Pilato, 1995; Kayastha et al. 2023a, b: *Paramacrobiotus gadabouti* Kayastha et al., 2023, *P. fairbanksi*; Zawierucha et al. 2023: *Cryoconicus kaczmareki* Zawierucha et al., 2018], or at least males seldom appear in their populations (a potential facultative parthenogenesis, see Morek et al. 2021: *Milnesium* Doyère, 1840), and so pass unnoticed by researchers. Importantly, there is insufficient detailed data for most tardigrade lineages to allow a correlation between their broad geographic distribution and the occurrence of parthenogenesis. The correlation should be studied in detail when more data becomes available. The next sections will address the supposition that cosmopolitism is more widespread among parthenogens than among bisexuals, and whether there are convincing arguments for cosmopolitism as a general pattern of distribution for limno-terrestrial tardigrades.

Means of meiofauna dispersal

Due to its diminutive body size and potentially infinite population sizes, meiofauna is most often viewed as capable of direct dispersal over both short and long distances [Zullini 2018, Fontaneto 2019; although see Jenkins et al. (2007) for an alternative explanation based on a meta-analysis]. However, empirical evidence supporting this supposition varies, depending on the faunal group studied. Cáceres and Soluk (2002) demonstrated that different components of zooplankton (rotifers, microcrustaceans, mites, flatworms, polychaetes) exhibited varying abilities for dispersal and colonization. One of the oldest hypotheses regarding dispersal vectors is aeolian (wind-mediated) transport or anemochory. This hypothesis received early support, when in

1953, White showed that a phytopathogenic nematode was capable of dispersal through wind transport (White 1953). Since then, the aeolian hypothesis has been confirmed for a variety of micrometazoans, predominantly other nematodes, because of their economic relevance (Nkem *et al.* 2006, Ptatscheck *et al.* 2018, Rivas *et al.* 2018). Nevertheless, a high potential for survival in a desiccated state following wind dispersal has been confirmed for such varied groups as rotifers, collembolans, mites, gastrotrichs, microcrustaceans, and tardigrades (Ptatscheck *et al.* 2018, Rivas *et al.* 2018, Arenas-Sánchez *et al.* 2024).

The second most important hypothesis regarding the dispersal of microorganisms is animal-mediated transport (zoochory), either on a dispersal vector's body (ectozoochory; Coughlan *et al.* 2017) or within it (endozoochory; Brochet *et al.* 2010). Usually, birds were examined in that respect (Figuerola and Green 2002) due to the migratory character of many species, but mammals can also transfer microorganisms which become temporarily trapped among their hair. Less researched vector groups include molluscs, particularly snails (Grønvold and Nansen 1984, Türke *et al.* 2018), and earthworms (Grønvold 1979). Recently, Ingels *et al.* (2020) provided evidence for the phoresis and potential dispersal of 20 different meiofaunal taxa on loggerhead sea turtles *Caretta caretta* (Linnaeus, 1758). The importance of animals as dispersal vectors for most meiofauna groups remains understudied in comparison with aeolian dispersal, but must be taken into consideration when routes of dispersal are investigated.

Dispersal by rain splash (dynamic hydrochory) has been documented for nematodes (Grønvold 1984), and later independently observed for Greenlandic populations of the genus *Echiniscus* C.A.S. Schultze, 1840, and is hypothesized as the third potential way of dispersal for tardigrades (Kristensen 1987). In contrast to the abovementioned anemochory and zoochory, dispersal by rain is by definition a mechanism for short-distance dispersal, which a priori precludes its role in shaping meiofaunal biogeographies on a global scale. For this reason, I will not consider hydrochory in the synthesis sections devoted to tardigrades.

Means of tardigrade dispersal: anemochory

Wind has been suspected to play a key role in the passive dispersal of tardigrades for a long time, and indeed it received reliable support, coming mainly from the indirect evidence of tardigrade distributions, along with the findings from empirical studies. Janiec (1996) was the first to reveal short-distance dispersal in maritime Antarctic limno-terrestrial tardigrade assemblages (alongside rotifers and nematodes) through the analysis of the contents of traps designed to capture wind-transmitted microfauna. Further molecular studies with a large geographic coverage corroborated the hypothesis that wind is the main dispersal factor for several limno-terrestrial tardigrade species, such as *E. testudo* (Jørgensen *et al.* 2007, 2013), *E. lineatus* (Gąsiorek *et al.* 2019a), or *E. perarmatus* (Gąsiorek *et al.* 2022a). *Echiniscus testudo* is a truly cosmopolitan species (Gąsiorek *et al.* 2019b) exhibiting limited genetic structuring among geographically distant populations (Jørgensen *et al.* 2007). The latter two species are pantropical and exhibit similar population genetic patterns (Gąsiorek *et al.* 2019a, 2022a). Given their geographic ranges are limited latitudinally, and correspond with the direction of trade winds, it is unlikely that birds, whose main migratory routes are

mostly meridional (Newton 2008), served as vectors in the case of *E. lineatus* and *E. perarmatus* (Gąsiorek *et al.* 2019a). Instead, such a pattern likely reflects recent wind-mediated dispersal, that has had insufficient time to allow genetic population subdivision to occur (Jørgensen *et al.* 2013). Anemochory was further supported as the most likely explanation for the pantropical nature of the entirety of clade E, comprising *c.* 10 spp. of *Milnesium* (see Morek *et al.* 2021). In that paper, the remaining clades A–D and F comprised species, for the most part, limited to a single zoogeographic region (e.g. Palaearctic, Afrotropics), with clade E constituting the only exception. The mixed biogeographic origins of its taxa (i.e. Oriental-Neotropical) indicated dispersal as a possible speciation factor. The aeolian hypothesis effectively explains the pantropical geographic distributions observed in tardigrades, i.e. potential dispersal via trade winds, distributions which are difficult to attribute to the zoochory hypothesis (see below). Alternatively, generalist lowland species could easily undergo dispersal via rafts, a concept already demonstrated for various animals (Thiel and Gutow 2005).

Distinguishing between dispersal vectors is not always straightforward, as demonstrated for the tardigrade genus *Mopsechiniscus* du Bois-Reymond Marcus, 1944 (Guidetti *et al.* 2017). Members of this relic, evolutionarily isolated lineage dwell in the *Nothofagus* Blume temperate rainforests of South America, Australia, and Tasmania, and on barren circum-Antarctic islands. Resolving the dispersion method of *Mopsechiniscus* is currently problematic, as it remains uncertain whether the genus was dispersed via wind or by seabirds since both could have facilitated dispersal of this taxon. Expanding the genetic dataset for this taxon would enable molecular clock reconstructions, and depending on the splitting age of particular lineages within *Mopsechiniscus*, could clarify which dispersal factor was pivotal in the divergence of the genus.

Means of tardigrade dispersal: zoochory

Even though zoochory has long been surmized to play a role in tardigrade dispersal, trustworthy empirical evidence has remained scarce (Nelson *et al.* 2018). In 1962, Fox and García-Moll described *Claxtonia molluscorum* (Fox and García-Moll, 1962) from faeces of the land snail *Bulimulus guadalupensis* (Bruguière, 1789), thus they conjectured that the species could be a commensal/parasite of the latter (Fox and García-Moll 1962); such relationships are extremely rare among tardigrades. Notably, the specimens exited the digestive tract of the snails intact, thereby marking the first example of gastropod-mediated tardigrade dispersal. Interestingly, *Claxtonia molluscorum* was recently shown to exhibit a broad tropical distribution (Gąsiorek *et al.* 2024). Recently, two studies independently demonstrated that land snails serve as vectors for the dispersal of representatives of the genera *Macrobiotus* C.A.S. Schultze, 1834 (Vuori *et al.* 2022) and *Milnesium* (Książkiewicz and Roszkowska 2022). Although the potential for snail dispersal exists, albeit to a limited extent (Aubry *et al.* 2006), the idea that it could effectively disperse tardigrades over large distances seems implausible. Such a capability is a prerequisite for playing a significant role in shaping global biogeographies. Consequently, malaco(endo)zoochory seems to be important only on a local geographic scale.

According to theoretical assumptions, birds should be one of the main tardigrade vectors. Ironically, evidence for this is weak

and unconvincing. Mogle *et al.* (2018) is likely the most widely cited study that aimed to present the disjunctive distributions of several limno-terrestrial tardigrade species belonging to the genera *Doryphoribius* Pilato, 1969, *Milnesium*, and *Oreella* Murray, 1910 in North America as corroborating bird-mediated dispersal along bird migratory routes. The huge weakness of this study was that the authors assumed species identification using morphological characteristics was sufficient to claim they were dealing with single species living in both Nearctic and Neotropical regions. In light of recent studies on tardigrade crypsis (see e.g. Morek *et al.* 2021 for *Milnesium*), this supposition can no longer be considered well-reasoned. Mogle *et al.* (2018) reported tardigrades in bird nests and also regarded this as evidence for bird-mediated dispersal. However, it is not unreasonable to expect that tardigrades would be present in nests as they are often built with the addition of mosses used to increase their thermal insulation (Deeming *et al.* 2020). The presence of tardigrades in nest mosses is therefore unsurprising, and does not constitute evidence of bird-mediated dispersal. In my opinion, this only strengthens the hypothesis that birds transport tardigrades over short distances. The single case of ornitho(endo)zoochory for tardigrades was reported by Robertson *et al.* (2020), who found species of the limno-terrestrial genera *Adropion* Pilato, 1987, *Macrobiotus*, and *Isohypsibius* Thulin, 1928 in the faeces of the sub-Antarctic shorebird *Attagis malouinus* (Boddaert, 1783).

Long-distance dispersal, paleogeography, and geographic distributions of tardigrades

Vicariance, that is the shaping of geographic ranges by geological events that lead to separation of a population, and long-distance dispersal (LDD), are two major factors contributing to the distribution of organisms (Gillespie *et al.* 2012). In the case of meiofauna, discriminating between the two might not be straightforward, as incidence data are scarce, re-discovering previously encountered species in the same locality—infrequent (see e.g. Suzuki *et al.* 2017 and re-collecting attempts of *Thermozodium esakii* Rahm, 1937 on Kyūshū), fossil evidence may be lacking (Mapalo *et al.* 2021), and the resulting occurrence pattern is discontinuous. For example, *Pseudechiniscus ehrenbergi* Roszkowska *et al.*, 2020 was initially genetically verified as present in Italy and Mongolia based on the *COI* marker (Cesari *et al.* 2020, Roszkowska *et al.* 2020). This finding could be explained by either poor sampling in the central part of Eurasia, or a disjunctive geographic range as a result of LDD. Subsequently, following enhanced sampling in other parts of the globe, it was suggested that *P. ehrenbergi* is probably also present in the Afrotropics and South-East Asia (Gąsiorek *et al.* 2022a). Therefore, these new records shifted the balance between the two possible scenarios in favour of LDD.

In theory, the ability of tardigrades to enter cryptobiosis, a phenomenon diversified among tardigrade evolutionary lineages, and their different reproductive strategies (sexual vs. asexual), should favour easy dispersal in those taxa reproducing parthenogenetically (see Bertolani *et al.* 1990 for *Ramazzottius* Binda & Pilato, 1986; Guidetti *et al.* 2019 for *Paramacrobiotus* Guidetti *et al.*, 2009 as examples of limno-terrestrial tardigrades) and those with a strong cryptobiotic potential (Roszkowska *et al.* 2023), as they can increase their population numbers rapidly and easily endure in a desiccated state. Species that reproduce

sexually and have difficulty surviving in an anhydrobiotic state are likely to exhibit more restricted geographic ranges. The most comprehensive dataset addressing LDD vs. palaeogeography in tardigrades was presented in Morek *et al.* (2021). The research elaborated on the global distribution of the genus *Milnesium* (more than 60 spp. were included; this is likely one of the most speciose tardigrade genera comprising hundreds of species), and revealed that LDD (later independently reported by Guil *et al.* 2022 for the same genus) accounted for less than 15% of all examined species. Conversely, more than 70% of species had geographic ranges limited to a single zoogeographic region. Finally, only *c.* 10% of species were widespread and probably anthropogenically dispersed. In other words, the phylogeographic analyses clearly indicated that palaeogeographic origin is more prevalent in *Milnesium* than LDD. What is more, the breakup of Gondwana (> 150 Mya) was suggested as a significant geological factor contributing to the evolution of this genus (Morek *et al.* 2021). The split between the Northern vs. Southern Hemisphere taxa is noticeable among several tardigrade lineages, such as Echiniscidae (Kristensen 1987, Gąsiorek *et al.* 2022a) and Eohypsibiidae (Hansen *et al.* 2016). The emerging picture is that the majority of tardigrade species inhabiting a given region are of endemic origin (hypothesis 1: species that usually reproduce sexually and with relatively weak cryptobiotic ability) but a small fraction of the fauna (10–20%) is ecdemic, that is of non-indigenous origin, and have achieved colonization via LDD (hypothesis 2: species that usually reproduce asexually and possess strong cryptobiotic abilities; species that form the 'biogeographic noise' that blurs the distinction between zoogeographic regions). A number of well-documented cases of tardigrade LDD are discussed in the next two paragraphs.

Widespread distributions: pantropical species

Pantropical geographic distributions seem to be common among limno-terrestrial tardigrades, including the genus *Kristenseniscus* Gąsiorek *et al.*, 2019, representatives of the subgenus *Meridioniscus* Gąsiorek *et al.,* 2023 (Gąsiorek *et al.* 2021b), and, again, clade E of *Milnesium* (Morek *et al.* 2021). Ample genetically supported cases have also been reported in the genera *Echiniscus* (Gąsiorek *et al.* 2019a, 2022a: *E. lineatus*, *E. perarmatus*; Fig. 1A) and *Claxtonia* Gąsiorek & Michalczyk, 2019 (Gąsiorek *et al.* 2024: *C. molluscorum*). As predicted by the theoretical assumptions, all examples are parthenogenetic, exhibit limited phylogeographic structuring of their populations despite having been collected from different continents, and have greater endurance to cycles of desiccation and rehydration. Moreover, the pantropical distribution can best be explained by aeolian LDD, perhaps aided by anthropogenic introduction to new habitats (Gąsiorek *et al.* 2019a), thus suggesting the marginal role of birds in transporting and shaping tardigrade biogeographies. Curiously, although commonly assumed to conduce tardigrade dispersal, no anthropogenic influence was found when formally tested for near cruise ship routes and at scientific research stations located on the South Shetland Islands and the Antarctic Peninsula (McInnes and Pugh 2013). Last but not least, Muñoz *et al.* (2004) have already shown that aeolian LDD is a pivotal driving force for Southern Hemisphere cryptogams (e.g. mosses, lichens, liverworts), which harbour tardigrade microhabitats. All
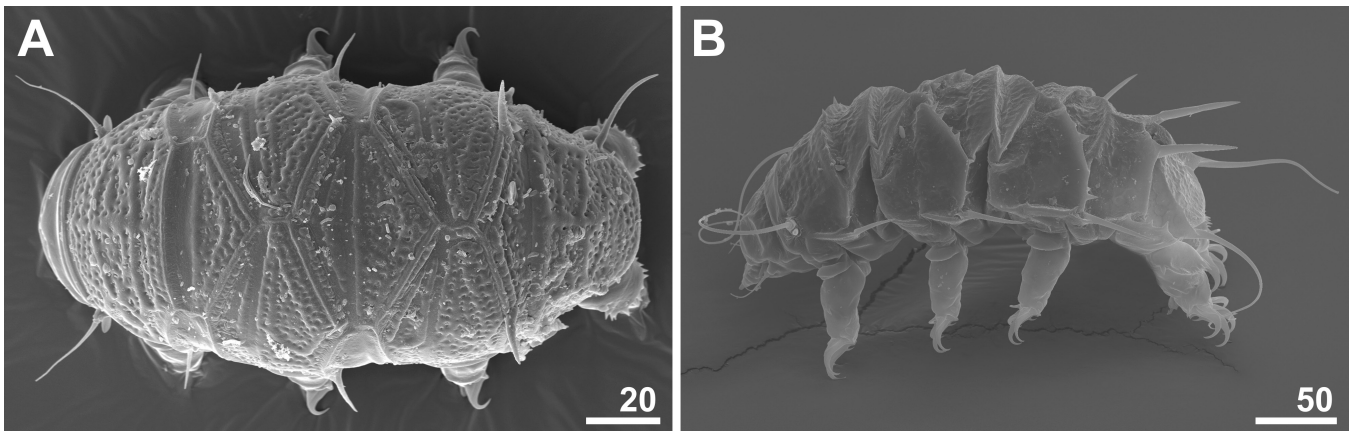
Figure 1. A, *Echiniscus lineatus* Pilato *et al.,* 2008 is a typical pantropical species (individual from Celebes, the Malay Archipelago). B, *Acanthechiniscus islandicus* (Richters, 1904) is a typical polar (High Arctic) species (individual from Þingvellir, Iceland). Scale bars are in micrometres.

of the above augments the impression that wind is the primary factor influencing the dispersion of pantropical species.

Widespread distributions: high mountain insular and polar species

Tropical tardigrades have received much less attention compared with polar and cold stenothermic taxa. The latter have benefitted from decades of systematic sampling, especially in the Arctic (Fig. 1B), that has resulted in extensive incidence data. Several classical examples of species distributed only in high mountains and in polar regions (insular distributions) include the following genera: *Bertolanius* Özdikmen, 2008 and *Eohypsibius* Kristensen, 1982 (Hansen *et al.* 2016), *Borealibius* Pilato *et al.,* 2006 (Pilato *et al.* 2006), the *Claxtonia wendti* complex (Gąsiorek *et al.* 2024), *Cryoconicus* Zawierucha *et al.,* 2018 (Zawierucha *et al.* 2018, 2023), or *Cornechiniscus holmeni* (Petersen, 1951) (Gąsiorek and Michalczyk 2020) and *Echiniscus lapponicus* Thulin, 1911 (Dastych 1988). This type of discontinuous distribution can be interpreted in two ways, namely, either it is associated with aeolian LDD, or with the contraction of a previously broader geographic range resulting from temperature increase. Localities at high elevations would serve as postglacial refugia in the latter scenario, as suggested for Eohypsibiidae (Hansen *et al.* 2016), whereas LDD is more probable for *Claxtonia* and *Cornechiniscus holmeni* (Gąsiorek *et al.* 2024, Gąsiorek and Michalczyk 2020). Importantly, these mechanisms are not mutually exclusive and it is probable that both have shaped tardigrade biogeography throughout their evolution.

ELEVATIONAL DIVERSITY GRADIENTS

Altitude is one of the factors affecting tardigrade distribution, with species richness seen to increase at least slightly at higher elevations (Horning *et al.* 1978 for the New Zealand fauna; Dastych 1988 for the Polish fauna; Kaczmarek *et al.* 2011 for the Costa Rican fauna; Gąsiorek *et al.* 2022a for the South African fauna). Despite this, tardigrade biodiversity surveys are usually conducted in more easily accessible low-lying areas, thus introducing a sampling bias that significantly impacts our understanding of faunal distribution at the continental scale

(first noted by Jørgensen 2001 through the GIS mapping of the African tardigrade fauna but see a contrasting pattern for the Neotropical tardigrade fauna presented by Ugarte *et al.* 2023). A high percentage of endemics at higher altitudes is consistent with probably limited dispersal of many evolutionary lineages among tardigrade faunas (Morek *et al.* 2021). These palaeoendemics, which evolved in small, constricted areas in high mountain regions (see e.g. Cai *et al.* 2023), are hypothesized to be typically sexually reproducing, restricted to a single zoogeographic region, and are relatively rare (Gąsiorek *et al.* 2022a). The prevalence of the EiE paradigm in tardigrade biogeography, is in part, a result of poor taxonomies that failed to adequately delineate similar-looking species and the location of fieldwork that was primarily undertaken in easily accessible lowland areas. Importantly, insufficient taxonomic distinctions prevented the identification of species boundaries, whereas fieldwork concentrated in low-land areas contributed to an incomplete understanding of high-altitude ecosystems, and their faunal composition and distribution.

TARDIGRADE FAUNAS: COSMOPOLITAN OR REGIONAL?

The vast majority of tardigrade diversity remains undiscovered and unnamed (Bartels *et al.* 2016), thus hampering the drawing of conclusions on their distributions. Nevertheless, some regionalization of tardigrade species at a continental scale was noticed at the beginning of this century (Pilato and Binda 2001). This publication preceded the era of integrative taxonomy and DNA barcoding in tardigradology (Cesari *et al.* 2009, Jørgensen *et al.* 2018), advancements that allowed the separation of closely related species previously hidden within species complexes. However, Pilato and Binda (2001) had envisioned the shift of paradigms in tardigrade biogeography from cosmopolitism to 'localism' by highlighting the biogeographic structuring visible in five eutardigrade genera. Later, formal analyses conducted on the global tardigrade fauna (McInnes and Pugh 1998, 2007), provided answers to a number of general questions: (i) what is the fraction of cosmopolitan species among the global limno-terrestrial fauna, (ii) whether limno-terrestrial tardigrades

Table 1. Well-documented cases of restricted geographic distributions among tardigrade taxa. Taxa reported only once in the literature were discarded as their true geographic range may be broader[c]

Genus/complex of species	Distribution	Reference
Antechiniscus	Post-Gondwanan (South America, Australia, Tasmania, New Zealand)	Kristensen 1987
Barbaria	Mostly Neotropical, southern Nearctic and Antarctic	Gąsiorek *et al.* 2022b
Bertolanius	Arctic and alpine habitats in Holarctic mountains[a]	Hansen *et al.* 2016
Borealibius	Arctic and alpine habitats in Holarctic mountains	Pilato *et al.* 2006
Cryobiotus	Glacial habitats in the Palaearctic	Dastych 2019
Cryoconicus	Polar and alpine habitats	Guidetti *et al.* 2019
Echiniscus brunus complex	Afro-Oriental	Dey *et al.* 2024a
Eohypsibius	Arctic and alpine habitats in Holarctic mountains	Hansen *et al.* 2016
Halobiotus	Polar-cold temperate seas in the Holarctic	Kristensen 1982
Limmenius	New Zealand and Tasmania	Claxton 2004
Milnesioides	Australia and Tasmania	Claxton 2004, Morek *et al.* 2024
Mopsechiniscus	Post-Gondwanan (South America, Tasmania, Antarctica)	Guidetti *et al.* 2017
Novechiniscus	Western Nearctic	Kristensen 1987
Oreella	Post-Gondwanan (South America, Australia, Tasmania, New Zealand, Antarctica)[b]	Dastych *et al.* 1998
Parechiniscus	Western Palaearctic	Kristensen 1987
Proechiniscus	Eastern Nearctic (Greenlandic)	Kristensen 1987
Ramajendas	Antarctic	Tumanov 2022
Ramazzottius baumanni complex	Neotropical	Dey *et al.* 2024b
Ramazzottius szeptyckii complex	Afro-Oriental-Australasian	Claxton 2004, Dey *et al.* 2024b
Stellariscus	Eastern Palaearctic	Gąsiorek *et al.* 2018

[a]Recently found in high-elevation Andean forests (Ramsay *et al.* 2021); detailed data lacking.
[b]Questioned with a High Arctic record (Calloway *et al.* 2011); taxonomic affinity of the Canadian species is uncertain (P. Gąsiorek and R.M. Kristensen, personal observations).
[c]Stec *et al.* (2022) noticed that the *Macrobiotus ariekammensis* complex occurs in Arctic and alpine habitats (all known records came from Palaearctic mountains). However, the record of *M. adelges*, now considered a synonym (probably incorrectly) of *M. ariekammensis*, came from the Pieniny Mts (Dastych 1988). This mountain range is well known for its relatively mild climatic conditions and, consequently, that is why several tardigrade species known for their xerothermic preferences can be found so far north (e.g. *Cornechiniscus cornutus*, *Parechiniscus chitonides*). Thus, the complex was not included in the table given its ecogeographic status is unclear.

evolved in Gondwana or in Laurasia. Even at that time, when our understanding of tardigrade diversity was in its infancy, cosmopolitan species were estimated to account for less than 3% of all species (McInnes and Pugh 1998). Strong biogeographic correlations were also uncovered, suggesting that the former Laurasian (roughly corresponding with the Holarctic region) tardigrade fauna was derived, whereas the post-Gondwanan faunas (Neotropical, Afrotropical, Oriental, and Australasian) comprise many old evolutionary lineages. Additionally, the discreteness of the North American vs. European tardigrade fauna was detected (McInnes and Pugh 2018). Further signs of regionalization were disclosed by Cesari *et al.* (2016), who demonstrated the pan-Antarctic character of *Acutuncus antarcticus* Pilato & Binda, 1997, which is both unique to the Antarctic and the most common eutardigrade species in Antarctica. A synopsis of all reliable evidence for tardigrade regionalization is given in Table 1; even a cursory glance will allow the reader to conclude that cases of strict biogeographic structuring are common and numerous among tardigrades. There will be a great many more cases when intensive sampling is undertaken in regions of the world relatively devoid of study (compare the number of candidate endemics in the echiniscid fauna of South Africa in Gąsiorek *et al.* 2022a with the state of knowledge on African fauna in Jørgensen 2001 and McInnes *et al.* 2017).

CONCLUSIONS

The period of treating EiE as the starting point for considerations on limno-terrestrial tardigrade biogeography has ended and has been replaced by the 'regional structuring' approach, in which most faunal elements are specific to a given zoogeographic region, but are accompanied by more widely distributed (sometimes even cosmopolitan) species. A rigorous analysis of tardigrade biogeography at both the local and global scale requires an expansion of integrative data and verification of conspecificity via DNA barcodes (Faurby and Barber 2015, Topstad *et al.* 2021). There are barriers to dispersal of at least some tardigrade species (Incagnone *et al.* 2015), resulting from their cryptobiotic and thus colonization abilities. More cogent evidence was shown for aeolian (Sudzuki 1972) compared with avian-mediated dispersal (Mogle *et al.* 2018) of tardigrades, which does not exclude the utility of both means of LDD for these animals. Tardigrade biogeographies clearly exhibit variable patterns, ranging from endemism (understood as restriction to a single zoogeographic region/continent) to ubiquitous, cosmopolitan distributions in a few species; this pattern was first suggested in the Antarctic tardigrade genetic inventory (Velasco-Castrillón *et al.* 2015), which reported many operational taxonomic units that were restricted to Antarctica, but also confirmed the presence of several

cosmopolitan taxa (*Echiniscus merokensis* Richters, 1904, *E. testudo*), and, in parallel, in bdelloid rotifers (Fontaneto *et al.* 2008) representing the genera *Adineta* and *Rotaria* on a global scale.

CONFLICT OF INTEREST

The author has no conflicts of interest to declare.

DATA AVAILABILITY

Not applicable.

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