

Review

Catch me if you can, or how paradigms of tardigrade biogeography evolved from cosmopolitanism to ‘localism’

Piotr Gąsiorek^{1,2,*} 

¹Natural History Museum of Denmark, University of Copenhagen, Øster Voldgade 5-7, DK-1350, Universitetsparken 15, DK-2100, Copenhagen, Denmark

²Department of Invertebrate Evolution, Faculty of Biology, Jagiellonian University, Gronostajowa 9, 30-387 Kraków, Poland

*Corresponding author. Department of Invertebrate Evolution, Faculty of Biology, Jagiellonian University, Gronostajowa 9, 30-387 Kraków, Poland.
E-mail: piotr.lukas.gasiorek@gmail.com

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: cosmopolitanism; 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 cosmopolitanism 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 cosmopolitanism. 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); *Macrobotus hufelandi* C.A.S. Schultze, 1834; *Milnesium tardigradum* (Doyère, 1840); *Paramacrobotus 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. Petrušek *et al.* 2004 questioning cosmopolitanism 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; Ptscheck 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: *Paramacrobotus fairbanksi* Schill *et al.*, 2010; Kiosya *et al.* 2021: *Echiniscus tropicalis* Binda & Pilato, 1995; Kayastha *et al.* 2023a, b: *Paramacrobotus 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 cosmopolitanism is more widespread among parthenogens than among bisexuals, and whether there are convincing arguments for cosmopolitanism 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 dispersion via trade winds, distributions which are difficult to attribute to the zoochory hypothesis (see below). Alternatively, generalist lowland species could easily undergo dispersion 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 surmised 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 *Macrobotus* 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 dispersion. 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, *Macrobotus*, 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 dispersion in those taxa reproducing parthenogenetically (see Bertolani *et al.* 1990 for *Ramazzottius Binda* & Pilato, 1986; Guidetti *et al.* 2019 for *Paramacrobotus* 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 ecademic, 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

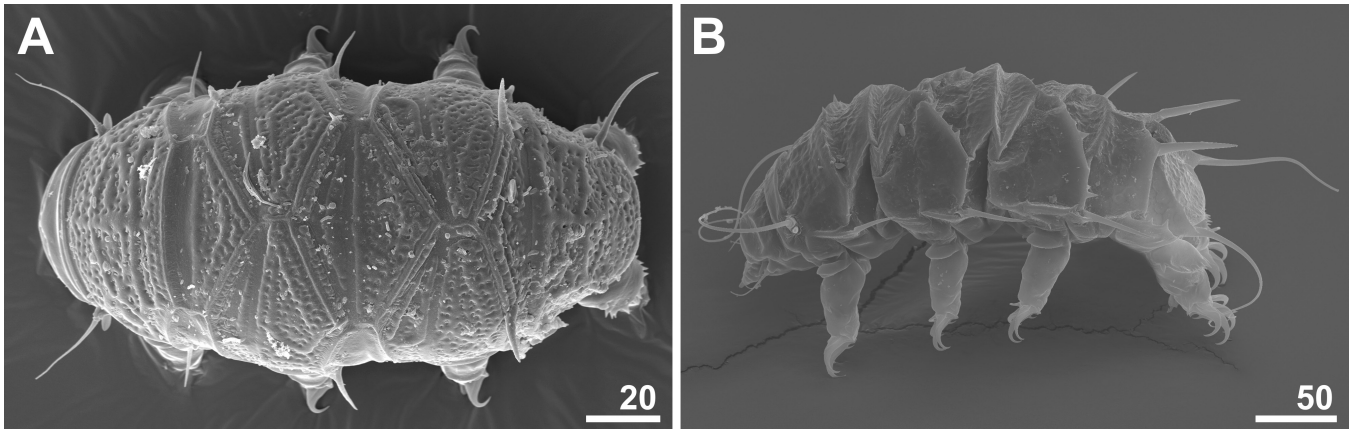


Figure 1. A, *Echiniscus lineatus* Pilato *et al.*, 2008 is a typical pantropical species (individual from Celebes, the Malay Archipelago). B, *Acanthechiniscus islandicus* (Richters, 1904) is a typical polar (High Arctic) species (individual from Þingvellir, Iceland). Scale bars are in micrometres.

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

^aRecently found in high-elevation Andean forests (Ramsay *et al.* 2021); detailed data lacking.

^bQuestioned 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).

^cStec *et al.* (2022) noticed that the *Macrobrotus 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.

ACKNOWLEDGEMENTS

The research received funding from the Polish National Science Centre via the 'Etiuda' programme (grant no. 2020/36/T/NZ8/00360). Brian Blagden, Diego Fontaneto, Łukasz Michalczyk, Nadja Møbjerg, and two anonymous reviewers kindly and significantly improved the draft of this paper by their comments.

CONFLICT OF INTEREST

The author has no conflicts of interest to declare.

DATA AVAILABILITY

Not applicable.

REFERENCES

- Aksenova OV, Bolotov IN, Gofarov MY *et al.* Species richness, molecular taxonomy and biogeography of the radicine pond snails (Gastropoda: Lymnaeidae) in the Old World. *Scientific Reports* 2018;**8**:11199. <https://doi.org/10.1038/s41598-018-29451-1>
- Arenas-Sánchez C, Brendonck L, García-Roger EM *et al.* Wind dispersal differences between rotifer cryptic species: a proof of principle from a wind tunnel experiment. *Hydrobiologia* 2024. <https://doi.org/10.1007/s10750-023-05349-6>
- Artois T, Fontaneto D, Hummon WD, McInnes SJ, Todaro MA, Sørensen MV, Zullini A. Ubiquity of microscopic animals? Evidence from the morphological approach in species identification. In: Fontaneto D (ed.), *Biogeography of Microscopic Organisms. Is Everything Small Everywhere?* Cambridge, UK: Cambridge University Press, 2011, 244–83. <https://doi.org/10.1017/CBO9780511974878.014>
- Aubry S, Labaune C, Magnin F *et al.* Active and passive dispersal of an invading land snail in Mediterranean France. *Journal of Animal Ecology* 2006;**75**:802–13. <https://doi.org/10.1111/j.1365-2656.2006.01100.x>
- Baas Becking LGM. *Geobiologie of Inleiding tot de Milieukunde*. Den Haag, Netherlands: W.P. Van Stockum & Zoon, 1934.
- Bartels PJ, Apodaca JJ, Mora C *et al.* A global biodiversity estimate of a poorly known taxon: phylum Tardigrada. *Zoological Journal of the Linnean Society* 2016;**178**:730–6. <https://doi.org/10.1111/zoj.12441>
- Beijerinck MW. *De Infusies en de Ontdekking der Backteriën*. Amsterdam, Netherlands: Jaarboek van de Koninklijke Akademie voor Wetenschappen, 1913.
- Bertolani R, Rebecchi L, Beccaccioli G. Dispersal of *Ramazottius* and other tardigrades in relation to type of reproduction. *Invertebrate Reproduction and Development* 1990;**18**:153–7. <https://doi.org/10.1080/07924259.1990.9672137>
- Brochet AL, Gauthier-Clerc M, Guillemain M *et al.* Field evidence of dispersal of branchiopods, ostracods and bryozoans by teal (*Anas crecca*) in the Camargue (southern France). *Hydrobiologia* 2010;**637**:255–61. <https://doi.org/10.1007/s10750-009-9975-6>
- Cáceres CE, Soluk DA. Blowing in the wind: a field test of overland dispersal and colonization by aquatic invertebrates. *Oecologia* 2002;**131**:402–8. <https://doi.org/10.1007/s00442-002-0897-5>
- Cai L, Krefl H, Taylor A *et al.* Climatic stability and geological history shape global centers of neo- and paleoendemism in seed plants. *Proceedings of the National Academy of Sciences of the United States of America* 2023;**120**:e2300981120. <https://doi.org/10.1073/pnas.2300981120>
- Calloway S, Miller WR, Johansson C *et al.* Tardigrades of North America: *Oreella chugachii*, a new species (Heterotardigrada, Echiniscoidea, Oreellidae) from Alaska. *Proceedings of the Biological Society of Washington* 2011;**124**:28–39. <https://doi.org/10.2988/10-08.1>
- Cesari M, Bertolani R, Rebecchi L *et al.* DNA barcoding in Tardigrada: the first case study on *Macrobotus macrocalix* Bertolani & Rebecchi 1993 (Eutardigrada, Macrobiotidae). *Molecular Ecology Resources* 2009;**9**:699–706. <https://doi.org/10.1111/j.1755-0998.2009.02538.x>
- Cesari M, McInnes SJ, Bertolani R *et al.* 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* 2016;**30**:635–49. <https://doi.org/10.1071/is15045>
- Cesari M, Montanari M, Kristensen RM *et al.* An integrated study of the biodiversity within the *Pseudechiniscus suillus-facettalis* group (Heterotardigrada: Echiniscidae). *Zoological Journal of the Linnean Society* 2020;**188**:717–32. <https://doi.org/10.1093/zoolinnean/zlz045>
- Claxton SK. The taxonomy and distribution of Australian terrestrial tardigrades. Ph.D. Thesis, Macquarie University, 2004.
- Coughlan NE, Kelly TC, Davenport J *et al.* Up, up and away: bird-mediated ectozoochorous dispersal between aquatic environments. *Freshwater Biology* 2017;**62**:631–48. <https://doi.org/10.1111/fwb.12894>
- Cracraft J. Continental drift and vertebrate distribution. *Annual Review of Ecology and Systematics* 1974;**5**:215–61. <https://doi.org/10.1146/annurev.es.05.110174.001243>
- Dastych H. The Tardigrada of Poland. *Monografie Fauny Polski* 1988;**16**:1–255.
- Dastych H. *Cryobiotus roswithae* gen. n., sp. n., a new genus and species of glacier-dwelling tardigrades from northern Norway (Tardigrada, Panarthropoda). *Entomologie heute* 2019;**31**:95–111.
- Dastych H, McInnes SJ, Claxton SK. *Oreella mollis* Murray, 1910 (Tardigrada): a redescription and revision of *Oreella*. *Mitteilungen aus den Hamburgischen Zoologischen Museum und Institut* 1998;**95**:89–113.
- Deeming DC, Dickinson AM, Broughton RE *et al.* Factors affecting thermal insulation of songbird nests as measured using temperature loggers. *Physiological and Biochemical Zoology* 2020;**93**:488–504. <https://doi.org/10.1086/711959>
- Dey PK, Gašiorek P, Michalczyk Ł. Convergent evolution of dark, ultraviolet-absorbing cuticular pigmentation in a new Afro-Oriental *Echiniscus brunus* species complex (Heterotardigrada: Echiniscidae). *Zoological Journal of the Linnean Society* 2024a. <https://doi.org/10.1093/zoolinnean/zlad132>
- Dey PK, López-López A, Morek W *et al.* Tardigrade Augean Stables - a challenging phylogeny and taxonomy of the family Ramazzottiidae (Eutardigrada: Hypsibioidae). *Zoological Journal of the Linnean Society* 2024b. <https://doi.org/10.1093/zoolinnean/zlad161>
- Faurby S, Barber PH. Extreme population subdivision despite high colonization ability: contrasting regional patterns in intertidal tardigrades from the west coast of North America. *Journal of Biogeography* 2015;**42**:1006–17. <https://doi.org/10.1111/jbi.12500>
- Faurby S, Jørgensen A, Kristensen RM *et al.* Phylogeography of North Atlantic intertidal tardigrades: refugia, cryptic speciation and the history of the Mid-Atlantic islands. *Journal of Biogeography* 2011;**38**:1613–24. <https://doi.org/10.1111/j.1365-2699.2011.02533.x>
- Faurby S, Jørgensen A, Kristensen RM *et al.* Distribution and speciation in marine intertidal tardigrades: testing the roles of climatic and geographical isolation. *Journal of Biogeography* 2012;**39**:1596–607. <https://doi.org/10.1111/j.1365-2699.2012.02720.x>
- Fenchel T, Finlay BJ. The ubiquity of small species: patterns of local and global diversity. *BioScience* 2004;**54**:777–84. [https://doi.org/10.1641/0006-3568\(2004\)054\[0777:tuossp\]2.0.co;2](https://doi.org/10.1641/0006-3568(2004)054[0777:tuossp]2.0.co;2)
- Figuerola J, Green AJ. Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. *Freshwater Biology* 2002;**47**:483–94. <https://doi.org/10.1046/j.1365-2427.2002.00829.x>
- Finlay BJ. Global dispersal of free-living microbial eukaryote species. *Science* 2002;**296**:1061–3. <https://doi.org/10.1126/science.1070710>
- Fontaneto D. Long-distance passive dispersal in microscopic aquatic animals. *Movement Ecology* 2019;**7**:10. <https://doi.org/10.1186/s40462-019-0155-7>

- Fontaneto D, Barraclough TG, Chen K *et al.* Molecular evidence for broad-scale distributions in bdelloid rotifers: everything is not everywhere but most things are very widespread. *Molecular Ecology* 2008; **17**:3136–46. <https://doi.org/10.1111/j.1365-294X.2008.03806.x>
- Fontaneto D, Barbosa AM, Segers H *et al.* The ‘rotiferologist’ effect and other global correlates of species richness in monogonont rotifers. *Ecography* 2012; **35**:174–82. <https://doi.org/10.1111/j.1600-0587.2011.06850.x>
- Fox I, García-Moll I. *Echiniscus molluscorum*, new tardigrade from the feces of the land snail, *Bulimulus exilis* (Gmelin) in Puerto Rico (Tardigrada: Scutechiniscidae). *Journal of Parasitology* 1962; **48**:177–81. <https://doi.org/10.2307/3275559>
- Gąsiorek P, Michalczyk Ł. Revised *Cornechiniscus* (Heterotardigrada) and new phylogenetic analyses negate the echiniscid subfamilies and tribes. *Royal Society Open Science* 2020; **7**:200581. <https://doi.org/10.1098/rsos.200581>
- Gąsiorek P, Suzuki AC, Kristensen RM *et al.* Untangling the *Echiniscus* Gordian knot: *Stellariscus* gen. nov. (Heterotardigrada: Echiniscidae) from Far East Asia. *Invertebrate Systematics* 2018; **32**:1234–47. <https://doi.org/10.1071/is18023>
- Gąsiorek P, Jackson K, Meyer H *et al.* *Echiniscus virginicus* complex: the first case of pseudocryptic allopatry and pantropical distribution in tardigrades. *Biological Journal of the Linnean Society* 2019a; **128**:789–805. <https://doi.org/10.1093/biolinnean/blz147>
- Gąsiorek P, Vončina K, Michalczyk Ł. *Echiniscus testudo* (Doyère, 1840) in New Zealand: anthropogenic dispersal or evidence for the ‘Everything is Everywhere’ hypothesis? *New Zealand Journal of Zoology* 2019b; **46**:174–81. <https://doi.org/10.1080/03014223.2018.1503607>
- Gąsiorek P, Vončina K, Ciosek J *et al.* New Indomalayan *Nebularmis* species (Heterotardigrada: Echiniscidae) provoke a discussion on its intragenetic diversity. *Zoological Letters* 2021a; **7**:6. <https://doi.org/10.1186/s40851-021-00172-0>
- Gąsiorek P, Vončina K, Zając K *et al.* Phylogeography and morphological evolution of *Pseudechiniscus* (Heterotardigrada: Echiniscidae). *Scientific Reports* 2021b; **11**:7606. <https://doi.org/10.1038/s41598-021-84910-6>
- Gąsiorek P, Vončina K, Bochnak M *et al.* Echiniscidae (Heterotardigrada) of South Africa. *Zootaxa* 2022a; **5156**:1–238. <https://doi.org/10.11646/zootaxa.5156.1.1>
- Gąsiorek P, Wilamowski A, Vončina K *et al.* Neotropical jewels in the moss: biodiversity, distribution and evolution of the genus *Barbaria* (Heterotardigrada: Echiniscidae). *Zoological Journal of the Linnean Society* 2022b; **195**:1037–66. <https://doi.org/10.1093/zoolinnean/zlab087>
- Gąsiorek P, Degma P, Michalczyk Ł. Hiding in the Arctic and in mountains: a (dis)entangled classification of *Claxtonia* (Heterotardigrada: Echiniscidae). *Zoological Journal of the Linnean Society* 2024. <https://doi.org/10.1093/zoolinnean/zlad029>
- Giere O, Schratzberger M. *New Horizons in Meiobenthos Research*. Cham, Switzerland: Springer, 2023. <https://doi.org/10.1007/978-3-031-21622-0>
- Gillespie RG, Baldwin BG, Waters JM *et al.* Long-distance dispersal: a framework for hypothesis testing. *Trends in Ecology and Evolution* 2012; **27**:47–56. <https://doi.org/10.1016/j.tree.2011.08.009>
- Gronvold J. On the possible role of earthworms in the transmission of *Ostertagia ostertagi* third-stage larvae from feces to soil. *Journal of Parasitology* 1979; **65**:831–2. <https://doi.org/10.2307/3280379>
- Gronvold J. Rain splash dispersal of third-stage larvae of *Cooperia* spp. (Trichostrongylidae). *Journal of Parasitology* 1984; **70**:924–6. <https://doi.org/10.2307/3281640>
- Gronvold J, Nansen P. The possible role of slugs (*Agriolimax* spp.) in the transmission of infective larvae of *Cooperia oncophora*. *Journal of Helminthology* 1984; **58**:239–40. <https://doi.org/10.1017/S0022149X00027048>
- Gross V, Treffkorn S, Reichelt J *et al.* Miniaturization of tardigrades (water bears): morphological and genomic perspectives. *Arthropod Structure & Development* 2019; **48**:12–9. <https://doi.org/10.1016/j.asd.2018.11.006>
- Guidetti R, McInnes SJ, Cesari M *et al.* Evolutionary scenarios for the origin of an Antarctic tardigrade species based on molecular clock analyses and biogeographic data. *Contributions to Zoology* 2017; **86**:97–110. <https://doi.org/10.1163/18759866-08602001>
- Guidetti R, Cesari M, Bertolani R *et al.* High diversity in species, reproductive modes and distribution within the *Paramacrobiotus richtersi* complex (Eutardigrada, Macrobiotidae). *Zoological Letters* 2019; **5**:1. <https://doi.org/10.1186/s40851-018-0113-z>
- Guil N. Molecular approach to micrometazoans. Are they here, there and everywhere? In: Fontaneto D (ed.), *Biogeography of Microscopic Organisms. Is Everything Small Everywhere?* Cambridge, UK: Cambridge University Press, 2011, 284–306. <https://doi.org/10.1017/CBO9780511974878.015>
- Guil N, Guidetti R, Cesari M *et al.* Molecular phylogenetics, speciation, and long distance dispersal in tardigrade evolution: a case study of the genus *Milnesium*. *Molecular Phylogenetics and Evolution* 2022; **169**:107401. <https://doi.org/10.1016/j.jympev.2022.107401>
- Hansen JG, Kristensen RM, Bertolani R *et al.* Comparative analyses of *Bertolanius* species (Eohypsibiidae; Eutardigrada) with the description of *Bertolanius birnae* sp. nov. from northern polar regions. *Polar Biology* 2016; **40**:123–40. <https://doi.org/10.1007/s00300-016-1931-0>
- Heger TJ, Mitchell EAD, Leander BS. Holarctic phylogeography of the testate amoeba *Hyalosphenia papilio* (Amoebozoa: Arcellinida) reveals extensive genetic diversity explained more by environment than dispersal limitation. *Molecular Ecology* 2013; **22**:5172–84. <https://doi.org/10.1111/mec.12449>
- Hohberg K. Tardigrade species composition in young soils and some aspects on life history of *Macrobiotus richtersi* J. Murray, 1911. *Pedobiologia* 2006; **50**:267–74. <https://doi.org/10.1016/j.pedobi.2006.02.004>
- Hohberg K, Russell DJ, Elmer M. Mass occurrence of algal-feeding tardigrade *Apodibius confusus*, in the young soils of a post-mining site. *Journal of Zoological Systematics and Evolutionary Research* 2011; **49**:62–5. <https://doi.org/10.1111/j.1439-0469.2010.00600.x>
- Holt BG, Lessard J-P, Borregaard MK *et al.* An update of Wallace’s zoogeographic regions of the world. *Science* 2013; **339**:74–8. <https://doi.org/10.1126/science.1228282>
- Horning DS, Schuster RO, Grigarick AA. Tardigrada of New Zealand. *New Zealand Journal of Zoology* 1978; **5**:185–280. <https://doi.org/10.1080/03014223.1978.10428316>
- Incagnone G, Marrone F, Barone R *et al.* How do freshwater organisms cross the “dry ocean”? A review on passive dispersal and colonization processes with a special focus on temporary ponds. *Hydrobiologia* 2015; **750**:103–23. <https://doi.org/10.1007/s10750-014-2110-3>
- Ingels J, Valdes Y, Pontes LP *et al.* Meiofauna life on loggerhead sea turtles-diversely structured abundance and biodiversity hotspots that challenge the meiofauna paradox. *Diversity* 2020; **12**:203. <https://doi.org/10.3390/d12050203>
- Janiec K. Short distance wind transport of microfauna in maritime Antarctic (King George Island, South Shetland Islands). *Polish Polar Research* 1996; **17**:203–11.
- Jenkins DG, Brescacin CR, Duxbury CV *et al.* Does size matter for dispersal distance? *Global Ecology and Biogeography* 2007; **16**:415–25. <https://doi.org/10.1111/j.1466-8238.2007.00312.x>
- Jørgensen A. Graphical presentation of the African tardigrade fauna using GIS with the description of *Isohypsibius malawiensis* sp. n. (Eutardigrada: Hypsibiidae) from Lake Malawi. *Zoologischer Anzeiger* 2001; **240**:441–50. <https://doi.org/10.1078/0044-5231-00052>
- Jørgensen A, Møbjerg N, Kristensen RM. A molecular study of the tardigrade *Echiniscus testudo* (Echiniscidae) reveals low DNA sequence diversity over a large geographical area. *Journal of Limnology* 2007; **66**:77–83. <https://doi.org/10.4081/jlimnol.2007.s1.77>
- Jørgensen A, Faurby S, Persson DK *et al.* Genetic diversity in the parthenogenetic reproducing tardigrade *Echiniscus testudo* (Heterotardigrada: Echiniscoidea). *Journal of Limnology* 2013; **72**:136–43. <https://doi.org/10.4081/jlimnol.2013.s1.e17>
- Jørgensen A, Kristensen RM, Møbjerg N. Phylogeny and integrative taxonomy of Tardigrada. In: Schill RO (ed.), *Water Bears: The Biology*

- of *Tardigrades*. Dordrecht: Springer, 2018, 95–114. https://doi.org/10.1007/978-3-319-95702-9_3
- Kaczmarek Ł, Goldyn B, Welnicz W *et al.* Ecological factors determining Tardigrada distribution in Costa Rica. *Journal of Zoological Systematics and Evolutionary Research* 2011;**49**:78–83. <https://doi.org/10.1111/j.1439-0469.2010.00603.x>
- Kaczmarek Ł, Mioduchowska M, Kačarević U *et al.* New records of Antarctic Tardigrada with comments on interpopulation variability of *Paramacrobiotus fairbanksi* Schill, Förster, Dandekar and Wolf, 2010. *Diversity* 2020;**12**:108. <https://doi.org/10.3390/d12030108>
- Kayastha P, Stec D, Slugocki Ł *et al.* Integrative taxonomy reveals new, widely distributed tardigrade species of the genus *Paramacrobiotus* (Eutardigrada: Macrobiotidae). *Scientific Reports* 2023a;**13**:2196. <https://doi.org/10.1038/s41598-023-28714-w>
- Kayastha P, Szydło W, Mioduchowska M *et al.* Morphological and genetic variability in cosmopolitan tardigrade species—*Paramacrobiotus fairbanksi* Schill, Förster, Dandekar & Wolf, 2010. *Scientific Reports* 2023b;**13**:17672. <https://doi.org/10.1038/s41598-023-42653-6>
- Kiosya Y, Vončina K, Gašiorek P. Echiniscidae in the Mascarenes: the wonders of Mauritius. *Evolutionary Systematics* 2021;**5**:93–120. <https://doi.org/10.3897/evolsyst.5.59997>
- Kristensen RM. The first record of cyclomorphosis in Tardigrada based on a new genus and species from Arctic meiobenthos. *Zeitschrift für Zoologische Systematik und Evolutionsforschung* 1982;**20**:249–70. <https://doi.org/10.1111/j.1439-0469.1983.tb00552.x>
- Kristensen RM. Generic revision of the Echiniscidae (Heterotardigrada), with a discussion of the origin of the family. In: Bertolani R (ed.), *Biology of Tardigrades. Selected Symposia and Monographs U.Z.I., Vol. 1*. Modena, Italy: Mucchi, 1987, 261–335.
- Książkiewicz Z, Roszkowska M. Experimental evidence for snails dispersing tardigrades based on *Milnesium inceptum* and *Cepaea nemoralis* species. *Scientific Reports* 2022;**12**:4421. <https://doi.org/10.1038/s41598-022-08265-2>
- Leasi F, Sevigny JL, Laflamme EM *et al.* Biodiversity estimates and ecological interpretations of meiofaunal communities are biased by the taxonomic approach. *Communications Biology* 2018;**1**:112. <https://doi.org/10.1038/s42003-018-0119-2>
- Mapalo MA, Robin N, Boudinot BE *et al.* A tardigrade in Dominican amber. *Proceedings of the Royal Society B* 2021;**288**:20211760. <https://doi.org/10.1098/rspb.2021.1760>
- McInnes SJ. Zoogeographic distribution of terrestrial/freshwater tardigrades from current literature. *Journal of Natural History* 1994;**28**:257–352. <https://doi.org/10.1080/00222939400770131>
- McInnes SJ, Pugh PJA. Biogeography of limno-terrestrial Tardigrada, with particular reference to the Antarctic fauna. *Journal of Biogeography* 1998;**25**:31–6. <https://doi.org/10.1046/j.1365-2699.1998.251176.x>
- McInnes SJ, Pugh PJA. An attempt to revisit the global biography of limno-terrestrial Tardigrada. *Journal of Limnology* 2007;**66**:90–6. <https://doi.org/10.4081/jlimnol.2007.s1.90>
- McInnes SJ, Pugh PJA. The impact of tourists on Antarctic tardigrades: an ordination-based model. *Journal of Limnology* 2013;**72**:128–35. <https://doi.org/10.4081/jlimnol.2013.s1.e16>
- McInnes SJ, Pugh PJA. Tardigrade biogeography. In: Schill RO (ed.), *Water Bears: The Biology of Tardigrades*. Dordrecht: Springer, 2018, 115–29. https://doi.org/10.1007/978-3-319-95702-9_4
- McInnes SJ, Michalczuk Ł, Kaczmarek Ł. Annotated zoogeography of non-marine Tardigrada. Part IV: Africa. *Zootaxa* 2017;**4284**:1–74. <https://doi.org/10.11646/zootaxa.4284.1.1>
- Mills S, Lunt DH, Gómez A. Global isolation by distance despite strong regional phylogeography in a small metazoan. *BMC Evolutionary Biology* 2007;**7**:225. <https://doi.org/10.1186/1471-2148-7-225>
- Møbjerg N, Halberg KA, Jørgensen A *et al.* Survival in extreme environments - on the current knowledge of adaptations in tardigrades. *Acta Physiologica* 2011;**202**:409–20. <https://doi.org/10.1111/j.1748-1716.2011.02252.x>
- Mogle MJ, Kimball SA, Miller WR *et al.* Evidence of avian-mediated long distance dispersal in American tardigrades. *PeerJ* 2018;**6**:e5035. <https://doi.org/10.7717/peerj.5035>
- Morek W, Surmacz B, López-López A *et al.* 'Everything is not everywhere': Time-calibrated phylogeography of the genus *Milnesium* (Tardigrada). *Molecular Ecology* 2021;**30**:3590–609. <https://doi.org/10.1111/mec.15951>
- Morek W, Walach K, Lamond E *et al.* Phylogenetic position, validity and diversity of the genus *Milnesioides* (Eutardigrada: Apochela). *Zoological Journal of the Linnean Society* 2024. <https://doi.org/10.1093/zoolinnean/zlad027>
- Muñoz J, Felicísimo AM, Cabezas F, Burgaz AR, Martínez I. Wind as a long-distance dispersal vehicle in the Southern Hemisphere. *Science* 2004;**304**:1144–7. <https://doi.org/10.1126/science.1095210>
- Nelson DR, Marley NJ. The biology and ecology of lotic Tardigrada. *Freshwater Biology* 2000;**44**:93–108. <https://doi.org/10.1046/j.1365-2427.2000.00586.x>
- Nelson DR, Bartels PJ, Guil N. Tardigrade ecology. In: Schill RO (ed.), *Water Bears: The Biology of Tardigrades*. Dordrecht: Springer, 2018, 163–210. https://doi.org/10.1007/978-3-319-95702-9_7
- Newton I. *The Migration Ecology of Birds*. Amsterdam, Netherlands: Elsevier, 2008. <https://doi.org/10.1016/B978-0-12-517367-4.XS000-1>
- Nkem JN, Wall DH, Virginia RA *et al.* Wind dispersal of soil invertebrates in the McMurdo Dry Valleys, Antarctica. *Polar Biology* 2006;**29**:346–52. <https://doi.org/10.1007/s00300-005-0061-x>
- Oliveira U, Brescovit AD, Santos AJ. Sampling effort and species richness assessment: a case study on Brazilian spiders. *Biodiversity and Conservation* 2017;**26**:1481–93. <https://doi.org/10.1007/s10531-017-1312-1>
- Petrusek A, Černý M, Audenaert E. Large intercontinental differentiation of *Moina micrura* (Crustacea: Anomopoda): one less cosmopolitan cladoceran? *Hydrobiologia* 2004;**526**:73–81. <https://doi.org/10.1023/b:hydr.0000041612.08425.f0>
- Pilato G, Binda MG. Biogeography and limnoterrestrial tardigrades: are they truly incompatible binomials? *Zoologischer Anzeiger* 2001;**240**:511–6. <https://doi.org/10.1078/0044-5231-00061>
- Pilato G, Guidetti R, Rebecchi L *et al.* Geonemy, ecology, reproductive biology and morphology of the tardigrade *Hypsibius zetlandicus* (Eutardigrada: Hypsibiidae) with erection of *Borealibius* gen. n. *Polar Biology* 2006;**29**:595–603. <https://doi.org/10.1007/s00300-005-0094-1>
- Platšček C, Traunspurger W. The ability to get everywhere: dispersal modes of free-living, aquatic nematodes. *Hydrobiologia* 2020;**847**:3519–47. <https://doi.org/10.1007/s10750-020-04373-0>
- Platšček C, Gansfort B, Traunspurger W. The extent of wind-mediated dispersal of small metazoans, focusing nematodes. *Scientific Reports* 2018;**8**:6814. <https://doi.org/10.1038/s41598-018-24747-8>
- Ramsay BPL, Marley NJ, Bilton DT *et al.* The structure of tardigrade communities at fine spatial scales in an Andean *Polylepis* forest. *Neotropical Biodiversity* 2021;**7**:443–54. <https://doi.org/10.1080/23766808.2021.1943216>
- Rivas JA Jr, Mohl JE, Van Pelt RS *et al.* Evidence for regional aeolian transport of freshwater micrometazoans in arid regions. *Limnology and Oceanography Letters* 2018;**3**:320–30. <https://doi.org/10.1002/lol2.10072>
- Robertson MW, Russo NJ, McInnes SJ *et al.* Potential dispersal of tardigrades by birds through endozoochory: evidence from Sub-Antarctic white-bellied seedsnipe (*Attagis malouinus*). *Polar Biology* 2020;**43**:899–902. <https://doi.org/10.1007/s00300-020-02680-9>
- Roszkowska M, Grobys D, Bartylak T *et al.* Integrative description of five *Pseudechiniscus* species (Heterotardigrada: Echiniscidae: the *suillus-facettalis* complex). *Zootaxa* 2020;**4763**:451–84. <https://doi.org/10.11646/zootaxa.4763.4.1>
- Roszkowska M, Goldyn B, Wojciechowska D *et al.* How long can tardigrades survive in the anhydrobiotic state? A search for tardigrade anhydrobiosis patterns. *PLoS One* 2023;**18**:e0270386. <https://doi.org/10.1371/journal.pone.0270386>
- Segers H, De Smet WH. Diversity and endemism in Rotifera: a review, and *Keratella* Bory de St Vincent. *Biodiversity and Conservation* 2008;**17**:303–16. <https://doi.org/10.1007/s10531-007-9262-7>

- Stec D, Vončina K, Kristensen RM *et al.* The *Macrobotus ariekammensis* species complex provides evidence for parallel evolution of claw elongation in macrobiotid tardigrades. *Zoological Journal of the Linnean Society* 2022;**195**:1067–99. <https://doi.org/10.1093/zoolinnean/zlab101>
- Sudzuki M. An analysis of colonization in freshwater micro-organisms II. Two simple experiments on the dispersal of wind. *Japanese Journal of Ecology* 1972;**22**:222–5. https://doi.org/10.18960/seitai.22.5_222
- Suzuki AC, Kagoshima H, Chilton G *et al.* Meiofaunal richness in highly acidic hot springs in Unzen-Amakusa National Park, Japan, including the first rediscovery attempt for Mesotardigrada. *Zoological Science* 2017;**34**:11–7. <https://doi.org/10.2108/zs160108>
- Tessens B, Monnens M, Backeljau T *et al.* Is 'everything everywhere'? Unprecedented cryptic diversity in the cosmopolitan flatworm *Gyatrix hermaphroditus*. *Zoologica Scripta* 2021;**50**:837–51. <https://doi.org/10.1111/zsc.12507>
- Thiel M, Gutow L. The ecology of rafting in the marine environment. II The rafting organisms and community. *Oceanography and Marine Biology* 2005;**43**:279–418. <https://doi.org/10.1201/9781420037449-9>
- Tilquin A, Kokko H. What does the geography of parthenogenesis teach us about sex? *Philosophical Transactions of the Royal Society B* 2016;**371**:20150538. <https://doi.org/10.1098/rstb.2015.0538>
- Topstad L, Guidetti R, Majaneva M *et al.* Multi-marker DNA metabarcoding reflects tardigrade diversity in different habitats. *Genome* 2021;**64**:217–31. <https://doi.org/10.1139/gen-2019-0218>
- Tumanov D. End of a mystery: Integrative approach reveals the phylogenetic position of an enigmatic Antarctic tardigrade genus *Ramajendas* (Tardigrada, Eutardigrada). *Zoologica Scripta* 2022;**51**:217–31. <https://doi.org/10.1111/zsc.12521>
- Türke M, Lange M, Eisenhauer N. Gut shuttle service: endozoochory of dispersal-limited soil fauna by gastropods. *Oecologia* 2018;**186**:655–64. <https://doi.org/10.1007/s00442-018-4058-x>
- Ugarte PDS, Suzuki LP, Cruvinel LG *et al.* Georeferenced database and interactive online map of limnoterrestrial and freshwater Tardigrada from Central and South America. *Biota Neotropica* 2023;**23**:e20231498. <http://doi.org/10.1590/1676-0611-BN-2023-1498>
- Večeřa M, Divišek J, Lenoir J *et al.* Alpha diversity of vascular plants in European forests. *Journal of Biogeography* 2019;**46**:1919–35. <https://doi.org/10.1111/jbi.13624>
- Velasco-Castrillón A, McInnes SJ, Schultz MB *et al.* Mitochondrial DNA analyses reveal widespread tardigrade diversity in Antarctica. *Invertebrate Systematics* 2015;**29**:578–90. <https://doi.org/10.1071/IS14019>
- Vuori T, Calhim S, Vecchi M. A lift in snail's gut provides an efficient colonization route for tardigrades. *Ecology* 2022;**103**:e3702. <https://doi.org/10.1002/ecy.3702>
- White JH. Wind-borne dispersal of potato-root eelworm. *Nature* 1953;**172**:686–7. <https://doi.org/10.1038/172686a0>
- Zawierucha K, Stec D, Lachowska-Cierlik D *et al.* High mitochondrial diversity in a new water bear species (Tardigrada: Eutardigrada) from mountain glaciers in Central Asia, with the erection of a new genus *Cryoconicus*. *Annales Zoologici* 2018;**68**:179–201. <https://doi.org/10.3161/00034541anz2018.68.1.007>
- Zawierucha K, Štefková Kašparová E, McInnes S *et al.* Cryophilic Tardigrada have disjunct and bipolar distribution and establish long-term stable, low-density demes. *Polar Biology* 2023;**46**:1011–27. <https://doi.org/10.1007/s00300-023-03170-4>
- Zullini A. Cosmopolitanism and endemism in free-living nematodes. *Biogeographia* 2018;**33**:33–9. <https://doi.org/10.21426/B633034658>