Environmental Issues

Ubiquity and Cosmopolitanism of Protists Questioned

This brief article is based on a recent review that contained a detailed discussion of ubiquity and cosmopolitanism of protists and literature evidence (Foissner 2004). Further, this review commented on bacteria and microfungi for which, due to new molecular methods, there now seems to be a restricted distribution of certain taxa.

As early as 1913, Beijerinck, a Dutch microbiologist, formulated his famous metaphor "in microorganisms, everything is everywhere, the environment selects". Quickly this phrase became a fundamental paradigm in microbial and protistan ecology, likely driven by the intuitive view that such minute organisms must have simple ecologies. Although this was soon disproved, Beijerinck's view survived, especially among ecologists. The few taxonomists who opposed an overall cosmopolitanism of protists were largely ignored, in spite of the good evidence they presented. Only when biodiversity research became fashionable did the problem actually become new, especially because newly developed molecular methods showed that many morphospecies of small organisms, such as bacteria, protists, rotifers and microcrustaceans, are composed of several species with sometimes distinct areals.

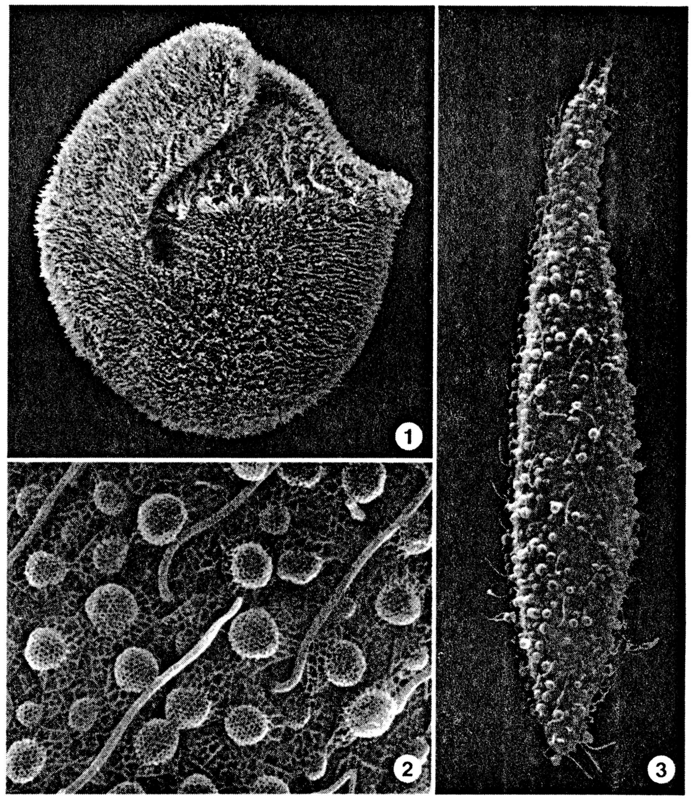
Why is endemicity so difficult to prove in protists?

A lot of drawbacks make endemicity difficult to prove in protists: (i) compared to higher plants and animals, they are extremely difficult to recognize due to their microscopic size; (ii) many species are dormant (encysted) most of their life, only when appropriate conditions set in do they excyst and become visible; (iii) compared to macroscopic organisms, most protists have few distinct morphological features which, additionally, are often difficult to recognize; (iv) protistology was never a mainstream science and thus few people contributed; and (v) the use of holarctic identification literature for species from other biogeographical regions classifying "minor" differences as "site variations".

These and other problems, such as the widespread occurrence of misidentifications, cause (i) reliable distribution data being scant; (ii) rare and possibly locally distributed species being heavily undersampled; and (iii) more than 50% of the actual diversity being undescribed in many protistan groups. In other words, we know mainly the euryoecious species, which are more abundant and widely distributed.

Contrasting views

Today, a "cosmopolitanism school", represented mainly by Fenchel and Finlay (2003), and a "moderate endemicity school", represented, inter alia, by myself and Ralf Meisterfeld, fight for the best arguments. Fenchel and Finlay argue that the small size and high abundance of microorganisms favor global dispersal and thus low rates of allopatric speciation. They explain the lack of certain microorganisms in certain areas as a result of uneven sampling efforts.



Figs. 1–3. Flagship ciliate species with restricted geographic distribution. Fig. 1: Bresslauides discoideus *is a long, rapacious moss and soil ciliate, up to 600 µm long, occurring only in Laurasian areas. Figs. 2 & 3: I discovered this still undescribed trachelophyllid ciliate in a salt marsh on the north coast of Venezuela. It is a slender species about 200 µm long covered with nicely faceted, 3–5 µm-sized lepidosomes. The unique, hat-like shape of the lepidosomes shows that this species represents a new genus likely restricted to South America or Gondwanan areals.*

The moderate endemicity model refers to the many eyecatching "flagship" species which have never been found in other well investigated areas, and emphasizes that most protists are much older than multicellular organisms and, thus, had sufficient time to acquire considerable diversity. This is supported by the continuous discovery of new flagship species showing our ignorance about even conspicuous taxa (Figs. 1-3). However, the most convincing argument for a restricted distribution of microorganisms comes from the data presented under the next heading.

Minuteness and high abundance do not necessarily cause global distribution: evidence from macrofungi, mosses, and ferns

Macrofungi, mosses and ferns often have larger areals than flowering plants and large animals. But few are true cosmopolitans and many of them have rather restricted areals, although their main dispersal means (spores) are usually in the size (5–50 μm) of large bacteria and small protists and are produced in astronomical numbers. This simple fact, which has been completely ignored by the cosmopolitanism model, shows that there is no ecological or other reasons to assume global distribution of all protists.

Conclusion: not everything is everywhere

Flagship species, reliable distribution data, and molecular investigations show that restricted geographic distribution of microorganisms occurs in limnetic, marine, terrestrial, and fossil ecosystems. The data available suggest a multifactorial model in which diversity, dispersal, and provincialism of microorganisms are determined by historic events (split of Pangaea etc.), time, small size, high individual numbers, and limited cyst viability. I estimate that about one third of the free-living protists, described and undescribed, have restricted distribution.

Key literature

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Fenchel T. and Finlay B.J. 2003. Is microbial diversity fundamentally different from biodiversity of larger animals and plants? *Europ. J. Protistol.* **39**:486–490.

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Working Groups

The African Great Lakes

SIL's African Great Lakes Group has had an important role in stimulating international research on the three largest East African lakes, the very deep rift valley lakes Tanganyika and Malawi and the huge (69,000 km^2) but shallower Lake Victoria. This group was initiated in 1987 at the SIL Congress in New Zealand in response to reports that drilling for oil had started on the shores of Lake Tanganyika, which could endanger the priceless faunas, fisheries and water supplies of the four riparian countries: Tanzania, Zambia, Burundi and the Democratic Republic Congo. All three lakes support fisheries of vital importance for their rapidly rising human populations. They are also well known as biodiversity hotspots with spectacular endemic faunas including flocks of cichlid fishes unique to each of the lakes of international significance as they offer special opportunities to investigate how new species evolve and coexist.

The group's first task was to organize an international 'Symposium on Resource Use and Conservation of the African Great Lakes' on Lake Tanganyika at the University of Burundi in 1989 (Lowe-McConnell, *et al.* 1992). The widely circulated recommendations from this and subsequent meetings were then used to help obtain international funds for fisheries and biodiversity projects.

The 1990s saw a veritable explosion of research on all three lakes which are now facing serious threats caused by the rapid rise in human populations, leading to over fishing and pressures on their unique faunas from sedimentation and pollution following changes of land use in the lake basins. International projects, involving well over a hundred scientists, have concentrated on limnological conditions affecting fish production, the ecology of the communities, and underwater observations of behavior, spawning a huge bibliography of papers and widely scattered reports. Their findings, together with those from papers given at fisheries conferences and international symposia organized by specialist groups (IDEAL - International Decade of East African Lakes, SIAL - Speciation in Ancient Lakes, PARADI - Biological Diversity of African Fresh and Brackish Waters, and GLOW - Great Lakes of the World) have been collated and assessed as 'Recent Research in the African Great Lakes: fisheries, biodiversity and cichlid evolution' (Lowe-McConnell 2003). Published as a Special Issue of Freshwater Forum this can be obtained from the Freshwater Biological Association (contact: *info@fba.org.uk*) or the author (*ro.mconnell@virgin.net*).

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Cosmopolitanism and Microbes

In the previous issue (Vol. 43, September 2004) of SILnews Professor Foissner questions our view that small organisms (e.g., protozoa) have cosmopolitan distribution – in the sense that habitat properties alone, rather than historical contingencies, determine where in the biosphere any particular microbial species thrives.

Ours is not a theory for protozoa alone. We have shown that small organisms in general tend to have wide geographical distribution, and those smaller than about 1 mm do appear to occur wherever their habitat requirements are met. These observations link to current ideas in community ecology predicting that large population sizes will correlate with wide geographical distribution, due to high probabilities of dispersal and low extinction rates (Finlay and Fenchel 2004; Fenchel and Finlay 2004). We recognise that some protists appear to be confined to particular climatic zones. They may, for example, show pantropical or bipolar distribution, but note that trans-tropical gene flow of 'bipolar' planktonic foraminifera has been shown (Darling *et al.* 2000).

Wide geographical distribution also has an impact on the number of species because of the lowered probability of allopatric speciation. This is reflected in the relatively modest global species richness of protists and smaller meiofauna – notwithstanding that some species remain to be discovered. At the local scale (e.g., a freshwater pond, or a few square metres of soil), the diversity of small organisms will always exceed that of larger organisms.

The disagreement is only a question of degree. Foissner suggests that maybe 33% of all ciliates show some degree of endemism. We tend to believe that this estimate is inflated, but even if true, it presents a situation that is markedly different to that of macrofauna and –flora for which cosmopolitan distribution is extremely rare (save for anthropogenic introductions). Macrofauna and –flora may be confined to mountaintops, river systems, old lakes or limited areas within continents: the flora of the Cape Province (South Africa), for example, includes more than 60% endemic species. The vast number of animals and plants with restricted geographical distributions explains their huge global species diversity.

We agree with Foissner that it is difficult to prove (or disprove) that every protist species occurs on all continents or in all oceans. New species are discovered every year and they are by definition endemic until found elsewhere. In 1995 we (Fenchel *et. al.* 1995) studied the protist biota of a marine anaerobic water column in a Danish fjord. No one previously had looked for anaerobic flagellates in such habitats and among other things we described a peculiar and very characteristic euglenoid flagellate (*Postgaardi mariagerensis*). Within a year it was found in samples collected in the anaerobic layers of a saline lake in Antarctica (Simpson *et al.* 1996/97) and soon after it was reported from the bottom of the Santa Barbara Basin off California (Bernard *et al.* 2000). So one should not give up the hope that some of the "endemic ciliates" will, after all, turn up elsewhere - once someone looks for them in the right places.

Foissner further questions our argument that large population sizes are required for large-scale dispersal by referring to the fact that mushrooms, mosses and ferns produce enormous numbers of spores and that these species should therefore have cosmopolitan distributions. In fact, representatives of these groups do tend to have very wide distributions, and this may be attributed to their spore dispersal ability, so the argument is not really at variance with our view. But the argument is also not quite valid. A huge number of spores is not equivalent to a huge population size. If an individual fern produces a million spores in its lifetime, on average only one millionth of these will survive to produce a new fern – the rest will succumb. The meaningful population size of ferns is, in the present context, the number of reproductive individuals. Five ferns may, perhaps, inhabit a square metre, but this area will also host something like 10^8 soil protists. *

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* A single Agaricus campestris releases 1.6×10^{10} spores (Schwantes 1996)!