

Past President's Address: Protistan Biogeography: Why All The Fuss?¹

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ABSTRACT. Conflicting hypotheses regarding the distribution of protistan species on our planet have led to rather impassioned arguments in the recent literature, and heated discussions at scientific meetings. Both sides of this debate have mounted seemingly credible arguments for endemism on the one hand, or ubiquitous dispersal of protists on the other. At present, the controversy appears unending, perhaps because it is fueled by a convergence of unresolvable issues involving the enormous phylogenetic breadth of species presently encompassed by the term “protist,” the application of multiple species concepts to these taxa, the inability of extant techniques and technology to plumb the depths of microbial diversity in natural ecosystems, and a lack of knowledge regarding the relationship between dispersal rates and rates of evolution of protists. These issues have made it difficult to erect and test hypotheses concerning the distribution of protists. In the absence of definitive experimental or observational information, preconceived attitudes regarding protistan distributions have dominated the interpretation of the available data. On the positive side, the debate has led to the development and application of new approaches to the study of protistan diversity, and stimulated discussions involving how (and why) we define protistan species.

Key Words. Biogeography, diversity, endemism, protists, species concept.

PROTISTAN biogeography has become a highly controversial topic in recent years. Opposing views have asserted that this highly diverse, predominantly microscopic group of organisms is composed primarily of species that have limited geographical distributions on the one hand, or whose distributions are cosmopolitan on the other. The resulting disagreement has generated some highly polarized attitudes, lively discussions, and a number of publications constructed to support either viewpoint (Fenchel 2005; Finlay 2002; Finlay and Clarke 1999b; Foissner 1999, 2006). These differing views regarding the distribution of protists on our planet have been extrapolated to form far-reaching corollaries related to the overall global diversity of these species. Specifically, it has been proposed that global protistan species diversity is extremely high because most species have limited geographical ranges (Foissner 1999), while supporters of the alternative view contend that total protistan diversity is much lower than that of macroorganisms because most protistan species have global dispersal (Finlay et al. 1996).

There appears to be no easy resolution to this controversy because both factions have mounted ostensibly credible arguments. I offer that this apparently unresolvable issue is a consequence largely of four main interrelated factors: (1) the extremely broad diversity of species that fall within the term “protist,” (2) the use of different (or multiple) species concepts to describe protistan species, (3) the present inability of extant approaches to sufficiently characterize protistan diversity in most natural ecosystems, and (4) a general lack of information on the relationship between rates of dispersal, rates of speciation, and constraints on speciation for protists.

It is not my intent in this article to argue one side or the other of this ongoing debate; in part because both sides may be correct (simply not for the same organisms), and in part because much of the disagreement is semantic and therefore not exceedingly productive. My goal is to provide an overview of a topic that has spun out of perspective during the last several years. I pose questions at the beginning of each of four sections below that provide the context for the comments/opinions in each section. To some degree they are rhetorical but I hope that these questions, and the comments that follow, might encourage researchers on both sides of the debate to consider which parts of their own positions might be uncertain or open for compromise. In doing so, I trust that some

interesting new perspectives and fruitful avenues of research will emerge.

THE ISSUE, AND WHAT'S AT STAKE

The contention that most protistan taxa are globally distributed across our planet is based largely on the generalized, inverse relationship that exists between organismal size and population size, and the relative ease of dispersal for microscopic organisms (Fenchel and Finlay 2003, 2004; Finlay 2002; Finlay and Clarke 1999b; Finlay, Esteban, and Fenchel 2004; Finlay and Fenchel 1999). Microbes can have enormously large population sizes. Fenchel (2005) has estimated that a 1-ha area of a shallow aquatic ecosystem contained as many as 10^{16} protists. Many of the species comprising this gargantuan number would be undetectable to observers using routine methods of microscopy and culture that are presently used in ecological studies. Similarly, 1 km^2 of surface area in a typical oceanic ecosystem may contain 10^{17} protists in the top 100 m of the water column, assuming a conservative estimate of 10^3 protists/ml. These are extraordinary numbers, and extinction of species with such enormous population sizes would be extremely unlikely, especially for taxa that possess cysts or life histories that provide refuge during periods of adverse conditions. The unlikelihood of extinction, coupled with the ability to be easily dispersed (the microbiologist's credo has generally been “everything is everywhere”) has made for a very convincing argument that all protists (or perhaps at least those $< 1 \text{ mm}$ in size) should be cosmopolitan.

The corollary, and important consequence, of extremely large population size and ubiquitous dispersal is that, while “local” species diversity may be quite high, “global” diversity of protists would be expected to be low. Total diversity should be low because endemism does not allow for the evolution of numerous, regionally restricted species (such as we see with many macroorganisms), and local diversity should be high because there is a good possibility that a single sample of an environment will yield much of the total diversity contained within the protists. To support their case, Fenchel and Finlay (2003) have noted the presence of large numbers of cosmopolitan protistan morphospecies in a freshwater and a marine environment (Fig. 1), and they have cited global-scale surveys that have demonstrated a latitudinal gradient in species richness for larger organisms but not for protistan species (Hillebrand and Azovsky 2001).

On the other hand, high levels of endemism among protistan species would imply that global protistan diversity might be extraordinarily high. Foissner (2006) reviewed information indicating restricted distributions for several protistan groups, and promoted the use of “flagship” species (species with conspicuous

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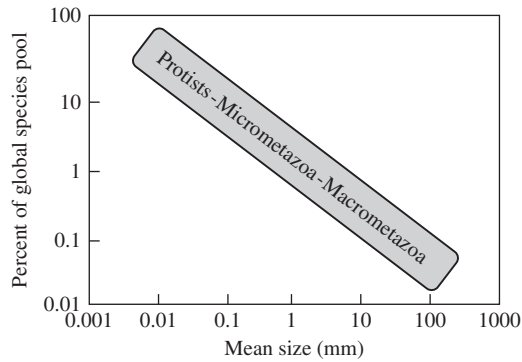


Fig. 1. Are protistan species distributed worldwide, and is total species diversity low? Information derived from Fenchel and Finlay (2004) that summarizes the authors' surveys of Priest Pot, a freshwater pond in the English Lake District and Nivå Bay, an estuarine ecosystem in Denmark. A high percentage of the protistan morphospecies that were observed have been characterized as cosmopolitan species, and this percentage is inversely related to organismal size.

morphologies whose presence/absence can be easily demonstrated in samples) as a means of testing whether protists had restricted or global distributions. While Finlay and Fenchel (1999) estimated that there are approximately 20,000 protistan species, Foissner (1999) estimated that there may be 30,000 species of ciliates alone. Clearly, there are diverging views with significant consequences for our conceptualization of protistan diversity.

Apples and oranges; the enormous taxonomic breadth of protists. (*Why would we expect any generality to apply to all protists?*)

Phylogenetic schemes for protists have varied since their discovery more than three centuries ago, and indeed the landscape here is still highly active and rapidly changing (Burki et al. 2007; Lane and Archibald 2008). One unfortunate bit of this legacy from which we are still emerging as a scientific community is the five

kingdom system of Whittaker (1969) in which all single-celled, eukaryotic organisms were placed into a single Kingdom, the Protista. While that system served scientists well for many years, it is now widely recognized as a poor conceptualization of the evolutionary relationships among eukaryotes. New hypotheses regarding eukaryote evolution have begun to shed light on the relationships among taxa within this diverse group of organisms (Adl et al. 2005) (also, see Fig. 2). Despite the difficulties with the evolutionary implications of "protist," the term remains in common usage and still has a great deal of practical application in ecology and other fields. Yet, the huge taxonomic/phylogenetic breadth of these species greatly complicates the study of "protistan" diversity, ecology, and biogeography (regardless of the species concept that one applies; see next section).

Protistan species span a tremendous range of sizes (<1.0 to >100,000 μm), and comprise a bewildering array of morphologies, life histories, environmental tolerances, and behaviors. Most ecologists and/or taxonomists of multicellular organisms deal with very narrowly defined groups, whether they realize it or not. Most museums have curators that specialize in a phylum of animals or plants, or perhaps even lower taxonomic groupings for particularly speciose groups. Yet, each of these collections constitutes a relatively minor component of the total phylogenetic diversity on the eukaryotic branch of the Tree of Life (shaded boxes in Fig. 2). All other forms of eukaryotic life are encompassed by or include species conforming to the general definition of "protist."

Why, then, would one assume that a single characterization of the distributions of these organisms is sufficient or appropriate? It seems highly unlikely that all protists display ubiquitous dispersal or endemism. A weak relationship between size and dispersal seems undeniable, but is it likely that it is the sole determinant across all protistan taxa? A few protistan taxa have cell volumes that are similar to bacteria (<1 μm^3) while others have biovolumes that are >10⁵ μm^3 . It seems unrealistic to assume the same level of dispersal for organisms spanning such a large size range. It is noteworthy that not even bacteriologists can agree on whether or not bacteria are truly cosmopolitan (Cohan 2002). Interestingly,

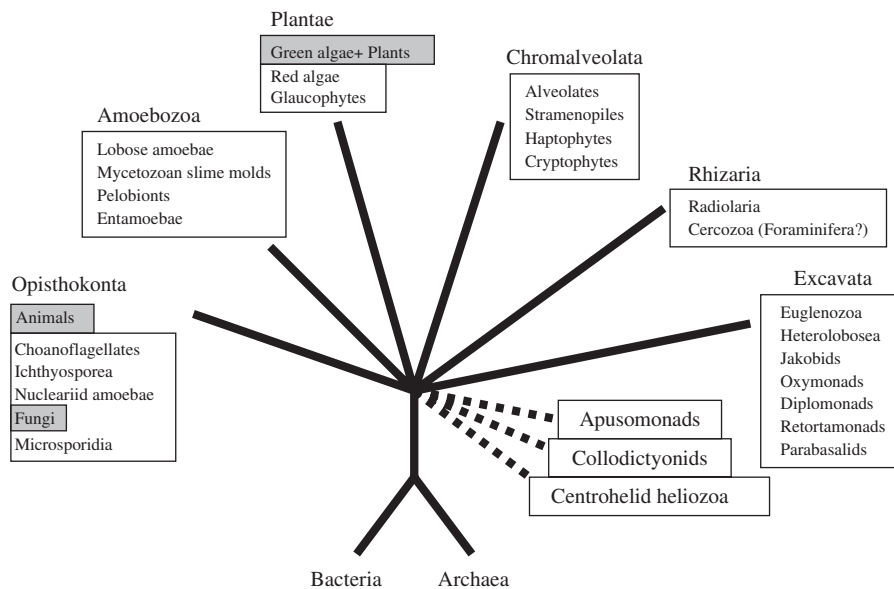


Fig. 2. Protistan phylogenetic breadth is vast. Although a final consensus has not yet been reached regarding the evolutionary relationships among all protistan groups, it is clear that the phylogenetic breadth of single-celled eukaryotes far exceeds that of the multicellular plants and animals. In this figure, adapted from Simpson and Roger (2004), multicellular taxa are indicated by the shaded boxes. Unicellular eukaryotes are indicated by the clear boxes. The enormous breadth of the protists has resulted in the development of different taxonomic schemes for different groups. In turn, the existence of multiple collection, preservation, and processing techniques required for these various taxonomies has greatly complicated ecological studies of these species.

much of the controversy with bacteria has to do with the species concept used to define these microorganisms. This also appears to be the main crux of the matter with protists (see next section).

One potentially useful feature of the tremendous diversity among protists is that these species display a wide range of life histories. Most species reproduce asexually (one possible reason for their vast population sizes and potential cosmopolitan existence) but many different reproductive modes exist. These differing modes may present a mechanism for testing hypotheses regarding global distributions. On a broad scale, one might hypothesize that sexually reproducing taxa would experience different constraints on establishing and maintaining populations on a global scale, and thus different degrees of endemism than species that reproduce asexually. To my knowledge, there has been no systematic comparison of sexual/asexual protistan species with respect to endemism/ubiquity, but such a comparison might yield interesting differences in the global distribution of these taxa. That is, the same diversity that make protists difficult to define as a single group may provide tools to examine some of the fundamental questions regarding their distributions. That is not to say that problems with the species concept for protists will be circumvented, however, and those problems are central to the issue of protistan biogeography.

Protists, and their identity crisis. (*What do arguments of global/endemism distribution of species mean if we can't settle on a species concept?*)

The debate over protistan biogeography during the past few years has evolved for many investigators in the community into a discussion regarding the species concept and the existence of cryptic species within protistan morphospecies. This focus is appropriate because it has been noted that the controversy regarding the distributions of protists is largely an issue related to the species concept (Schlegel and Meisterfeld 2003).

A central tenet of the cosmopolitan hypothesis has been the adherence to the general ideas contained in the Cohesion Species Concept and the Morphological Species Concept (Meglitsch 1954; Templeton 1989). The former defines a species as a group of organisms whose divergence is capped by one or more forces of cohesion. In the case of asexual organisms (encompassing many protists), the cohesive force is natural selection, and the criteria in question are phenotypic morphological traits (hence, the Morphological Species Concept). Indeed, morphological criteria have constituted the “gold standard” for protistan taxonomy for centuries. For fossil protists, morphological features remain essential criteria for species descriptions and identification (Knoll et al. 2006).

Despite the long and fruitful history of the morphological species concept in protistology, morphology alone has been deemed inadequate by many investigators who feel that other features of protists reveal sufficient differences among strains that we must recognize and accept the presence of cryptic species within many morphospecies. Examples include compatible and incompatible mating types within some species of ciliates (Coleman 2001; Nanney 1999), and the existence of ecologically or physiologically distinct groups of morphologically indistinguishable forms of heterotrophic flagellates (Boenigk et al. 2006a, b) or minute phototrophic protists (Fawley, Fawley, and Owen 2005). These findings imply the application of the Biological Species Concept (Mayr 1944), the Ecological Species Concept (Van Valen 1976), or the Evolutionary Species Concept (Simpson 1961). Many researchers working with bacteria have defined “ecotypes” for genetically similar strains of bacteria that show minor physiological differences and typify particular environments or locations (Ward 2006). This falls short of defining “species,” but it captures the ecological significance of differences present among closely related strains of microorganisms. The same terminology has sometimes been applied to protists (Choi and Peters 1992).

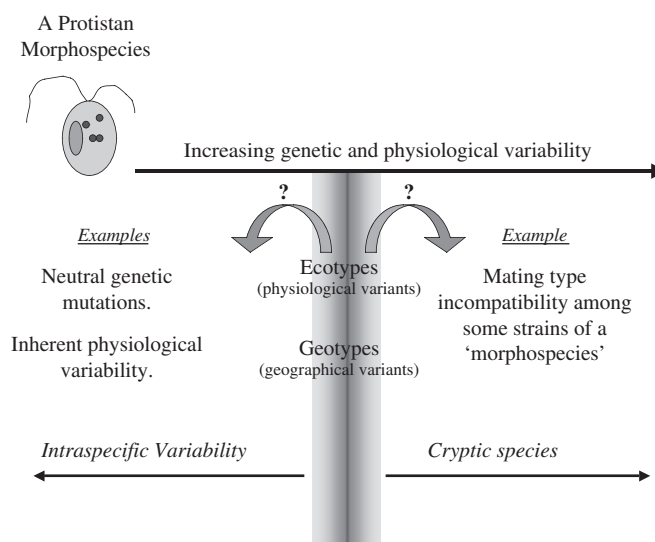


Fig. 3. The morphospecies concept, and the “fuzzy line” that discriminates between species. To many, the morphospecies remains an acceptable species concept, and physiological and genetic variation within a morphospecies is expected and within tolerable limits. To others, the morphospecies harbors significant (and presently unknown) numbers of cryptic species. Opinions vary widely, and consequently opinions regarding total protistan diversity and geographical distributions remain unreconciled.

DNA sequence information has been increasingly applied in recent years to help define microbial taxa. Molecular taxonomies hold great potential but a major impediment to their adoption, as with other species concepts, is establishing the amount of genetic dissimilarity that should be accepted as intra-specific. Rates of evolution for the same gene in different taxonomic groups may vary. Here again, the enormous breadth of the protists creates difficulties. Heterogeneous rates of evolution make the use of any single gene problematic as the “gold standard” for molecular taxonomy across very broad phylogenetic boundaries. A combination of genes may some day prove useful for supporting a purely molecular taxonomy, but sequencing and bioinformatic capabilities have not yet advanced to the point of making that approach realistic.

None of the species concepts described above is foolproof, and none is universally applicable, resulting in proposals that protistan species should be defined based on a combination of morphology, DNA sequences, physiology and ecology (Schlegel and Meisterfeld 2003). This is a formidable task that is taking place at a slow pace (Modeo et al. 2003). As a consequence, drawing the species line between closely related taxa remains quite difficult for many protistan types, and many scientists presently draw that line differently (Fig. 3). While some investigators choose to simply accept that a morphospecies contains substantial intra-species variability, others believe that many morphospecies are composed of multiple entities that should be elevated to species level. Still others might compromise and accept the morphospecies concept yet choose to recognize that strains within a morphospecies may constitute genetically distinct (and presumably ecologically distinct) entities (Dolan 2005). In short, species demarcations are subjective; they are opinion, if not downright arbitrary in some cases. The fact that species distinctions are individual opinions was noted as far back as Darwin in *The Origin of Species*. The important message here is that our inability to resolve the core issue of defining protistan species makes it quite difficult to productively discuss the distribution of these species across broad geographical scales.

Plumbing the depths of community composition: the inadequacy of methodology. (*What do arguments of global*

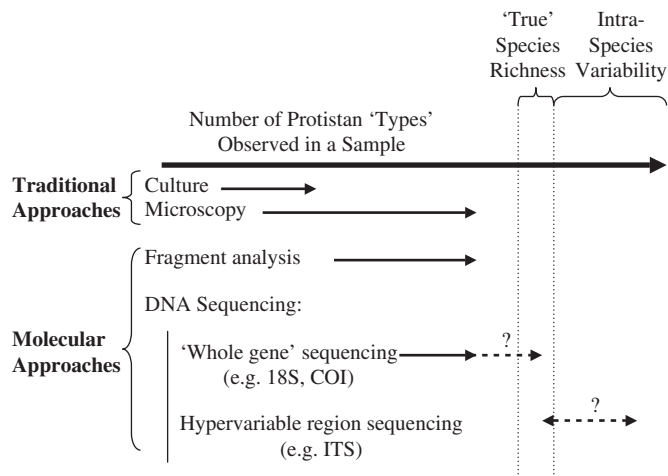


Fig. 4. Different approaches for assessing protistan assemblage composition and species richness in natural ecosystems. Traditional methodologies involving microscopy (light microscopy, electron microscopy) and culture methods provide a very limited view of total protistan diversity. Molecular approaches offer the potential for a much more accurate assessment of total protistan diversity, but are not yet capable of plumbing the depths of microbial diversity when applied on a routine basis (solid vs. dotted lines).

distribution mean if we cannot yet plumb the depths of diversity in any particular environment?

Assessment of the biogeographic patterns of protists, or establishing the absence of certain species in particular environments, presupposes the ability to accurately identify protistan taxa *and* to detect them in natural communities even if they are present at very low abundance. To address the heart of the debate regarding the distributions of protistan taxa, it is not sufficient to simply establish that a taxon is not present at high abundance in a natural community. It is necessary to establish that it is not present at all. That is NOT an easy task. Foissner (2006) has suggested that this can be accomplished for protistan species (flagship species) that should be obvious in a sample if they are present. On the other hand, Finlay et al. (2004) noted that it is problematic to claim endemism simply because flagship species have not been observed. The point is well taken in the case of microorganisms, even conspicuous ones, because sampling is sporadic and sparse no matter how thorough the attempt. Therefore, confirming the *complete* absence of a species from an environment is a formidable task.

A pivotal question then becomes “Do any of our existing methods provide us with certainty that they can establish the presence of truly rare taxa in a given habitat?” The short answer to that question is, unfortunately, not yet (Fig. 4). Species richness of microbial communities is insufficiently sampled by all extant approaches. Traditional approaches of microscopy cannot distinguish many of the morphologically non-descript forms, and culture methods cannot reveal the fastidious ones. DNA-based taxonomy and sequence-based approaches also do not yet provide adequate capacity, but they are on the verge of dramatically altering this situation as sequencing power increases and computational methods improve.

The great potential of molecular techniques to characterize the composition of natural protistan assemblages and to estimate species richness have resulted in their rapid adoption by microbial ecologists, but two significant impediments must be overcome for this information to be useful for addressing questions of protistan diversity and biogeography. First, most approaches are presently unable to assess the many rare taxa that characterize virtually all microbial communities. The inability to enumerate most rare taxa

undermines the accuracy of diversity estimates presently obtained using sequence data (Bent and Forney 2008). In this regard, the use of rarefaction curves and coverage values as indicators of exhaustive sampling of microbial communities must be taken with caution at present. These values have sometimes been interpreted as verifications that sampling has accurately assessed the total species richness of an environment when in fact the approaches are designed to compare richness estimates from different samples for a standardized sampling effort (Hughes and Hellmann 2005). High values can provide a false sense of understanding because the estimates are only valid if the collection method is appropriate for all species. DNA is not extracted with the same effectiveness from all individuals, and not present in equal amounts in all species. Differences in the efficacy of DNA extraction, greatly differing gene copy number among taxa, and variability in the amplification efficiency can and do alter the microbial eukaryotic diversity “perceived” by genetic approaches as presently applied.

The second impediment to using sequence information for assessing protistan diversity and species distributions involves the method employed for converting sequence data into taxonomic information. Once again, the species concept is the problem. Guidelines for reconciling traditional protistan taxonomy with DNA sequence data are rare in the literature, but are necessary as molecular taxonomy gains acceptance within the scientific community (Caron et al., unpublished). The general approach thus far has been to demarcate taxa (operational taxonomic units) by grouping sequences according to some arbitrary value of sequence similarity. However, the specific methods and values employed have varied from study to study, and the specific value chosen for this purpose can dramatically affect the predicted number of taxa in a sample (Fig. 5).

Until these issues are resolved, the reality is that existing molecular methods are able to characterize only a portion of the protistan diversity present in nature. This state-of-the-art of molecular ecology has not gone unnoticed, and it has been noted that these methods presently do not provide much greater resolution for observing protistan diversity than traditional approaches of microscopy and culture (Fenchel 2005). The power of genetic methods will unquestionably improve, however, and are already able to characterize a different component of the community than is possible using traditional methods. For example, Savin et al. (2004) compared morphological and molecular methods (DGGE and cloning/sequencing) to examine the diversity of phytoplankton in the Bay of Fundy. The methods yielded similar levels of diversity but very different taxonomic compositions. The authors concluded that either method captured only a portion of the true diversity. Genetic approaches offer tremendous promise for assessing microbial diversity in the future, but at present they remain largely that . . . potential.

In fairness, molecular approaches have already improved our understanding of the composition of natural protistan assemblages beyond traditional methods of microscopy and culture. Rank abundance curves of phylotype diversity have revealed the presence of an incredibly large number of “rare” taxa in most habitats (Fig. 6). Although we are not yet able to completely characterize all of the forms present, it is reassuring that such methods may be close at hand for bacteria (Sogin et al. 2006) and that, historically, breakthroughs in eukaryote ecology have rapidly followed advances in bacterial ecology (Caron et al., unpublished). Interestingly, the presence of a “rare biosphere” appears to indicate the presence of a large component of the assemblage that may not be ecologically important most of the time but nevertheless remains present. The results of Countway et al. (2005) indicate that at least some of this “rare biosphere” can grow and become dominant in the protistan assemblage following perturbation. In that way, the ecological function of communities may be preserved even though individual species conducting most of these

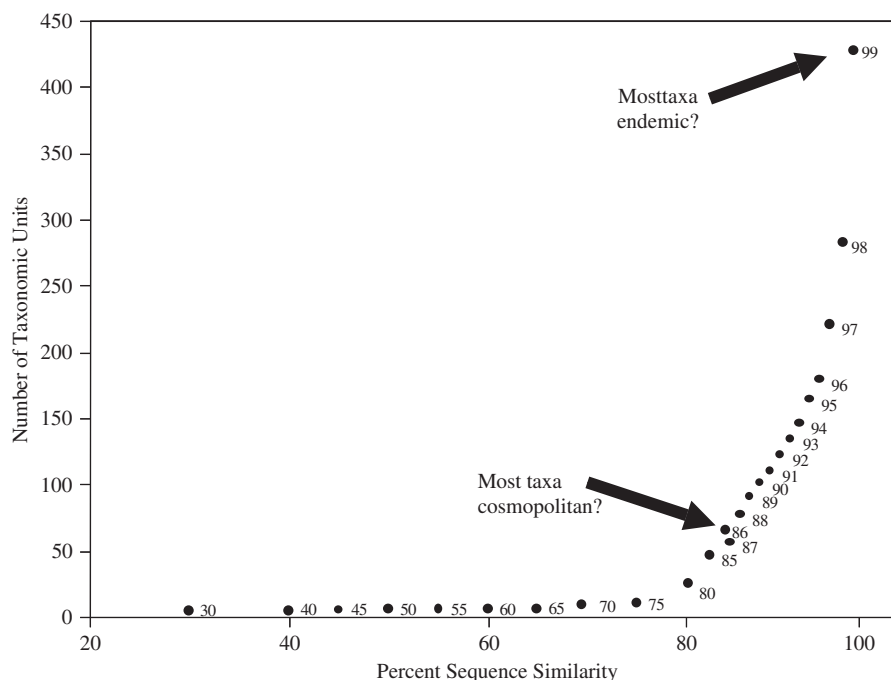


Fig. 5. Consequences of varying the percentage of sequence similarity for establishing molecular operational taxonomic units. This example presents the results for 970 partial 18S sequences from environmental clone libraries obtained from samples collected in the western North Atlantic by Countway et al. (2005).

processes change. Are these results indicative of a ubiquitously dispersed protistan assemblage? The answer is presently unclear because much of the rare biosphere remains undetectable to extant methods.

Some important determinants of protistan biogeography, and what we know about them. (*What constitutes a “habitat” for a protistan species, how effective is dispersal in connecting them, and how do dispersal rates compare to rates of mutation?*)

Finlay et al. (2004) made the distinction between “ubiquity” (which admittedly is a rather difficult term in the real world) and “ubiquitous dispersal,” claiming that most protists have ubiquitous dispersal. They are not necessarily found everywhere because suitable habitats may not be present everywhere, but they should be present in suitable habitats present around the world. Important questions then become, how does one define a suitable habitat? Is that based on chemical/physical data? Is it based on habitat size? How do rates of dispersal among these suitable habitats compare with rates of genetic mutation? What constitutes “significant” genetic mutation? Answers to these and similar questions are essential to evaluating the proposed existence of protistan biogeography. Unfortunately, we actually have very little factual information about most of these determinants. The biogeographies of species are affected by a variety of factors, and these factors interact in complex ways that confound our ability to accurately predict whether we should expect to observe cosmopolitan or endemic distributions of protists across our planet.

When it comes to dispersal, (organismal) size matters, but perhaps not in a simple linear inverse relationship (Fig. 1). It is unclear how effective dispersal mechanisms might be for connecting freshwater and soil ecosystems (atmospheric transfer; migratory birds, etc.). The ocean ostensibly provides a more contiguous environment, and one could postulate that marine protists might exhibit considerably faster rates of dispersal than some terrestrial or freshwater species. However, everything is relative . . . to rates of genetic divergence. We know little of the rates of significant mu-

tation within the protistan genome, and how that compares with rates of the dispersal of protists across the face of the planet. This is a fundamental gap in our knowledge that might help shed light on the validity of the data that have been used to support the endemism hypothesis. This is a topic for which population genetics is ideally suited. Studies have reported genetic differences within protistan morphospecies (Boenigk et al. 2006b; Scheckenbach et al. 2006). These differences are consistent with geographic ranges of taxa in some cases, while in other cases they are not (Katz et al. 2005). Are these genetic differences indicative of cryptic species within morphotypes, or are these differences merely accumulated neutral mutations that have no ecological significance (Fenchel 2005)? In few cases have genetic differences been linked to physiological differences among protistan strains (Ryneron and Armbrust 2004), but this is an area of research that is still young and ripe for progress.

If we accept the Cohesion Species Concept (and its manifestation as the Morphological Species Concept) for protists, then environmental/ecological constraints on species forms are important determinants in maintaining the morphospecies that we see in nature. Morphological variability might not be limitless or continuous if available niches in nature are finite, and natural selection might maintain relatively low protistan species diversity globally. Thus, similar environmental parameters in different regions of the world should harbor the same protistan morphospecies. This expectation is consistent with claims of the ubiquitous distributions for some protists (Finlay and Clarke 1999a).

Yet, the existence of endemic macroorganisms worldwide makes it hard to imagine that some degree of endemism among microorganisms does not exist (setting aside the problem of the species concept for a moment). We recognize as fact that many macroscopic species have restricted geographical distributions (i.e. biogeographies). Protists live and interact with these endemic species in complex communities. Proponents of the cosmopolitan hypothesis must either contend that the same ecological niches for

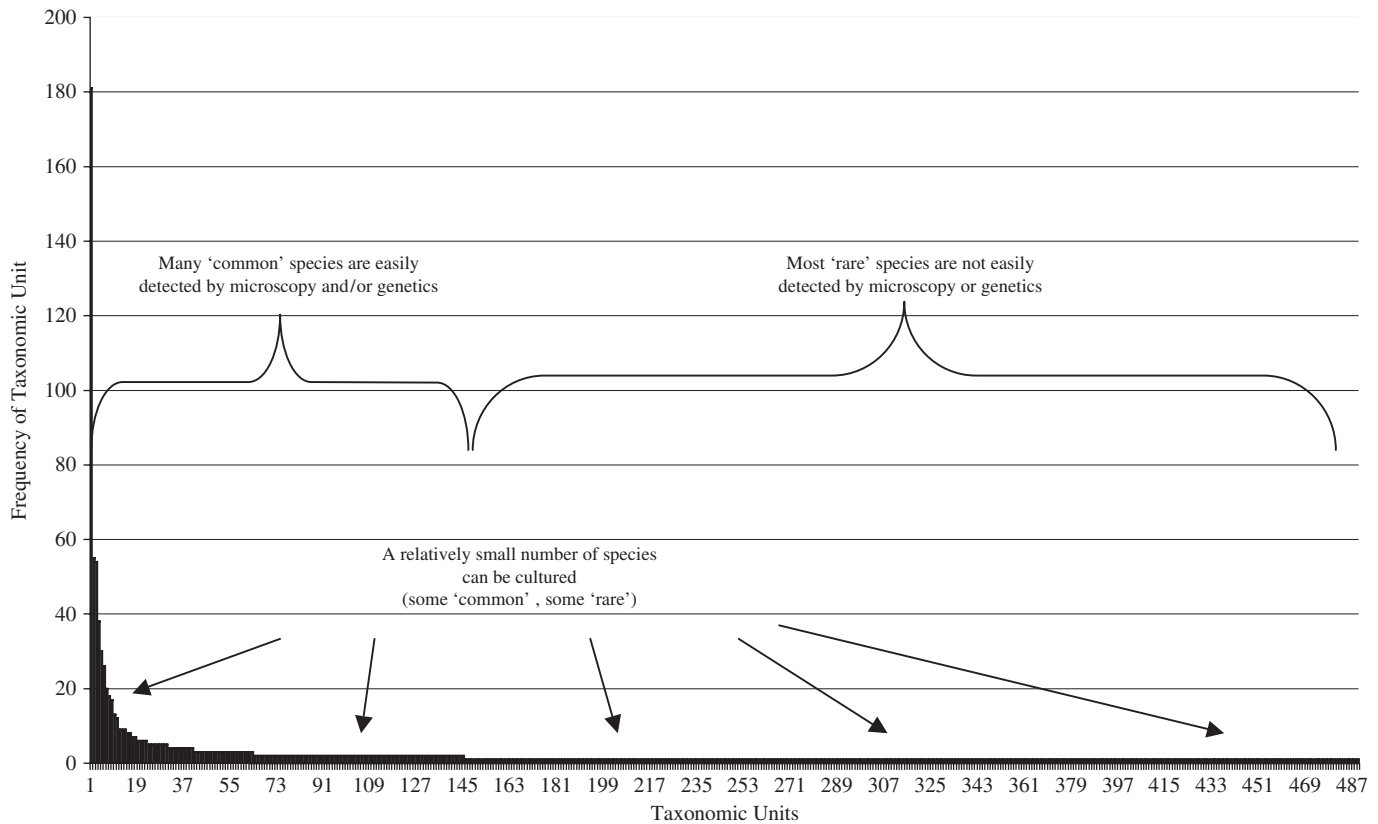


Fig. 6. “Taxon-level” calling of sequence-based, operational taxonomic units from $\approx 1,200$ partial 18S sequences from six depths, collected on a single date from the San Pedro Channel, eastern North Pacific. A total of 488 OTUs were observed based on 95% similarity in an automated pairwise alignment program (Caron et al., unpublished data).

protists exist among endemic macroscopic species that can be filled by the same set of cosmopolitan protists, or accept the possibility that unique protistan taxa may exist that fill niches that are specific to each community of endemic macroorganisms. It is even conceivable that genetically and physiologically distinct protists possessing similar morphologies might co-exist with endemic macroorganisms from different regions. Gross morphological similarities could be a result of convergent evolution owing to the existence of “similar” niches in different regions with analogous endemic species (e.g. marsupial mammals of Australia and eutherian mammals of other continents). This situation is consistent with the prevalence of convergent morphologies among some groups of physiologically diverse and phylogenetically distant phytoplankton taxa (Potter et al. 1997). Most ecologists would characterize the latter protistan types as different species, despite gross similarities in their morphologies.

Unfortunately, we have little or no understanding of the fundamental and realized niches of most protistan species at this time, and therefore evaluating the opposing hypotheses noted in the two previous paragraphs is not yet possible. It seems probable that some of both possibilities have occurred in evolutionary history. In order to exploit the huge amount of genetic information that is now emerging, and will continue to accumulate in the future, there is presently a critical need to greatly expand our understanding of the ecological niches of protists, and to establish the relationship between that genetic information and their morphology, behavior and physiology. This is an area where additional research might greatly improve our conceptualization of the species concept for protists, and thereby impact the debate regarding the global distribution of these taxa.

SEMANTICS, PRECONCEPTIONS, AND FINDING COMMON GROUND

We are faced with the situation that some protistologists take exception to the idea that microbes might have discrete distributions (real biogeographic patterns), while others consider it a paradigm. However, there is a reasonable amount of confusion regarding terminology that clouds the debate regarding whether or not protistan species (or other microbes) possess ubiquitous distributions. Many researchers expect that the potential for ubiquity presupposes that every species will be found everywhere across the planet, but species can be discontinuous in their distributions and still be globally distributed. The confusion arises because, when some researchers discuss the biogeography of microbes, they are referring to the (locally) discontinuous distributions of (globally distributed) microbial species (Ramette and Tiedje 2006). Notwithstanding this semantic confusion, claims of true endemism have been common for protistan as well as bacterial taxa (Foissner 2006; Papke et al. 2003).

A significant component of the controversy seems to stem from preconceived notions of endemism or ubiquity, and often the same type of data (or even the same data set) has been used to support either argument. For example, recent molecular diversity studies have been used to point out the presence of apparently endemic phylotypes as well as ubiquitously distributed ones. This selective use of information seems oddly common in the endemism vs. ubiquity debate, and it is undoubtedly fostered by the inadequacy of the data sets that are presently available, and the application of different species concepts or species-level distinctions. This is not to say that some compromise positions have not been voiced. A

few studies have proposed that some protistan species appear to be globally distributed while others exhibit limited geographical distributions (Petz et al. 2007; Schlegel and Meisterfeld 2003). One study of ciliate distributions in the Arctic and Antarctic reported that most limnetic species were not ubiquitously distributed; while 13% were common to collection sites in both locales, many appeared to be unique (i.e. endemic) (Petz et al. 2007). Is this intermediate position so outlandish, or is it simply less pleasing that nature is messy?

The bottom line seems to be that the limits of geographical distributions of protists, if they exist, are very difficult to define. If claims of endemism are going to stand the test of time, they need to be substantiated with evidence that “endemic” species are truly absent outside their geographical ranges (not just “undetectable” by extant methods). That is a difficult task for most taxa, although there are some exceptions. On the other hand, it is very easy to argue that species are ubiquitously distributed if one uses an expansive definition of the term “species.” If claims of ubiquity are to be accepted, there is a need to clearly define (as a community) the characters by which these taxa are defined and, consequently, the degree of variability that is considered intraspecific variability. As we move (hopefully) towards a resolution to this debate, we may find that there was never as much controversy as there appears to be at present. I expect that one important outcome will be that we will have gained a much better understanding of the relationships between morphology, genetics, physiology, and the ecological niches of protists. We will also learn much regarding the structure of protistan assemblages, how they function, and how they respond to environmental change.

As a protistan ecologist attempting to summarize the sides of this debate, I try to take heart in the projected “victory” of either side. If protists exhibit a high degree of endemism, I am fascinated by the possibility that protistan diversity might be almost limitless. It is always rewarding and exciting to observe a new taxon through the microscope, or isolate and culture a species with unique physiological/ecological abilities. On the other hand, if protistan species are globally distributed and species richness is limited, then some day I might actually be able to survey all of the species that are present in nature, and do it in my backyard. Sarcasm aside, it is highly improbable that this debate will find an easy resolution, in large part because it is a debate that methodology cannot presently address, and ultimately based on species distinctions that are a matter of opinion; opinions that may always differ.

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