

Global Dispersal of Free-Living Microbial Eukaryote Species

Bland J. Finlay

The abundance of individuals in microbial species is so large that dispersal is rarely (if ever) restricted by geographical barriers. This "ubiquitous" dispersal requires an alternative view of the scale and dynamics of biodiversity at the microbial level, wherein global species number is relatively low and local species richness is always sufficient to drive ecosystem functions.

During the great age of natural history exploration in the 19th century, it became abundantly clear that many animal species—especially the larger ones—had restricted geographical distributions. In many cases, isolation had apparently led to speciation, resulting for example in distinctive island faunas (1). A rather different picture was provided by the small band of traveling naturalists who were equipped with microscopes. Most hoped to discover new and exotic species of microbial eukaryotes (e.g., protozoa, diatoms, and other microalgae), but their hopes were dashed by the lack of novelty they found. As early as 1887, the microscopist W. H. Maskell conceded that the ciliated protozoa living in the fresh waters of New Zealand were basically identical to those known from Europe (2). At around this time, similar ideas also began to appear with respect to the prokaryotes (bacteria). Beijerinck's pioneering use of enrichment culture techniques showed that diverse types of bacteria could be cultured from almost any type of natural material (3), and species recorded from a particular habitat type located in geographically distant places were usually similar if not identical to each other.

Traces of Ubiquitous Eukaryotes

Recent evidence indicates that these ideas can be extended to the microbial eukaryotes. There is, for example, no evidence that flagellated protozoan morphospecies have biogeographies (4)—communities from adjacent sites are not more similar to each other than they are to those from more distant sites. The same flagellate genotype has been isolated from a shallow inland fjord in Denmark and from hydrothermal vents in the Pacific (5). The same planktonic foraminiferan morphospecies are common to both Arctic and Antarctic waters, and some of these are also genetically identical (6). All 86 freshwater ciliated protozoan morphospecies identified from a volcanic crater lake in Australia in the late 1990s were already known from Northern Europe by the mid-1930s (7, 8).

There are strong indications that protozoa

(Fig. 1) and other microbial eukaryotes in general do not have biogeographies, and one obvious explanation is that they are simply so abundant that continuous large-scale dispersal sustains their global distribution. The local abundance of microbial eukaryote species is, indeed, impressively large. An average-sized protozoon with a mass of about 1 ng typically has an areal abundance roughly 12 orders of magnitude greater than that of an average-sized mammal (Fig. 2A), so sheer weight of numbers might be expected to drive large-scale dispersal for purely statistical reasons. When we consider the many forces in the natural environment that must drive the dispersal of small organisms (e.g., hurricanes, global oceanic circulation, labyrinthine groundwater networks, damp fur and feathers), it is not surprising that some spectacular examples have been recorded by explorer-naturalists. While the *Beagle* was sailing in oceanic waters of the tropical Atlantic, Darwin (9) scraped from the mast and sails a fine layer of dust that was rich in freshwater

diatoms. These had been deposited by the combined agency of a tornado and the Harmattan blowing from West Africa.

Local/Global Species Ratios

Doubtless, most of these diatoms were dead by the time they were recovered, but many microbial species can exist for long periods in states such as resting cysts or spores. For example, when a small sample of sediment was collected from a freshwater pond and examined microscopically, 20 ciliate species were detected and identified, but after a variety of enrichment techniques were used over a period of 100 days, the species number had risen to 137 (10), indicating that the "seedbank" of species was very large.

If ubiquitous dispersal is typical of most (if not all) microbial eukaryotes, we would expect relatively low global species richness. This appears to be true for one of the best studied groups, the free-living ciliates [~3000 species (11)], and independent estimates place the species richness of all free-living protozoa somewhere in the range of 10,000 to 20,000 (12, 13). These are relatively small numbers compared with 5 million species of insects (14). The main difference, of course, is that many insect species have geographically restricted ranges, and similar niches located in geographically isolated regions of the world tend to be occupied by



Fig. 1. A small sample from the variety of free-living protozoan species, drawn to scale next to a pinhead. Virtually all species fall within the size range 0.002 to 2 mm.

Centre for Ecology and Hydrology (Windermere), Ferry House, Ambleside, Cumbria LA22 0LP, UK. E-mail: bjf@ceh.ac.uk

dissimilar species, which in many cases evolved in these regions. We can expect the local/global species ratio to be significantly higher for microbial eukaryotes than it is for larger animals, and this too appears to be the case (15). Whereas the numbers of species of bivalves and gastropods living in the 2-hectare semi-enclosed Nivå Bay (Denmark) represent <0.1% of the global marine totals, the number of ciliate species there represents more than 10% of the global marine total—a figure that continues to increase with current intensive studies.

The proportion of the global species number that can be found in a local area is partly a function of sampling effort. In one of the most

intensive recent efforts (>700 hours of observation with an electron microscope), 80% of the global species total in the flagellate genus *Paraphysomonas* were found in <0.1 cm² of sediment from a freshwater pond in England (16). High local/global species ratios will also produce relatively flat species-area curves, distinguishing them from animal groups with locally restricted species, such as the insects (Fig. 2B).

If there is little support for the idea that microbial eukaryote species are geographically restricted, the existence of “endemic” microbial species becomes questionable (17)—a conclusion that is supported by evidence that additional sampling effort tends to deprive microbial

species of their endemic status (18–20). In any event, the virtual impossibility of disproving the existence of endemic species elsewhere in the biosphere probably makes the argument for endemic microbial eukaryotes untenable.

Random Dispersal

We expect the abundance of individuals within a species at neighboring locations to be correlated because of the “stream of migrants” (21). For larger organisms, this correlation tends to break down at large spatial scales, but for microbial eukaryotes with high dispersal rates, species maintain consistent patterns of abundance or rarity on a global scale (22) (Fig. 3A). Microbial eukaryotes are probably dispersed by forces that are essentially random, implying that the primary spatial distributions should also be random. This is not usually obvious, especially when the randomness is masked by subsequent population growth in nonrandom spatial niches. But for those species that are dispersed to places where there is little probability of population growth (e.g., a soil type for which a species is ill adapted), the spatial distribution of the species should remain close to random. The signature of this randomness has recently been detected (22) (Fig. 3B).

As the fundamental driver of random dispersal is high absolute abundance, and as organism size and abundance are inversely related (Fig. 2A), there must be some size range where ubiquitous dispersal becomes less likely and where species are more likely to be geographically restricted (Fig. 4). The organism size range where this change occurs is generally believed to be about 1 to 10 mm (23, 24), but no one really knows, and a considerable international effort (25) is currently directed at pinning it down.

Cryptic Species

The morphospecies is a particularly useful species concept for the protozoa because of the strong link between body form [particularly the

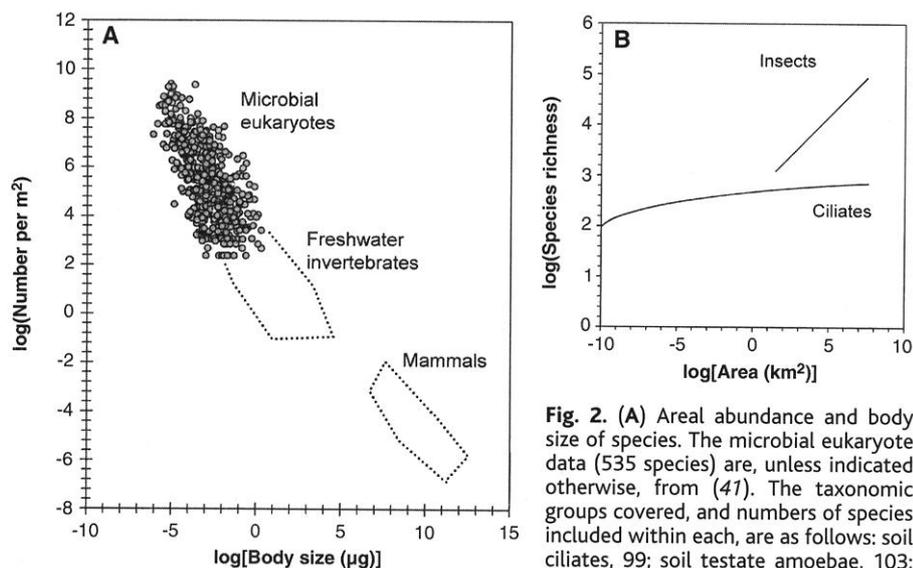
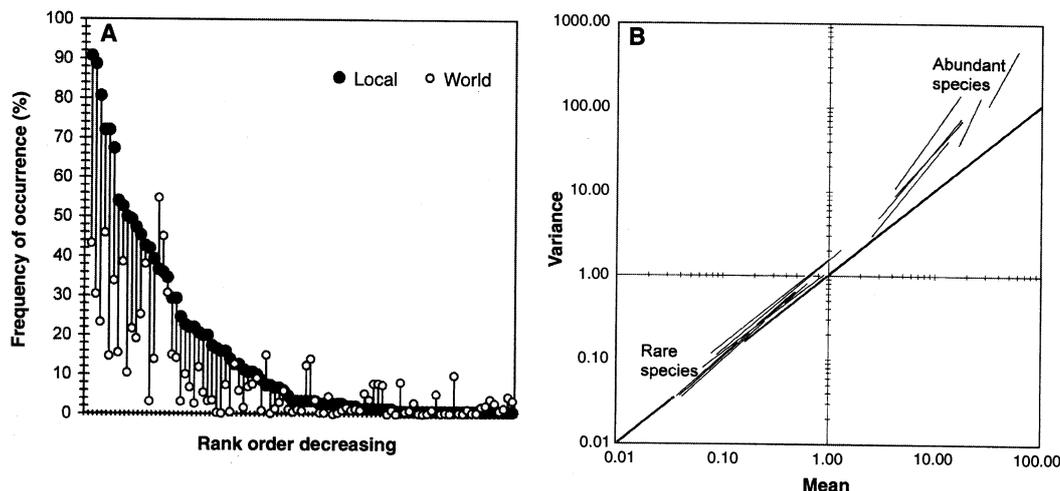


Fig. 2. (A) Areal abundance and body size of species. The microbial eukaryote data (535 species) are, unless indicated otherwise, from (47). The taxonomic groups covered, and numbers of species included within each, are as follows: soil ciliates, 99; soil testate amoebae, 103; freshwater ciliates, 113; freshwater

Paraphysomonas, 32; soil flagellates, 5; soil naked amoebae, 17 (42); deep-sea foraminifera, 3; marine benthic ciliates, 104; freshwater naked amoebae, 29 (43); brackish-water flagellates, 3; epipelagic freshwater algae, 27 (44). The data box for freshwater invertebrates is taken from (45) and that for mammals from (46). (B) Species-area curves. The relatively flat curve for ciliates is based on data in (47). The steeper slope for insects is based on data in (14). One general equation relating the cumulative increase in species number with increasing area is $S = cA^z$, where S is number of species, A is area, and c and z are constants. Here, the slope z takes values of 0.043 and 0.31 for ciliates and insects, respectively.

Fig. 3. (A) Frequency of detection of 95 ciliate species in 150 soil samples from a 1-hectare upland grassland in Scotland, and of the same species in 606 soil samples collected worldwide. Spearman's rank correlation coefficient indicates that the level of agreement between the local and global data sets is highly significant ($P < 0.001$). [Adapted from (22)] (B) Spatial distributions of six rare and six abundant species of testate amoebae living in soil. Each line is the regression through six data points for a species. The longer thick line represents the equivalence of variance and mean (= random distribution). The abundant species have aggregated distributions, but the spatial distributions of the rare species are very close to that of randomness. [Adapted from (22)]



structure of the feeding apparatus (26)] and the way the protozoan functions in the natural environment (12). But morphospecies may hide layers of variation of different types, including clonal or sexual lifestyles (or a combination of the two). In sexual populations, periodic sex occurs between individuals in closed gene pools known as sibling species (27). Different sibling species may be genetically extremely divergent. Others may be genetically identical to each other [e.g., the ciliate *Tetrahymena americanis* harbors eight sibling species, each with an identical sequence of 190 bases in a variable region of the 23S rRNA (27)], so in some ciliates at least, genetic isolation and genetic divergence are not correlated.

It is possible that different, morphologically indistinguishable sibling species carry unique phenotypic traits that enable specialized exploitation of resources within their natural habitat, but there is no conclusive evidence supporting this. One example could have been provided by the three genotypes discovered (28) within the foraminiferan morphospecies *Orbulina universa*. Each genotype appeared to be adapted to specific environmental conditions in the ocean, but upon closer examination by scanning electron microscopy, it was discovered that the genotypes could actually be distinguished according to morphological features. Even if it is discovered that they do fill different ecological niches, recall that individual sibling species can have very wide geographical distributions, and isolates from various parts of the world have been shown to be capable of mating with each other (29, 30).

Morphospecies might also harbor large numbers of physiological species that conceivably could have disjunct distributions, but this is unlikely. The remarkable ability of microbial eukaryotes to tolerate or adapt to very wide

ranges of ecologically important factors such as temperature and salinity (31) indicates that the number of physiological "species" lying within morphospecies may not be great. Tom Fenchel (32) has recently isolated a marine *Paraphysomonas* that grows well in fresh water, and an isolate of the ciliate *Uronema* from the high Arctic could be adapted to grow at 37°C. Local adaptation in combination with ubiquitous dispersal will increase the probability of finding the same morphospecies, sibling species, or "physiological species" in the same suitable habitat type, wherever that habitat exists worldwide (18, 33, 34).

Conclusions

First, free-living microbial eukaryotes, all of which have body sizes less than about 2 mm, are probably sufficiently abundant to have worldwide distribution. And as prokaryotes are much smaller and several orders of magnitude more abundant (35, 36), they are even less likely than microbial eukaryotes to be restricted by geographical barriers (37). This view is supported by analyses of recombination rates in the natural environment indicating very high migration rates [e.g., intercontinental exchange of viable bacterial cells on time scales similar to bacterial generation time (38)].

Second, the species richness that constitutes the microbial "seedbank" of any recognizable ecosystem is large, and probably a significant proportion of global diversity. This implies that microbially mediated ecosystem functions will never be compromised by lack of microbial diversity (39), and this appears to be the case so long as the "ecosystem" remains within the physicochemical limits of microbial life.

Finally, the fundamental characteristics of biodiversity at the microbial level (astronomical abundance of individuals within species populations, potentially very short generation times, high dispersal rates, low speciation rates, and relatively flat species-area curves) differ markedly from those of macroscopic organisms, and one might have reservations about inserting such alien organisms into any of the contemporary neutral theories of biodiversity and biogeography [e.g., (40)]. But microbes merely provide extreme values for the parameters on which these theories are based, and they may even have something to offer—particularly in testing how far the theoretical framework can be stretched while retaining the capacity to predict microbial species richness and relative species abundance.

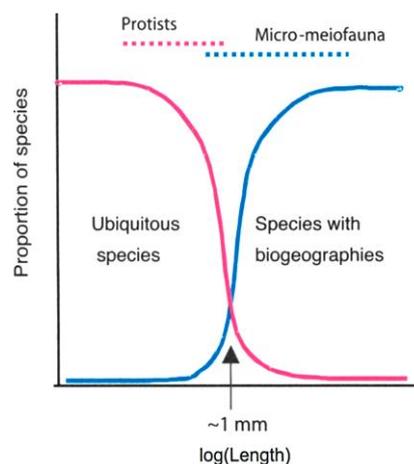


Fig. 4. Large mammal species obviously have biogeographies, whereas microbial species do not. Shown here is a hypothetical model of the ubiquity-biogeography transition, which is believed to be located in the species size range 1 to 10 mm. The real slopes of the "ubiquity" and "biogeography" curves are not yet known.

References and Notes

- S. Anderson, *Q. Rev. Biol.* **69**, 451 (1994).
- W. M. Maskell, *Trans. N.Z. Inst.* **20**, 3 (1887).
- C. B. van Niel, in *Martinus Willem Beijerinck, His Life and Work*, G. van Iterson, L. E. Dooren de Jong, A. J. Kluyver, Eds. (Science Tech., Madison, WI, 1983), foreword.
- D. J. Patterson, W. J. Lee, in *The Flagellates*, B. S. C. Leadbeater, J. C. Green, Eds. (Taylor & Francis, London, 2000), pp. 269–287.
- M. S. Atkins, A. P. Teske, O. R. Anderson, *J. Euk. Microbiol.* **47**, 400 (2000).
- K. F. Darling et al., *Nature* **405**, 43 (2000).
- B. J. Finlay, G. F. Esteban, J. L. Olmo, P. A. Tyler, *Ecography* **22**, 138 (1999).
- G. F. Esteban, B. J. Finlay, J. L. Olmo, P. A. Tyler, *J. Nat. Hist.* **34**, 159 (2000).
- C. Darwin, *Proc. Geol. Soc. London* **2**, 26 (1846).
- T. Fenchel, G. F. Esteban, B. J. Finlay, *Oikos* **80**, 220 (1997).
- B. J. Finlay, J. O. Corliss, G. Esteban, T. Fenchel, *Q. Rev. Biol.* **71**, 221 (1996).
- B. J. Finlay, in *Encyclopedia of Biodiversity*, S. Levin, Ed. (Academic Press, San Diego, CA, 2001), vol. 4, pp. 901–915.
- J. O. Corliss, in *Nature and Human Society: The Quest for a Sustainable World*, P. H. Raven, T. Williams, Eds. (National Academy Press, Washington, DC, 1999), pp. 130–155.
- K. J. Gaston, *Funct. Ecol.* **6**, 243 (1992).
- T. Fenchel, *Oikos* **68**, 375 (1993).
- B. J. Finlay, K. J. Clarke, *Nature* **400**, 828 (1999).
- B. J. Finlay, T. Fenchel, *Protist* **150**, 229 (1999).
- G. F. Esteban, B. J. Finlay, N. Charubhun, B. Charubhun, *J. Zool. London* **255**, 139 (2001).
- W. Foissner, *Protist* **150**, 363 (2001).
- J. Kristiansen, *Nova Hedwigia* **122**, 23 (2001).
- G. Bell, *Science* **293**, 2413 (2001).
- B. J. Finlay, G. F. Esteban, K. J. Clarke, J. L. Olmo, *Protist* **152**, 355 (2001).
- J. H. Lawton, *Oikos* **81**, 3 (1998).
- R. M. May, *Philos. Trans. R. Soc. London Ser. B* **330**, 293 (1990).
- Natural Environment Research Council (www.nerc.ac.uk/funding/thematics/mfmb/abstracts2.shtml).
- T. Fenchel, *Prog. Protistol.* **1**, 65 (1986).
- D. L. Nanney, in *Species: New Interdisciplinary Essays*, R. W. Wilson, Ed. (MIT Press, Cambridge, MA, 1999), pp. 93–118.
- C. de Vargas et al., *Proc. Natl. Acad. Sci. U.S.A.* **96**, 2864 (1999).
- T. Stoeck, E. Przybos, H. J. Schmidt, *Eur. J. Protistol.* **34**, 348 (1998).
- A. W. Coleman, A. Suarez, L. J. Goff, *J. Phycol.* **30**, 80 (1994).
- L. E. Noland, M. Goidics, in *Research in Protozoology*, T. T. Chen, Ed. (Pergamon, Oxford, 1967), vol. 2, chap. 4.
- T. Fenchel, personal communication.
- J. Kusch, *Protist* **149**, 147 (1998).
- N. Bowers, T. T. Kroll, J. R. Pratt, *Eur. J. Protistol.* **34**, 341 (1998).
- U.-G. Berninger, B. J. Finlay, P. Kuuppo-Leinikki, *Limnol. Oceanogr.* **36**, 139 (1991).
- T. Fenchel, *Annu. Rev. Ecol. Syst.* **19**, 19 (1988).
- _____, *Philos. Trans. R. Soc. London Ser. B* **343**, 51 (1994).
- M. S. Roberts, F. M. Cohan, *Evolution* **49**, 1081 (1995).
- B. J. Finlay, S. C. Maberly, J. I. Cooper, *Oikos* **80**, 209 (1997).
- S. P. Hubbell, *The Unified Neutral Theory of Biodiversity and Biogeography*, vol. 32 of *Princeton Monographs in Population Biology* (Princeton Univ. Press, Princeton, NJ, 2001).
- B. J. Finlay, unpublished data.
- P. J. Bischoff, O. R. Anderson, *Acta Protozool.* **37**, 17 (1998).
- O. R. Anderson, *J. Euk. Microbiol.* **44**, 393 (1997).
- C. M. Happey-Wood, *Hydrobiologia* **161**, 99 (1988).
- P. E. Schmid, M. Tokeshi, J. M. Schmid-Araya, *Science* **289**, 1557 (2000).
- J. Damuth, *Nature* **290**, 699 (1981).
- B. J. Finlay, G. F. Esteban, T. Fenchel, *Protist* **149**, 29 (1998).
- I thank A. Gooday, T. Fenchel, K. Vickerman, S. Brown, and K. J. Clarke for providing unpublished data for areal abundance of species. Supported by Natural Environment Research Council (UK) grants GST 2130 (Soil Biodiversity Thematic Programme) and NER/T/S/2000/01351 (Marine and Freshwater Microbial Biodiversity Thematic Programme).