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Does parasitism mediate water mite biogeography?

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Abstract

The biogeography of organisms, particularly those with complex lifestyles that can affect dispersal ability, has been a focus of study for many decades. Most Hydrachnidia, commonly known as water mites, have a parasitic larval stage during which dispersal is predominantly host-mediated, suggesting that these water mites may have a wider distribution than non-parasitic species. However, does this actually occur? To address this question, we compiled and compared the geographic distribution of water mite species that have a parasitic larval stage with those that have lost it. We performed a bootstrap resampling analysis to compare the empirical distribution functions derived from both the complete dataset and one excluding the extreme values at each distribution tail. The results show differing distribution patterns between water mites with and without parasitic larval stages. However, contrary to expectation, they show that a wider geographic distribution is observed for a greater proportion of the species with a non-parasitic larval stage, suggesting a relevant role for non-host-mediated mechanisms of dispersal in water mites.

Keywords: biogeography, water mites, non-parasitic larvae, parasitic larvae, worldwide distribution patterns

Introduction

Studies of the geographic distribution of organisms have greatly influenced our understanding of how species emerge and have provided arguments favoring the theory of evolution by natural selection proposed by Darwin (1859). Traditionally, two different mechanisms are invoked to explain organismal distribution: dispersal and vicariance (Zink *et al.* 2000; Jurado-Rivera *et al.* 2017). A basic assumption under the dispersal scenario is that anything is possible, even highly improbable events (de Queiroz 2014) such as dispersal across barriers thought to be impenetrable or over very long distances. Vicariance, in contrast, assumes that fragmentation of a previously continuous distribution and their derivatives account for the differential distribution of plants and animals under the same variables (Nelson & Platnick 1980; Yoder & Nowak 2006). Assuming the reliable identification of the organisms under study, the biological variables considered most significant under both scenarios are organism size, morphology, habitat, and life cycle (de Queiroz 2014).

Finlay (2002) proposed a model in which microscopic species (those in the size range of 0.002 to 2 mm) do not have structured geographic patterns, lack barriers, and do not show biogeographic discreteness. Water mites (Acari: Parasitengona: Hydrachnidia) are quasi-microscopic organisms, whose body sizes fall within the range given by Finlay. Water mites have a complex life cycle that includes many species with a parasitic larval stage, with high phoretic dispersal possibilities, two dormant phases, and two predatory stages as deutonymphs and adults. They may only leave the water during the phoretic stage, suggesting that the parasitic stage facilitates dispersal (Davids *et al.* 2006).

They have been included in the presumption that “Everything is everywhere, but the environment selects” (Baas-Becking 1934, reviewed in Fontaneto & Hortal 2013 and O’Malley 2008). Nevertheless, other biological traits may influence dispersal potential and determine the distribution patterns of microscopic species. According to Valdecasas *et al.* (2006), “...the law on size, abundance and distribution can lose its applicability in parasitic species” (p. 134) as their distribution may be conditioned by the biology of their host.

Although most recognized water mite species are thought to have a phoretic parasitic larval stage during their life cycle (Proctor *et al.* 2015), a few appear to have lost this stage (Smith 1999), which may have affected the geographic distribution range of some aquatic mite species. In this study, we investigate whether parasitic and non-parasitic water mites differ in the extent of their geographic distribution. In other words, does phoretic parasitism mediate water mite biogeographic distribution? We hypothesize that phoretic parasitic species have more opportunities to disperse and, thus, wider biogeographic ranges than non-parasitic species.

Material and Methods

Dataset

Approximately 7,000 species of water mites have been documented worldwide, according to a revision by Zhang *et al.* (2011). Only records accepted in the recent literature were used to compile our list of water mites with a parasitic larval stage. A species list with corresponding references confirming parasitism is provided in Appendix S1 (available at Doi: 10.6084/m9.figshare.11816673). For each species, information on host(s), habitat and distribution is also provided, as is the calculated geographic distance of the distribution range (in km). In total, 177 parasitic water mite species from several families were included in our analysis. The two species with only one locality were excluded from the analysis.

The non-parasitic dataset is an update of the list compiled by B. P. Smith (1999) and includes the following 22 species (for the references on distribution, see Appendix S1):

Thyas stollii = *Parathyas stollii* = *Acerbitas stollii*. References in Smith (1999).

Sperchon violaceus. Postulated reduced parasitism (Gerecke & Martin 2006; in Di Sabatino *et al.* 2010).

Sperchon turgidus. See Müller (2015).

Teutonia cometes. See Piersig (1896-1899). “Probably not parasitic” in Böttger (1972, page 306).

Brachypoda versicolor. References in Smith (1999).

Hygrobates neoocetoporus. References in Smith (1999).

Hygrobates nigromaculatus. Recently recognized as a valid species, distinct from its sister species *H. setosus* whose larvae parasitize Diptera (references in Gerecke *et al.* 2016)

Hygrobates longiporus. References in Smith (1999).

Limnesia connata. References in Smith (1999).

Limnesia koenikei. References in Smith (1999).

Limnesia marmorata. (see references in Gerecke *et al.* 2016)

Limnesia undulata. References in Smith (1999).

Physolimnesia australis. References in Smith (1999).

Forelia cookie. References in Smith (1999).

Pionacercus leuckarti. References in Smith (1999; no in Böttger 1972).

Piona annulata. References in Smith (1999).

Piona clavicornis. References in Smith (1999).

Piona novae-zealandiae. References in Smith (1999).

Piona pusilla. References in Smith (1999).

Unionicola inusitata (see Gerecke *et al.* 2016 for a discussion of hypotheses about its potential loss of lar-

val parasitism)

Arrenurus manubriator. References in Smith (1999).

Arrenurus rufopyriformis. References in Smith (1999).

We have excluded the following species listed by B. P. Smith (1999) from our study:

a) Species that Smith notated with a question mark: *Acherontacarus halacaroides*, *Unionicola formosa*, *U. intermedia*, *U. bonze*, *Taintaturus stoutae*, *Aturus scaber*, *Limnesia fulgida*, and *Neoacarus hibernicus*; b) Those conceptualized as ‘groups of species’: *Piona coccinea* group, *P. nodata* group, *P. rotunda* group, *P. clavicornis* group, *P. carnea* group and *P. conglobata* group; c) *Atractides nodipalpis*, which has been shown to have a parasitic larval stage (see Gerecke *et al.* 2016); d) *Estellacarus unguitarsus*, as only one species of *Estellacarus* is known to date and there are contradictory statements about its parasitic status: I. Smith (1984) reports it as a parasite of chironomids (Diptera), though B. P. Smith (1999) includes it as an *Estellacarus* (without species names) that lacks a parasitic stage, based on a personal communication from I. Smith; e) *Lebertia stigmatifera*, which parasitizes chironomids (Martin 2000); and f) *Limnesia maculata*, which also parasitizes chironomids. Böttger (1972), whom B. P. Smith (1999) cited as evidence of the species’ non-parasitic stage, clearly states in his paper that it is parasitic.

To quantify distribution ranges, we measured the linear distance between the two most extreme points of a given species’ distribution. This method allows a hierarchical ordering of distributions without overlaps, which have proven problematic when, for instance, distribution is quantified by area (see Valdecasas *et al.* 2006). Worldwide distributions of the selected species were gathered from compilations by K. Viets (1956) and K. O. Viets (1987), publications of single species, the website European Water Mite Research (<http://www.watermite.org/>; data last extracted on 23/02/2018) and the references cited in Appendix S1. First, we built a distribution map for each species and then we calculated the distance (in km) between the two farthest geographic points. All distances were rounded to the nearest whole number. Distances were measured using the distance measurement tool in Google Maps Engine and then corroborated using the haversine formula, which can be used to calculate the distance between two points on a sphere without considering ellipsoidal effects. Species known from only a single location, two from each dataset (parasitic and non-parasitic), were excluded from the comparison. We assumed that the present knowledge of water mite fauna and distribution represents an unbiased sample of water mites. However, bias may be present at the distribution range extremes, i.e., mites with only one locality record or mites with a worldwide distribution.

Statistical analyses

To compare the data variables under study, distance range of distribution, the use of single measures of location or dispersion, such as the mean or standard variation, may be misleading. If the parasitic stage significantly affects the dispersal capacity of water mite larvae, we would expect the empirical cumulative distribution function (ecdf) to be significantly different between the two datasets (Fig. 1). To compare ecdfs, we used the Kolmogorov-Smirnov (KS) test. This nonparametric test does not assume any particular distribution of the data, has no restriction on sample size, and is generally robust to the presence of outliers (reviewed in Feigelson & Babu 2019). It calculates the maximum distance between two ecdfs (D) and its probability (P). Shortcomings for the application of the KS test mentioned by Feigelson & Babu (2019) do not apply to our dataset. Additionally, as remarked by Sekhon (2011) (see also Abadie 2002), the bootstrapped version of the KS test is recommended over the non-bootstrapped one because it “provides correct coverage even when there are point masses in the distributions being compared” (p. 10). Furthermore, the

bootstrapped KS test was recently used to analyze other species distribution datasets, such as in Cyperaceae (Glon *et al.* 2017) and anurans (Ruland & Jeschke 2017).

We ran the `ks.boot` function in the Matching package (<http://sekhon.berkeley.edu/matching/>; last seen on 26/06/2020) for R (R Core Team 2019) with 10,000 resampling runs. The freely available packages for R `ggplot2` (Wickham 2016), `vioplot` (Adler & Kelly 2019), and `kSamples`, for the Anderson-Darling test (<https://cran.r-project.org/web/packages/kSamples/index.html>; last seen on 26/06/2020), were also used.

Results

A summary of the statistical values for the distance range of distribution of the two datasets, water mites with or without a parasitic larval stage, is shown in Table 1. Figures 1 and 2, respectively, show the histogram and the kernel density plot (ksd) of both datasets with all species and/or all species excluding the outliers. KSD plots are usually better to compare the distribution of two data sets because they are not strongly affected by the number of bins used in histograms (Wike, 2019). Tukey (1977) defines outliers as data points that are $[1.5 * IQR]$ (interquartile range) below the first quartile or above the third quartile. According to these criteria, 9 of the species with a parasitic larval stage are putative outliers (marked in yellow in Appendix S1. They belong to following genera: *Limnochares* (1 species), *Lebertia* (1), *Sperchon* (1) *Sperchonopsis* (1), *Piona* (2), *Pionopsis* (1), and *Unionicola* (2).

TABLE 1. Summary of the statistical values obtained from the distribution of distance range of water mites with a parasitic (PA) or a non-parasitic (NPA) larval stage. The following values are shown: minimum, first quartile (Q1), median, mean, third quartile (Q3) and maximum.

	Min.	Q1	Median	Mean	Q3	Max.
PA	157	2798	3814	5259	6114	17928
NPA	1225	3803	5094	6566	10100	16610

The range distribution of each set of water mite species is very different, as evident by the violin plot, which depicts density distribution, the median and the interquartile range (Figure 3). If we exclude outliers, distance values of water mites with non parasitic larval stage are higher than those with parasitic larval stage.

The KS test estimated that the maximum distance between ecdfs (D) is 0.28 with a p-value of 0.0921, indicating a 90.79% probability that the distributions are different. The stricter Anderson-Darling test (see: <https://asaip.psu.edu/articles/beware-the-kolmogorov-smirnov-test/>; last seen 26/06/2020) calculated a 90.3% probability that the ecdfs are different. The KS test of the dataset excluding the outliers sensu Tukey estimated D as 0.31 with a p-value of 0.0446, indicating a 95.54% probability that the distributions are different.

Discussion

Our results suggest that non-parasitic water mites have a wider distribution than parasitic ones, contrary to our initial hypothesis. This unexpected result, at first glance, seems counterintuitive. Nevertheless, it appears that being a parasite of an insect with a flying stage does not intensify water mite dispersion. Furthermore, we do not know how representative the selected species (i.e., the 177 parasitic and the 22 non-parasitic species) are for the more than 7,000 known species of water mites.

Dispersal of aquatic animals that are unable to withstand desiccation requires continuity of the habitat unless they are transported by other means, such as vegetative or animal propagules or physical process like the wind. For instance, this scenario is likely to be particularly true for stream-dwelling species found between basins. A similar situation occurs in species inhabiting ponds and lakes: these habitats can be considered continental islands (Vuilleumier 1970) and dispersal from them is prone to the same challenges as true islands, with desiccation being the main problem.

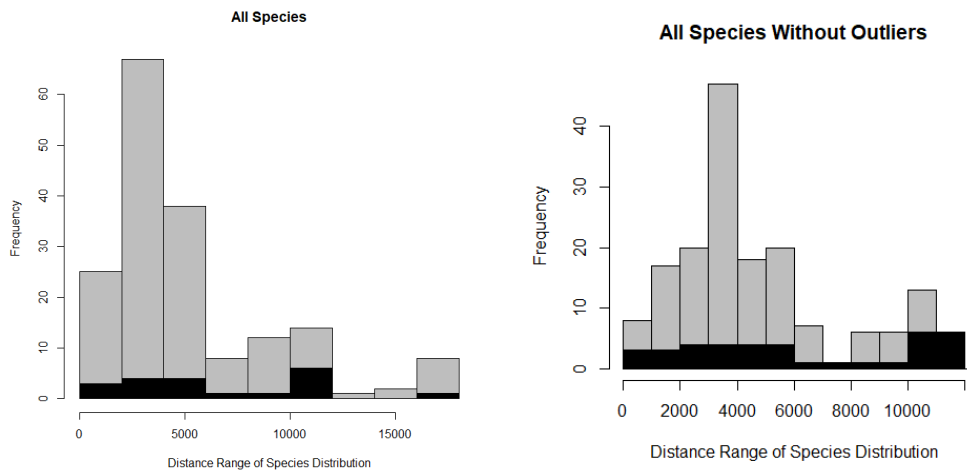


FIGURE 1. Histogram of water mites species with a parasitic (gray) or non-parasitic (black) larval stage, in terms of distance range of species distribution for either all species or all species excluding outliers sensu Tukey (1977).

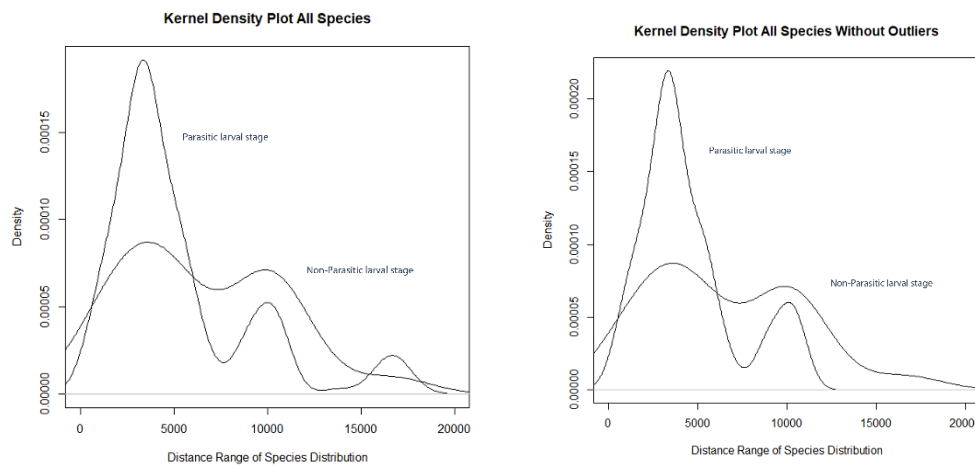


FIGURE 2. Kernel density plot of water mite larvae with a parasitic or non-parasitic stage, excluding outliers sensu Tukey (1977).

To bypass the consequences of habitat discontinuity, water mites, either during their dormant stage or as deutonymphs or adults, require an external biological or physical agent, such as a flying host, for dispersal.

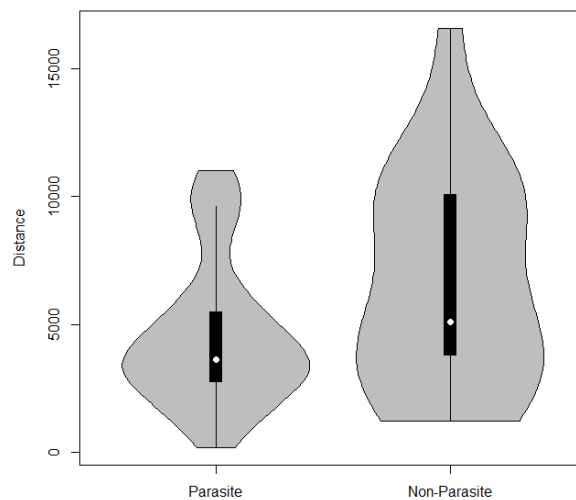


FIGURE 3. Violin plot showing the distribution of the distance variable for water mites with or without a parasitic larval stage, excluding outliers. The white dot represents the median of the distribution, the thick bar indicates the interquartile range, and the fine black line represents the remainder of the distribution. The shape of the plot shows the density of the distribution of the data, with the width indicating the probability of a data point having a given value.

The traditional view on the mechanism of dispersal of water mites is via “larval parasitism...on flying insects...egg masses attached to leaves or vegetable material transported by birds and humans” (Di Sabatino *et al.* 2000, p.54). This view is one that continues to the present: “[T]he only possibility to survive outside the aquatic habitats is at the larval/protonymphal stage by remaining attached to a host” (Gerecke 2020, p.5). However, Valdecasas (2019) found “uncertain if they have been viable” *Arrenurus* individuals in the gut contents of a duck in Bolivia, and A.J. Green recovered an intact adult and many eggs in a potentially viable state in the feces of ducks from Old Wives Lake in Saskatchewan in 2011 (pers. comm.). How common these other means of dispersal are in water mites is currently unknown. Dispersion mechanisms are integrated in a complex way with the biology of organisms. To add to this complexity, we can include the serendipity of apparently improbable causes (De Queiroz 2014), which may provide more clues to present-day animal distributions than exclusive mechanisms of dispersion. Clearly, much remains to be determined about the means of dispersal in water mites.

What may be true for water mites can also be said for other aquatic animals. In a recent review, Fontaneto (2019) discusses the dispersion and distribution of three microscopic aquatic microorganisms, rotifers, tardigrades, and nematodes; however, he does not cover the role of parasitism in dispersal, despite its potential importance for nematodes and other aquatic organisms. For aquatic insects with a terrestrial flying stage, finding a new aquatic habitat may be a hazardous task, particularly if they have additional cargo, such as parasitic water mite larvae, that may limit their range of dispersion or their ability to avoid predators, among other effects (Di Sabatino *et al.* 2000).

Although, it has been demonstrated that, in some cases, water mites do not negatively affect the dispersal ability of hosts and may even have a positive effect. For example, Conrad *et al.* (2002) found that parasitized males of the damselfly *Coenagrion puella* were more likely to disperse than non-parasitized ones.

Another possible explanation for our result is that the species with a very wide distribution are in fact species groups, a phenomenon found in other invertebrate groups (Tzedakis *et al.* 2013). That is, what we consider as a single species may actually constitute a complex of species that are difficult to differentiate on a morphological basis, thus leading to taxonomical errors. The presence of cryptic species, however, has not been extensively explored in water mites, except in a few cases (Martin *et al.* 2010; Stålstedt *et al.* 2013; Pešić & Smit 2016). The 22 species with a non-parasitic larval stage included in this study belong to six different water mite families, indicating that the non-parasitic condition independently evolved in the different species. Regardless of whether the water mite species have a parasitic larval stage or not, the idea that widely distributed species may belong to different putative species does not negate the fact that modern morphological characterizations suggest a common origin. It is tempting to test whether Tukey's (1977) statistical criteria for determining the outliers is in accordance with the criteria used to delimit them as species. This type of test could rigorously be done with molecular data (García-Jiménez *et al.* 2017).

A referee asked us to consider “Why do species with parasitic larvae have minor distribution areas?” In our opinion, the most parsimonious answer is that parasitism does not enhance dispersal, but limits it: First, if the host is faithful to its original habitat to which it may return, then there is no advantage of dispersal for the parasitic larvae. Second, if the host dares to move to another habitat, then the larval cargo may act as an impediment to dispersion.

Water mite larvae are easily found in the neuston layer at the interface between air and water. Due to their small size (approximately 0.25 mm) and their ability to endure periods without feeding, these larvae could be transported passively and quickly to other suitable habitats by operating winds (Maguire 1963; Bilton *et al.* 2001). Therefore, passive dispersal via the neuston layer may represent another mechanism contributing to the high level of dispersion found for non-parasitic water mite species, and should be further explored. In this sense, it is possible that, given enough time, any improbable means of dispersion may produce a successful dispersion event (De Queiroz 2014).

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