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FROM THE ARCHIVES

Protist Citation Classics Cosmopolitan Metapopulations?

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Background

We are, of course, pleased that the paper Finlay and Fenchel (2004) has received so many citations although several of them reflect disagreement regarding its contents (according to Clarivate's Web of Science the article received 180 citations by ay 02, 2019). The article treated a subject to which we had already contributed substantial research - reflected by the fact that the paper refers to twelve of our previous contributions to the topic (e.g. Finlay 2002).

It all started as a response to a paper by May (1988) that attempted to estimate the global number of terrestrial species according to size groups. It was found that the number of species increases with decreasing body size, but only down to a size around 1 cm; below that size

species numbers declined with decreasing size. May suggested that many small-sized species remain to be discovered and also that taxonomic resolution is poorer for small organisms. That species numbers should increase with decreasing size seemed in line with theoretical considerations that the environmental patchiness is a question of scale: a given area may seem like a homogenous habitat for a large mammal, but constitutes a myriad of different habitats for small organisms. And in fact, within a given limited area, for example one ha of sandy sea floor or forest, the biota contain many more small than large species. Fenchel (1993) argued that the immense population sizes of small organisms mean that they have a greater ability for dispersal. Therefore they do not have a biogeography in the sense that their distribution depends only on environmental parameters, but not on historical contingencies over geological time. So what applies on a local scale does not apply on a global scale and the observation that global species numbers decline for species below a size of about 1 cm is a true phenomenon. And actually only about 17,000 species of free-living protists have been described which is modest compared to e.g., insects with more than one million species or molluscs that include about 85,000 described species. The correlation between absolute population size and dispersal ability has been confirmed both empirically and by theoretical population biology (e.g. MacArthur and Wilson 1967 and Hubbell 2001).

Actually, the considerations in Fenchel (1993) were not really very original. Already e.g., Darwin and Ehrenberg had suggested that protist species have a cosmopolitan distribution. With regard to bacteria Baas Becking had already in 1931 stated that for bacteria: "Everything is everywhere, (but) the environment selects" (see Finlay 2002, de Wit and Bouvier 2006). This was based on the observation that by using enrichment cultures it is possible to obtain isolates of all kind of bacteria everywhere and this has been confirmed over and over again. Thus it is possible, for example, to isolate obligate thermophiles from ice cold sea water and obligate anaerobes from the aerobic water column. The argument was that the immense population sizes of bacteria combined with dispersal by wind, water currents or other mechanisms such as migrating birds constantly spread bacteria worldwide. The cells would remain viable for some time under unsuitable conditions, but may proliferate if the environment becomes suitable for growth. With respect to protozoa the monumental treatise on ciliates (Kahl 1930-35) had the subtitle : "*eine Bearbeitung der freilebenden und ectocommensalen Infusorien der Erde*" (A Treatise on the Free-

Living and Ecto-Commensal Infusoria on Earth) . The work was published in a series of books on the fauna of Germany and at the time there were very few surveys of ciliate biota outside of Europe and North America. And so the subtitle implied that the author took it for granted that ciliate species have a cosmopolitan distribution.

It has also been discussed to which extent the so called meiofauna (small metazoan species usually defined as measuring <2 mm) display biogeographical patterns or whether “everything is everywhere” (Giere 2009). It cannot be considered a settled question, but as in the case of protozoans it is to a large extent a problem of undersampling.

The question – in the case of protozoa – induced the present authors to collaborate in resolving the question: do protozoa have a biogeography or are they more like bacteria in that their presence is only contingent on the environment. The paper that we are “revisiting” (Finlay and Fenchel 2004) was based on two localities: a eutrophic freshwater pond in the English Lake District and a marine sandy bay north of Copenhagen. Both localities have over many decades been studied intensively with respect to the flora and fauna including the protists. For both sites we attempted to evaluate the fraction of species that could be considered to have a cosmopolitan distribution. To consider a species to have “cosmopolitan distribution” entails a set of criteria and we chose that it required the presence on both hemispheres, in all oceans and in at least two biogeographical regions. The result was that there was a clear relation between size and distribution: for the freshwater pond, heterotrophic eukaryote species those measuring < 0.2 mm in size were about 90% “cosmopolitan”, and among those measuring >2 cm there were none. The marine bay provided a similar picture, but the fraction of “cosmopolitan species” among the smallest organisms reached only about 70%.

Further Evidence

Our investigations into protists (mainly ciliates) geographical distributions initially used the morphospecies concept that we had previously proposed (Finlay et al 1996) in order to bring underpinning consensus to our studies (and those of others wishing to undertake similar examinations thereafter, e.g. Azovski and Mazei 2012). Also, ciliate species are relatively easy to identify by morphological characteristics, and we had the right taxonomic expertise within the research group.

To further pursue evidence for Baas Becking's "everything is everywhere, but the environment selects", and armed with the "morphospecies" concept, we focused research on two key areas: (1) protists thriving in distant and/or geographically-isolated aquatic habitats, i.e. biogeographical "islands" (McArthur and Wilson, 1967), and (2) presence and significance of protist "seedbanks". For the former, we must allude to our unexpected discovery of common brackish-water ciliate species (like those previously recorded from, e.g. the sandy sediments in Nivå Bay, Denmark) in an isolated crater lake in southern Australia, most likely as result of "dispersal and colonization" due to enduring sea-sprays from the Southern Ocean (Esteban et al 2000). Other "islands" that we sought out to investigate were closer to "home" (i.e. Europe, where a wealth of ciliate faunistic lists and their habitats are available), but they equally rendered interesting results; for instance, the finding of typical marine ciliates thriving in inland salt pans (of salinity like that of sea water) in central Spain at more than 300 km from the nearest coast line (Esteban and Finlay 2004). The environmental conditions in these isolated habitats made population growth of the ciliate species possible, independently of the habitats' geographical locations.

Ubiquitous dispersal of protists implies that every habitat may support a "seedbank" of species imported to that habitat by random dispersal. However, many of the species in the seedbank may never thrive due to lack of environmental conditions to develop population growth and, hence, they persist dormant/encysted (albeit viable) waiting for favourable conditions to emerge (Esteban and Finlay 2010). Finlay et al (1996) and Fenchel et al (1997) had demonstrated that natural habitats do support species-rich 'seedbanks' by manipulating natural samples using a large variety of enrichment cultures in order to offer micro-habitats to a variety of 'dormant' protist species. A few milliliters of pond sediment collected in one single occasion from one single pond depth and using multiple enrichment techniques increased the recorded ciliate species from 27 (first day of observations) to 137 after four months of painstakingly culturing subsamples.

There is also evidence for the rapid dispersal of protists over great distances. Thus Cairns Jr., Ruthven JA (1972) and McCormick, Cairns Jr. (1990) demonstrated the colonization of isolated freshwater ponds, Frederiksen et al.(2001) proved the rapid colonization of protozoa in soil on the volcanic island Surtsey that originated in a volcanic eruption in 1963 and is situated 33 km from the south coast of Iceland. Villerslev et al. (1999) using the detection of SSU rRNA genes

in cores from the Greenland glacier ice, demonstrated a long list of protists (and fungal spores) that had rained down on the ice cap during the Holocene period.

Some of the soundest evidence of random dispersal followed by cryptic (i.e., dormant or very low abundance) persistence in the 'seedbank' is probably the detection of species that would not thrive in the habitat where they have been found. The search of such ciliates was the target of work that we also published in *PROTIST* (Esteban and Finlay 2003), in which freshwater and other ciliates (not adapted to high salt concentrations) were found in a hypersaline lagoon after gradually diluting the original samples over a long period of time until the environment eventually became favorable for the ciliates' development.

For most rare protist species, undersampling is inevitable (Finlay and Fenchel 2004), and for that reason, "endemic" species are not (yet) found elsewhere. After all, all surveys are based on few ml of water or sediment, which is a minor fraction of even the smallest of lakes that include a great amount of different microhabitats. Having said that, there are superb examples of 'endemics' being 'dethroned' when sampling ranges expand to wider geographical regions, with *Loxodes rex* providing one of the finest examples; the ciliate has a cell size of 1-1.5 mm, with cyst formation (so far) unknown. The species was described as endemic to tropical Africa (Dragesco 1970), but when sampling expanded to other world regions it was found in swamps in Thailand (Esteban et al. 2001) and, more recently, all across Florida, USA (Hines et al 2016). The occurrence of a bipolar distribution of cold-adapted protists is also striking. For example, the ciliate *Euplotes nobilii* has been found in both the Arctic and the Antarctic and the two isolates share common pheromone-mediated cell signaling and display cross-mating (Di Guiseppe et al 2011).

Cryptic Species and Genotypes

With respect to sexual outbreeding in ciliates it has been found that nominal species may represent a complex of forms that cannot interbreed although they are morphologically very similar or identical; such sibling species or syngenes are then separate species in terms of the biological species concept. The classic example is the *Paramecium aurelia* complex (Sonneborn 1975). A similar complex has been found within the genus *Tetrahymena* (e.g. Nanney and McCoy 1976); given that the two genera are among the most intensively studied ciliates it is probable that the phenomenon is more widespread. A geographical distribution pattern of these forms has also

been suggested (Nanney 2004), but again this may be an effect of undersampling – most syngenes have been found in North America where search for different *Tetrahymena* genotypes has been most intensive.

All species show some genetic polymorphism which, to a large extent, represents neutral or near neutral mutations. The number of such neutral mutations that is maintained in populations is a function of absolute population size (Kimura 1983). And so it has also been considered whether such genetic differences show biogeographical patterns. The problem with this approach is, of course, that it requires an a priori idea of how many such variations in a given gene exist: when the number is high it is quite likely that when a representative of a species is collected at site A it will show another genotype than one collected at site B.

It has been attempted to demonstrate biogeographical distribution patterns of different genotypes of SSU rRNA genes (Bass et al. 2007), but the above mentioned problem of undersampling has not been taken into account. Finlay et al. (2006) obtained SSU rRNA sequences from isolates of the ciliate *Cyclidium glaucoma* collected in various freshwater sites in Europe, South East Asia, Japan, Africa, Australia, North American and South America and in adjacent marine localities. It resulted in 31 genotypes, but there were no geographical patterns, and identical genotypes were found in e.g., Australia and Denmark. The species occurs in salinities ranging from freshwater to hyperhaline water and there was a correlation between genotype and the salinity in which they occur and different isolates display differences with respect to their growth response to different salinities in laboratory cultures (Fenchel and Finlay 2006). But, for example, identical genotypes were found in Great Salt Lake in Utah and in a hyperhaline pond in Spain so that there is a correlation between their tolerance range to different salinities and their rRNA genes. It is unclear whether *C. glaucoma* is a sexual out breeder and if so, the different genotypes may represent sibling species such as in the *Tetrahymena* complex, but there is no indication that the different genotypes are confined to particular parts of Earth's surface.

Conclusion

The idea of a cosmopolitan distribution of protists and that their distribution depends exclusively on the habitat has met opposition (e.g. Nanney 2004, Stoeck et al 2007) and it seems to be almost

impossible to provide a final “proof” or “disproof” one way or the other. It is always possible to declare a species for being “endemic” (e.g. to a continent, a hemisphere, or a lake) as long as it has not been detected elsewhere. And it is not impossible that endemics within a certain geographical region actually do exist. But examples of such putative endemics are rare and the species in question have so far often later turned up in other locations. It is clear that some species display what botanists refer to as “ecotypes”, i.e. that populations within a nominal species somehow display genetically determined differences with respect to environmental preferences, e.g. the different salinity preferences in isolates of the ciliate *Cyclidium glaucoma* complex (Finlay et al. 2006) and in the flagellate *Bodo designis* (Koch and Ekelund 2005). But at least in these two cases such ecotypes (and identical genotypes) have also been found to have a widespread geographical distribution. And as far as asexual forms are concerned there is no theoretically based species concept.

The essential difference between macroscopic organisms and microbes is the immense absolute population sizes of the latter. This again explains the greater potential for dispersal and also for a high degree of genetic polymorphism. The great genetic distances in, e.g. rRNA genes, within complexes of syngenes or sibling species (Nanney et al. 1988) testify that the extant phenotypes of different species are ancient in a geological time scale – perhaps because allopatric speciation does not play a role for microbes.

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