

Protist diversity and distribution: some basic considerations

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Abstract This essay discusses protist species number and geographic distribution, both heavily influenced by undersampling and human introductions. The features of the ubiquity model and the moderate endemism model are compared. I recognize five main flaws of the ubiquity model, viz., the ignorance of the extraordinary possibilities protists have to speciate due to their short generation time and the likelihood that many persisted over geological time scales; that all protist species have high abundances; that their small size is a main reason for global distribution; the ignorance of human introductions; and the rejection of literature evidence on the occurrence of flagship species with restricted distribution in a wide variety of protists. Thus, the data available support the moderate endemism model which proposes about 300,000 extant, free-living protist species, of which one third might have a restricted distribution, i.e., is not cosmopolitan in spite of suitable habitats. To sum up, the distribution of protists, flowering plants, and larger animals has much in common, but protists usually have wider ranges and thus a higher proportion of cosmopolites. Future research should reconcile morphologic, genetic, and ecological species concepts because this is crucial for determining the number of protist species. Further, greatly intensified research is required on morphospecies in heterotrophic protists because their diversity has never been investigated in large areas of the earth.

Keywords Community structures of protists and multicellular organisms · Distribution models · Moderate endemism distribution model · Protist endemism · Protist species number · Ubiquitous distribution model · Undersampling

Introduction

The collection of papers in this issue of *Biodiversity and Conservation* was stimulated by the controversy whether or not micro-organisms have biogeographies. Indeed, several

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colleagues suggested me to compare my “moderate endemism model” (Foissner 1999, 2006) with the “ubiquity model” of Finlay et al. (1996, 2004). Thus, I provide here a brief essay not going in literature details which can be found in several recent reviews (Dolan 2005; Foissner 2006) and in the contributions contained in this issue.

Molecular studies greatly advanced our understanding of protist distribution and species number. However, we should not ignore the excellent evidence for protist endemism collected by generations of taxonomists, for instance, by Heimans (1969) in desmids, by Bonnet (1983) in testate amoebae, and by Dragesco and Dragesco-Kernéis (1986) in ciliates.

Distribution models

The current literature discusses two possibilities of protist distribution, viz., the “ubiquity model” of Finlay and Fenchel (Finlay et al. 1996; Fenchel and Finlay 2004) and the “moderate endemism model” of Foissner (1999, 2004, 2006). Both models have much in common, for instance, that most protists are cosmopolites.

At first glance, the distribution debate appears rather academic because the importance of protists is still widely neglected, although the “microbial loop” has now found a home in most ecological textbooks. However, when the consequences of the two models are compared, the significance of the distribution debate becomes obvious, extending from academic to applied issues (Table 1).

Undersampling and human introductions, the keys to understand protist diversity and distribution

Why is it so difficult to obtain reliable data on protist diversity and geographic distribution? There are several reasons (Foissner 1999, 2006), but a main problem is undersampling, that is, only a small proportion of the protists can be seen at any time because most species are in a dormant (cystic) stage waiting for optimal conditions to become active. Furthermore, the samples studied are usually very small, both in quantity and size, because all investigations must be done with the microscope, which is time-consuming and needs well trained taxonomists. Although various attempts have been made to correct morphologic and molecular data for this hidden diversity (Chao et al. 2006; Hong et al. 2006), we have only a vague knowledge how many of them are overlooked either because they are inactive or do not reproduce to detectable numbers. When only a single sample from a habitat is investigated, for instance, a composite sample from 100 m² forest soil, undersampling may miss 70% of the species actually present (Foissner 1999; Foissner et al. 2002).

Foissner (2006) emphasized the importance of biogeographic changes due to human introductions and provided several examples, for instance, the introduction of the very distinctive alga *Hydrodictyon* to New Zealand by imported fish and water plants from East Asia. Further impressive cases are contained in some contributions of the present issue, for instance, the introduction of the diatom *Asterionella formosa* to New Zealand (see contribution of Vanormelingen et al.). Thus, human-induced biogeographic changes of protist communities are as important as in plants and animals and should get much more importance in the biogeography debate.

Table 1 Comparison of distribution in macro-organisms and free-living protists

Features	Macro-organisms	Protists (micro-organisms)	
		Ubiquity model	Moderate endemicity model
1 Absolute abundance of individuals within morphospecies	Low	High	Low in the majority ($\geq 90\%$) of species, high only in some euryoecious species
2 Rates of migration	Low	High	Low for most of the rare species, high only for some euryoecious species
3 Proportion of global species pool found locally	Low	High	Moderate; usually highly over-estimated due to undersampling, see Foissner (1999) for an example
4 Rates of allopatric speciation	High	Low	Low, but see next entry
5 Rates of non-allopatric speciation	Low	?	High, e.g., parapatry, microallopatry, isolation-by-distance (Helbig 2005)
6 Cryptic persistence of species	Variable	High	High
7 Persistence of specific morphotypes over geological time scales	Low	High	Moderate
8 Large-scale distribution determined by historical contingencies, e.g., continental drift	High	Low	Moderate
9 Time for speciation	Low	?	High
10 Relative number of endemics	High	Low/none	Moderate ($\sim 30\%$)
11 Rates of species extinction	High	Low	Moderate
12 Global number of morphospecies	High	Low	High due to long time to speciate and non-allopatric speciation (see above)
13 Conservation	Needed	Not needed	Needed
14 Human introductions	Low	?	Likely high; see Foissner (2006) and several contributions in this issue

Based on Finlay et al. (2004), except for features (5, 9, 13) and the “moderate endemicity model”

Main flaws of the ubiquity model

I recognize five main flaws of the ubiquity model, viz., the ignorance of the extraordinary possibilities protists have to speciate because of their short generation times and the likelihood that many persisted over geological time scales; that all protist species have high abundances; that their small size is a main reason for global distribution; the ignorance of many human introductions both in the past and present; and the ignorance of literature data on the occurrence of species with restricted distribution in a wide variety of protists.

(1) Speciation is an ongoing process in most or even all organisms. I do not want to repeat the knowledge and problems of speciation and species delimitation in general and of protists in particular. The evidence from protists which left fossils argue for similar speciation mechanisms in protists, plants, and animals. For instance, speciation can be a

slow (10^6 years) or rapid (10^3 years) process (Norris 2001). In the present context, two issues are of paramount importance, both suggesting a high number of protist species.

Protists have short generation times, fostering mutations and thus speciation, although their genetic isolation is possibly less strict than in most plants and animals due to their wider distribution. Thus, there must be a large stock of relatively young species which not yet fully explored their potential area, simply for the lack of time to distribute. These then appear, *inter alia*, as endemics in our species lists. Considering that plants and animals can speciate in 10–20,000 years, for instance, fish in lakes (Martens 1997) and plants and animals in postglacial areas (Schluter 1998), there is no logical reason to assume that protists behave different, especially when considering their short generation time. Accordingly, local and regional endemics should be widespread. Unfortunately, these species often will be inconspicuous and thus difficult to recognize. However, some examples from ciliates and diatoms are reviewed in Foissner (2007) and Mann and Droop (1996), respectively.

Protists possibly survived the great extinctions in the earth's history better than larger organisms due to their smaller habitats. Thus, they could accumulate diversity over hundreds of millions of years. Such scenery is not only suggested by various paleontological data but also by recent studies, indicating that micro-organisms persisted in cold refuges during periods of greenhouse conditions (Stoeck et al. 2007).

(2) When compared to plants and larger animals, protists are indeed much more numerous, but only a few species, while the vast majority (>90%) have moderate, low, or very low abundances, as is the case in plant and animal communities (see ecological textbooks). This is obvious from all investigations in which species richness and the abundances of the individual species were carefully studied (Figs. 1, 2). Curiously enough, the high similarity in the structure of protist, plant, and animal communities never played a significant role in the discussion about protist diversity and distribution. Of course, rare species can become numerous and vice versa, just as pests in plant and animal communities. Usually however, rare species are rare throughout time and space, while abundant species are numerous at many times and globally; the latter are those we usually recognize and make protist samples from, e.g., Europe and Australia so similar. The rare species, many of which have been not yet discovered (Chao et al. 2006) and may be endemic, are not recognized in ordinary surveys due to undersampling discussed above.

(3) Often, the wide or cosmopolitan distribution of protists is assumed to be associated with their small size and high numbers (Fenchel 1993; Finlay et al. 1996, 2006), and Wilkinson (2001) suggested that this is especially likely for organisms having a size of below 100 μm . However, this is disproved by macrofungi, mosses and ferns, many of which have small areals in spite of appropriate habitats and minute spores (<50 μm) produced in high numbers (see explanation to Fig. 3). This was first recognized by Foissner (2006) and is supported by the detailed data of Frahm in this issue. Further, seeds of higher plants often have small size and special morphologic adaptations for air dispersal, but are not cosmopolites, although many of these “exotics” grow well in our home gardens. Interestingly, morphological adaptations for air dispersal are unknown in cysts and spores of micro-organisms, suggesting that this kind of distribution never played a major role.

Wilkinson (2001) founded the hypothesis on testate amoebae whose small resting cysts (usually <100 μm) often remain in the much larger and rather robust test. However, all test-less protists have only the small resting cysts for large scale distribution because the active specimens are too fragile. There are few resting cysts with a size of >100 μm , and thus size is possibly only one of several reasons for cosmopolitan or restricted distribution.

(4) Generations of taxonomists provided convincing evidence for restricted distribution of some protists, using so-called flagship species considered as “ultimate” proof of protist

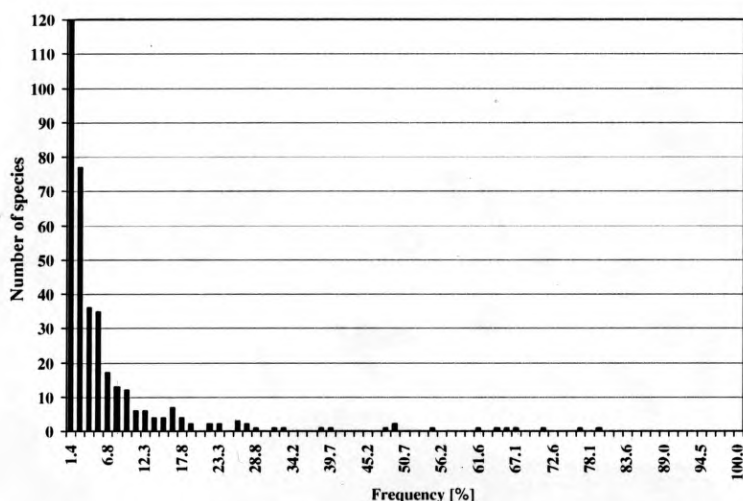


Fig. 1 Frequencies of 365 ciliate species in 73 samples from terrestrial habitats of Namibia (from Foissner et al. 2002)

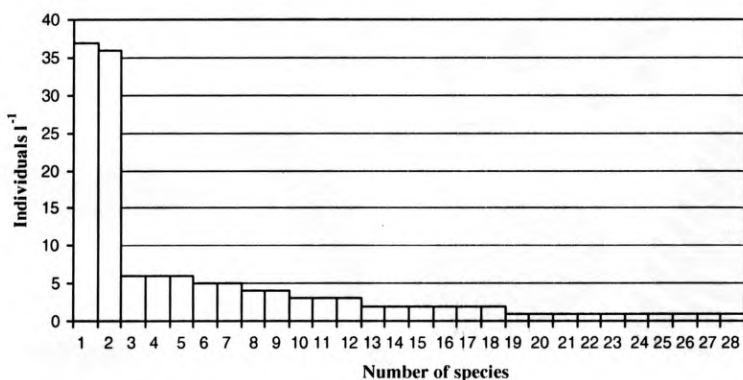


Fig. 2 Number of ciliate species and individuals in the free water of a pond in the Austrian Central Alps about 2,000 m above sea-level. The pond is ca 2,000 m² in size, but the average depth of the water is only 17 cm. Ciliates were rare in the free water, both qualitatively and quantitatively, possibly due to the acidic (pH 4.8–5.4) and dystrophic water. The individual numbers are averages of 14 sampling occasions between 10 July and 19 August. The dominant species were two common cosmopolites, viz., *Cyrtolophosis mucicola* and a species of the *Vorticella aquadulcis* complex

endemism by Foissner (2006). Tyler (1996) has summarized the reasons why flagship species have the greatest probability of real endemism: “Because they are so showy, or so novel, it is unlikely that such species would be overlooked if indeed they were widely distributed. If the Australian endemics occurred in Europe or North America they would have been seen there, long ago”. Foissner (2006) put together flagships from various protist groups, and some are shown in the contributions to this issue.

The ubiquity model has ignored all these evidence or rejected the data as caused by undersampling and misidentification (Mitchell and Meisterfeld 2005). This stimulated more detailed research showing, e.g., endemism of some testate amoebae beyond reasonable doubt (Smith and Wilkinson 2007).

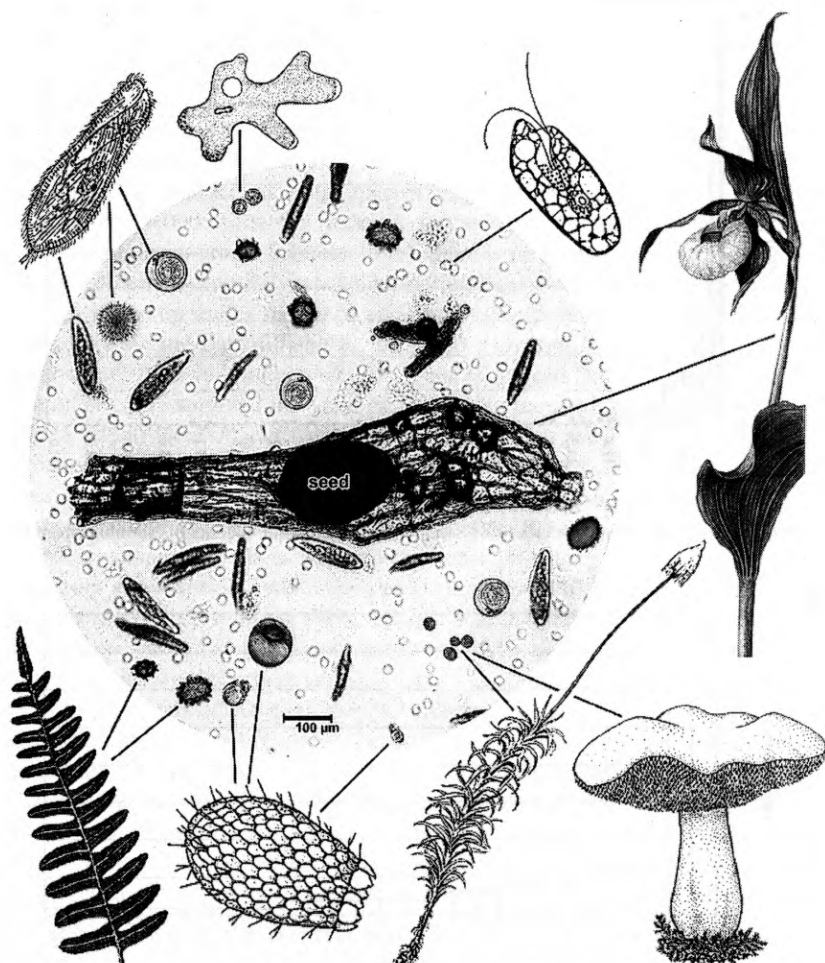


Fig. 3 This figure compares, at about the same magnification, trophic and cystic protists (ciliates, flagellates, naked and testate amoebae) with spores of macrofungi (mushrooms), mosses, ferns, and the minute seed of an orchid (*Vanda caerulescens*). Obviously, all are of minute size and very abundant, for instance, a single *Agaricus campestris* (mushroom) releases 1.6×10^{10} spores within 6 days (Webster 1983), which exceeds the abundance of ciliates in a m^2 of forest soil by several orders of magnitude (Meyer et al. 1989). While nobody denies that mushrooms, mosses, and ferns have biogeographies, protists are widely assumed to be cosmopolitan because their small size and high abundance favour air dispersal, an opinion flawed by this figure. Further, protist cysts lack adaptations for air dispersal, while seeds of many flowering plants have such adaptations, including the orchid seed shown which has wings of large-sized, air-filled cells

Protist species number and distribution: main challenges

The papers in this issue of *Biodiversity and Conservation* leave no doubt on the occurrence of endemic protists, i.e., of species with restricted distribution in spite of suitable habitats in other regions of the earth. We lack solid information on the number of protist species with restricted distribution, and the percentage highly depends on the species concept applied; my estimation of 30% (Table 1, Foissner 2006) of morphologic and/or genetic

and/or molecular endemics is a very crude figure based on some better known groups, such as testate amoebae, ciliates, and diatoms; further, it includes 15% undescribed rare and very rare species which bear the greatest probability for restricted distribution.

The existence of endemic protists evokes the first main question: why did they not spread globally, as the majority of species? Likely, the reasons are manifold: perhaps, many are young species not having sufficient time to disperse globally; others might have specific ecological demands found only in a certain habitat or region; many do not produce stable resting cysts for long range dispersal, for instance, protists from rainforests (Foissner 2006); and others might have evolved in regions not favouring wide dispersal.

The second main challenge is of more general nature, viz., to develop a species concept reconciling morphologic, genetic, and ecological features, as outlined by Weisse in this issue. Although this is a different task (Hey et al. 2003), it should be possible to reach some agreement for practical purposes, such as biodiversity and conservation issues. Further, morphological research has to be intensified greatly because large parts of the earth never have been investigated for, especially, heterotrophic protists, suggesting that more than 50% of their morphological diversity is still undescribed (Foissner 2006; Cotterill et al. in this issue). Likely, this will double or treble the number of species in many groups, such as ciliates and naked amoebae. Thus, genetic, molecular, and ecological features will possibly double or treble this figure again (for an example, see the contribution on ciliates in this issue).

Corliss (2000) estimated about 90,000 extant, free-living described protist species. Applying the figures mentioned above and a synonymy rate of 20%, we might arrive at about 300,000 species, excluding the fungi which probably constitute over a million species (Hawksworth 2001; Taylor et al. 2006).

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