The Ubiquity of Small Species: Patterns of Local and Global Diversity

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Small organisms (less than 1 millimeter in length) tend to have a cosmopolitan distribution. This is a consequence of huge absolute population sizes rather than any inherent properties of particular taxonomic groups. At the local scale, the diversity of small species exceeds that of larger organisms, but at the global scale this relation is reversed, because endemism is largely responsible for the species richness of large organisms. For small organisms, the relationship between species and area is flat, and a latitudinal diversity gradient is absent or weak. These patterns are explained by some of the assumptions underlying the unified neutral community model.

Keywords: biodiversity, microorganisms, meiofauna, protists, unified neutral community model

Almost a century ago, the Dutch microbiologist M. W. Beijerinck observed that particular species of bacteria occur anywhere on Earth's surface, provided their environmental requirements are met (Brock 1961). That is, habitat properties alone are needed to explain the presence of a given microbe, and historical factors are irrelevant. This is in contrast to macroscopic animals and plants, whose evolutionary history contributes to their present-day distribution: Radiation of particular taxonomic groups within the confines of particular continents, lakes, river systems, or oceanic islands, along with extinction episodes, results in disjunct distribution patterns. Studies have confirmed the ubiquitous distribution of bacteria at the genetic level (e.g., Hagström et al. 2000), although genetic differentiation of extreme thermophilic bacteria collected from mutually remote geothermal sites has recently been demonstrated (Whitaker et al. 2003). The cosmopolitan distribution of eukaryotic microbial species, or protists (protozoa and protophytes), was also suggested around the turn of the last century by Vladimir Schewiakoff (Fokin 2000). This view has since been taken for granted by most (if not all; see Foissner 1999) taxonomic experts on these organisms, even though some protist species are actually confined to particular climatic regions of Earth. Gislén (1940), in a survey of the fauna of Sweden, noted that in spite of that country's limited area and cool climate, it hosts an unexpectedly large fraction of the global pool of small animals. He suggested that the absence of migration barriers may explain this phenomenon. The wide or even cosmopolitan distribution of marine meiofauna (metazoans ranging from less than 1 millimeter [mm] to 2 mm long, such as nematodes and rotifers) has previously been considered a "paradox" because these organisms typically do not have a planktonic larval stage (Giere 1993).

May (1988) observed that most terrestrial animal species seem to measure approximately 1 centimeter (cm) and that below this size range, the numbers of described animal species decline rapidly with decreasing body size. This intuitively unexpected result could perhaps be attributed to a poorer taxonomic resolution for small organisms and to the fact that many of them still await discovery. Fenchel (1993) showed a similar relationship between body size and number of species for aquatic organisms, arguing that the phenomenon is real and may be explained by the cosmopolitan distribution of the smallest organisms. Since then we have tried to document these ideas and their implications with respect to different groups of protists (Finlay 2002, Finlay and Fenchel 2004). Most recently, we attempted to record all microscopically distinctive eukaryotic species within a 2-hectare (ha) shallow marine locality and in a eutrophic 1-ha pond. Next, through a systematic literature search, we recorded the global distribution of all observed species. In this way, we attempted to quantify the relation between body size and distribution range of aquatic organisms. We are supplementing these attempts with data on gene sequences and on physiological properties of protist isolates from different continents and climates. Together, the results support recent ideas on factors controlling the composition and diversity of biotic communities.

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Body size and species distribution: The underlying idea

The composition and diversity of a local biotic community depend primarily on the immigration and extinction of species populations (MacArthur and Wilson 1967), in addition to interspecific interactions such as competition and predation. The ability to disperse depends on many factors that may be specific to particular groups of organisms. Among microbes, some species form desiccation-resistant endospores or cysts that can be transported widely through the atmosphere. It has been calculated that some 10^{18} viable bacteria are thus transported between continents annually, but for many other microbes, desiccation is synonymous with instant death. The abundance of organisms is also important. As a crude generalization, the density of species populations is inversely proportional to body volume. One milliliter (mL) of lake water or seawater contains approximately 10^6 bacteria, 10^3 protists, and perhaps 10 zooplankton animals. In sediments, these numbers may be multiplied by a factor of 100: A pond 1 ha in area and 10 meters (m) deep will host perhaps 10^{18} bacteria, 10^{16} protists, and 10^{11} small animals. Thus, without inferring any particular high per capita ability for dispersal, unlikely events (such as transport on the feet of waterfowl to other lakes) will ensure conveyance of small species from place to place.

Another consequence of huge population sizes is that local extinction rarely, if ever, takes place. Declining population sizes caused by biotic interactions such as competition asymptotically approach zero, and eventual extinction depends on stochastic events. Therefore, declining population sizes will rarely lead to the total demise of populations that were initially very large. There will always be a pool of undetected microbes in these populations; they may not thrive or multiply at a given time and place, but some will survive long enough for immigration to secure a permanent presence. It should also be noted that a "rare" microbial species, with perhaps a total of 10^7 individuals in the aforementioned pond, is unlikely ever to be detected. This explains the observation that bacterial species can be isolated from habitats where they presumably do not belong, as in the case of obligate thermophilic bacteria recovered from cold seawater far from any site where they could thrive (Isaksen et al. 1994).

Fenchel and colleagues (1997) counted the number of ciliates in the sediment beneath 1 cm^2 of pond sediment and found approximately 1000 individuals representing 20 species. Subsamples of sediment collected immediately adjacent to the first sample were then exposed to different treatments (adding different potential food items, inoculations at different oxygen tensions, desiccation and subsequent rewetting, and other factors). Over the following weeks, this yielded another 110 species. The 130 species thus recorded beneath a few square centimeters of sediment surface corresponded to about 50 percent of all species recorded from the pond and about 8 percent of all named freshwater ciliates. Similarly, Persson (2002) was able to recover about 25 percent of all recorded plankton dinoflagellates and diatoms ever recorded from the seas along the Swedish west coast (Skagerrak and Kattegat) from a total of 100 mL of sediment samples. These data suggest that high rates of dispersal and low rates of local extinction lead to a situation in which "everything is everywhere," and that the microbial species found in a given habitat are a function only of habitat properties and not of historical factors.

Species concepts for large and small organisms

Considerations of biodiversity are generally based on the concept of morphospecies, which is probably the only viable operational approach when dealing with a large number of species, and with preserved specimens in particular. This approach implicitly reflects a concept of biological species, even though complexes of sibling species (that is, morphologically indistinguishable but genetically isolated forms) occur. In addition, clines or genetically isolated subpopulations may blur the distinction between closely related species. The central question here is whether the taxonomic resolution is cruder for small organisms. For small metazoans and many protist groups, the amount of morphological detail generally matches that of larger organisms: Representatives of groups such as ciliates, diatoms, and foraminiferans possess many morphological features, and in some cases polymorphic life cycles have led to an inflation of species numbers (Finlay et al. 1996). Certain protist groups (amoebae, several flagellate taxa) provide less detail at the light-microscopic level, but this has been compensated for through the use of electron microscopy (Patterson 1999).

Complexes of sibling species are known in some ciliates. The classical example is the *Paramecium aurelia* complex, consisting of 14 genetically isolated sibling species that are difficult to distinguish on the basis of morphological traits but cannot interbreed (most are obligate sexual outbreeders, but obligate self-fertilizers also occur within this complex). Many but not all of these sibling species have been recorded on several continents, and strains from distant continents readily interbreed. There are also complexes in which there is actually free gene flow between "sibling species," because different combinations are mating-compatible in a complex way (Finlay et al. 1996). The freshwater ciliate *Tetrahymena* includes a complex of many species, several of which cannot be distinguished morphologically but are characterized by their ability to mate and by genetic distances. Altogether, 39 such *Tetrahymena* species are known, including both sexual outbreeders and asexual forms. They have been sampled extensively in North America (85 percent of all sampling sites). Twenty-five species have been recorded outside of North America (in South America, the Pacific Islands, China, Australia, and Europe); of these, 20 have also been recorded in North America (Nanney 2004). Although there is no hard evidence to show that all the species occur on all continents, many do seem to occur worldwide. Given the biased distribution of sampling sites, the data do not exclude the worldwide distribution of all *Tetrahymena* species.

It is not known how many nominal species of protists represent such sibling-species complexes, nor whether the phenomenon is more common among protists than among metazoans. Overall, however, there is so far no strong evidence of geographically restricted sibling species among protists. In the case of small multicellular animals, Westheide and Schmidt (2003) have recently shown that geographically structured genetic variations do occur among populations of a meiofaunal polychaete species, indicating genetic isolation of remote populations. This is not necessarily inconsistent with a ubiquitous distribution of microbes, but it does indicate that small animals can display some geographically patterned genetic variation.

For sexual outbreeders, there is, at least in principle, a theoretically based species concept. But many protist groups are sexless or include sexless species; this applies, for example, to all naked amoebae and to many groups of flagellates. In these species, as in bacteria, evolution is clonal and the species concept is fundamentally arbitrary. For clonal organisms, there are no constraints to genetic divergence, and descendants from a cell will accumulate neutral mutations over time. Moreover, isolation is not a prerequisite for adaptive radiation (e.g., to new niches within a population) for these organisms, as it is, for example, in species complexes among apomictic vascular plants. Considerable genetic variation and clusters of genotypes within a nominal species can therefore be expected, and these effects have been demonstrated for bacterial species (Cohan 2002). Sequencing of genes (such as ribosomal RNA genes) from remote places could thus reveal patterns indicating some degree of geographical patterning, but the data available so far are very limited in the case of eukaryotic microbes.

Atkins and colleagues (2000) isolated a number of small heterotrophic flagellates from hydrothermal vents in the Pacific Ocean. All of the organisms they retrieved belonged to known and widespread nominal species. Gene sequencing revealed variation between populations, but there was no consistent geographic pattern when sequences were compared to sequences of isolates from elsewhere. The flagellate *Cafeteria roenbergensis* from a Pacific vent was genetically almost identical to a strain from a shallow-water habitat in Denmark, but it differed from a morphologically similar shallow-water isolate from the eastern coast of North America. So far, however, there are too few data to draw any firm conclusion from this approach.

Global distribution and phenotypic specialization

Organisms differ in their degree of specialization, but all are to some extent confined to particular types of habitats. Some protists grow only within a narrow temperature range. For example, the large freshwater ciliate *Neobursaridium gigas* grows only within the range of 22 degrees Celsius (°C) to 29°C. It therefore occurs only in tropical regions; it has been found in Africa, South America, and Southeast Asia (Dragesco 1968). Likewise, many foraminiferans have a pantropical distribution. Other marine protists are confined to cold seas or to porous sea ice, but identical species occur in the Arctic and Antarctic regions (Montresor et al. 2003). In the case of planktonic cold-water foraminiferans, gene flow between Arctic and Antarctic populations has been demonstrated (Darling et al. 2000).

One could also look at species that have unusually wide habitat niches. Most protist species occur either in fresh water or in the sea, but some morphospecies appear in both habitats. Isolates of different euryhaline protists have shown that strains from marine and hypersaline habitats grow equally well at all salinities, from fresh water to three times oceanic salinity, whereas the freshwater isolates generally will not grow in full-strength seawater. This suggests that freshwater strains lose the ability to cope with high salinities, but it still supports the correlation between particular morphospecies and specific tolerance limits. Strains of the marine ciliate *Uronema* (*U. marinum* and *U. nigriceps*) from arctic East Greenland and from temperate Denmark show a similar relationship between growth rate and temperature (both strains are able to grow within the temperature range of –0.1°C to 38°C), whereas a strain from the Red Sea grows relatively more slowly below 10°C.

We have so far implicitly discussed only free-living species. The distribution of host-specific symbiotic microbes is, of course, limited to the distribution of the host species. Furthermore, total symbiont population sizes are, depending on the abundance of the host, probably often small in an absolute sense, and so the arguments put forward here may not apply. However, even symbionts may have cosmopolitan distribution. The dinoflagellate *Symbiodinium* is a phototrophic endosymbiont in a variety of corals, bivalves, and some other marine invertebrates. Recent studies have shown that *Symbiodinium* comprises a number of genotypes that differ with respect to temperature tolerance and preferences for light intensity. However, the different genotypes do have a cosmopolitan distribution (LaJeunesse 2001).

Returning to free-living forms, it is evident that some genetically based adaptations to different habitats may occur within nominal protist species. Whether there is any real geographical structuring of such genetic variation within nominal species is difficult to disprove. Among macroscopic organisms, however, restricted geographic distribution applies not only to genetic variation within species but also to variation among species, families, and orders. Certainly nothing like this occurs among unicellular organisms: There are no microbial counterparts to the marsupial mammals confined to Australia, the penguins confined to the Southern Hemisphere, or the giant tortoises confined to the Galápagos. With the exception of species introduced by humans, representatives of the macrofauna of Australia are nearly all endemic to the continent. In comparison, Esteban and colleagues (2000) recorded 85 ciliate species from a crater lake in Tasmania; all but one (already known from Africa) had previously been found in Europe.

Every year a few new species of protists are discovered, usually when previously ignored habitat types are investigated.

Such newly discovered species are initially defined as endemic. However, experience has shown that such species are usually rediscovered in similar habitats worldwide—as soon as someone looks for them.

Size spectra and global distributions of organisms: Two aquatic sites

In an effort to quantify the relationship between body size and global distribution, we attempted to identify all the eukaryotes at two aquatic sites: a 1-ha eutrophic pond (Priest Pot) in the English Lake District and a 2-ha marine shallow-water habitat in the innermost part of Nivå Bay, the Sound, about 25 kilometers north of Copenhagen, Denmark (figure 1). Both sites had been subject to previous floristic and faunistic studies by other researchers; we analyzed these data along with the results of our own more recent surveys.

The species list for these sites is not complete, because we lack the taxonomic expertise to identify some groups (e.g., benthic diatoms at the marine site). Also, it is still possible to find additional species (especially among protists) not previously recorded at the sites. So far approximately 1200 species have been recorded from the freshwater site and approximately 700 from the marine site. These numbers are not quite comparable, in that the freshwater site includes amphibious species, whereas the marine data are confined to organisms that are permanently beneath the water surface. In both cases, most organisms are small. At the marine site, for example, 446 species are heterotrophic or phototrophic protists (most of these being either ciliates or flagellates). Of the remaining species, 131 belong to the meiofauna (animals less than 1 mm long; mainly nematodes, rotifers, gastrotrichs, turbellarians, and some crustaceans) and 106 to the macrofauna (mainly molluscs, crustaceans, polychaetes, coelenterates, and fish); we also found 19 species of macroalgae and 2 species of vascular plants. The size spectra of the two sites are similar (figure 2). Clearly, small organisms (less than 1 mm) dominate in terms of species numbers, supporting the general notion that there are many more species of small organisms than of large ones.

Figure 1. The two sampling sites. Above: The inner part of Nivå Bay, Denmark. The 2-hectare (ha) rectangular area sampled is delimited by the pier and by the submerged stone settings, which are remains of a never-completed naval harbor from the 18th century. The water depth is 1 to 1.5 meters (m); the purple color along the shore is caused by the mass occurrence of purple sulfur bacteria. Below: Priest Pot, a freshwater lake in the English Lake District. Its area is 1 ha and its maximum depth approximately 3.5 m; during summer it is stratified with an anoxic hypolimnion.

Determining the global distribution of large plants and animals is a relatively easy task. Regrettably, this is not so for small organisms, because of undersampling in many parts of the world. The vast majority of recordings of protists and meiofauna derive from Europe and North America, with many fewer from most other parts of the world. Data on marine meiofauna, for example, are almost absent from Australasia, where the protist biota has so far been covered

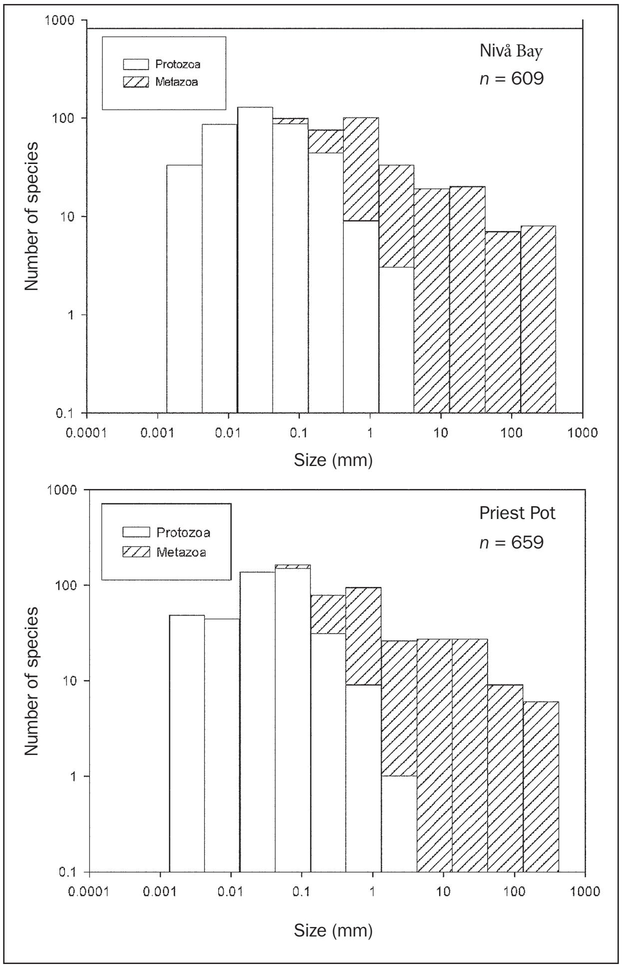

Figure 2. Size spectra of species of heterotrophic organisms (protozoa and animals) at Nivå Bay and Priest Pot. An organism's size is defined as its body length in millimeters.

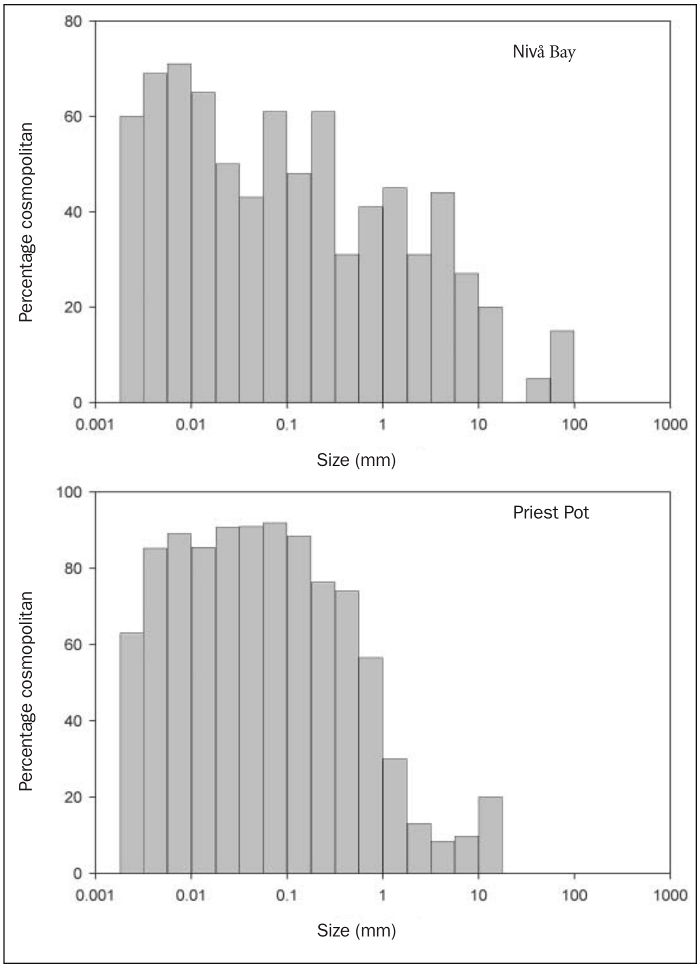

Figure 3. Percentage of organisms of different size groups (body lengths) with cosmopolitan distribution at a marine site (Nivå Bay, above) and a freshwater site (Priest Pot, below). Macrophytes have been omitted in both cases.

by only a handful of workers. Data are also scarce from South America, Southeast Asia, and Africa, although they are somewhat more complete for limnic than for marine organisms. A few species that could be identified only to the genus level had to be omitted from the analysis. Furthermore, we had to use a pragmatic definition of *cosmopolitan species* as species occurring in at least two oceans or two biogeographical regions and in both Northern and Southern Hemispheres. Because of undersampling of small species, their degree of cosmopolitanism may be underestimated.

Figure 3 shows the relationship between body size and the fraction of species with cosmopolitan distribution (macrophytes are omitted). The freshwater data suggest a sharp transition at a body size of approximately 1 mm, below which species tend to have a cosmopolitan distribution, whereas the marine data suggest a more gradual change. This difference, however, may be an artifact reflecting the incomplete records of marine meiofauna from the Southern Hemisphere. Aquatic macrophytes deviated from this pattern: For the limnic species measuring less than 10 cm, approximately 50 percent had a cosmopolitan distribution. In the case of the marine macroalgae, the relationship with size was not evident because of the limited number of species, but approximately half of the species had cosmopolitan distribution. We are unable to explain why macrophytes apparently have a wider distribution than similarly sized animals.

Both study sites represent shallow-water biota in a temperate climate zone. Organisms living there must be able to tolerate temperatures ranging from 0°C to 30°C, so conceivably they could thrive in almost any kind of climate. It is therefore not impossible that a similar study set in, for example, a tropical region would look somewhat different, showing a smaller fraction of cosmopolitan species. This does not, however, affect the difference between small and large organisms. The trend shown in figure 3 is real, demonstrating that small organisms have a wider distribution than larger organisms and that the smallest ones apparently are distributed worldwide.

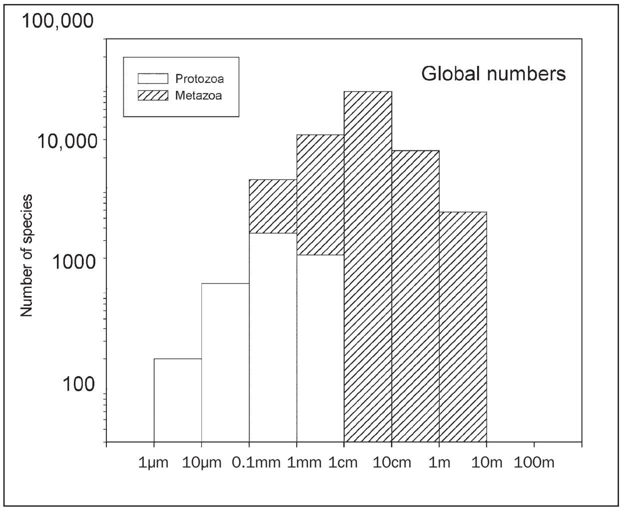

Figure 4. Size distribution (body lengths) of all described heterotrophic aquatic organisms.

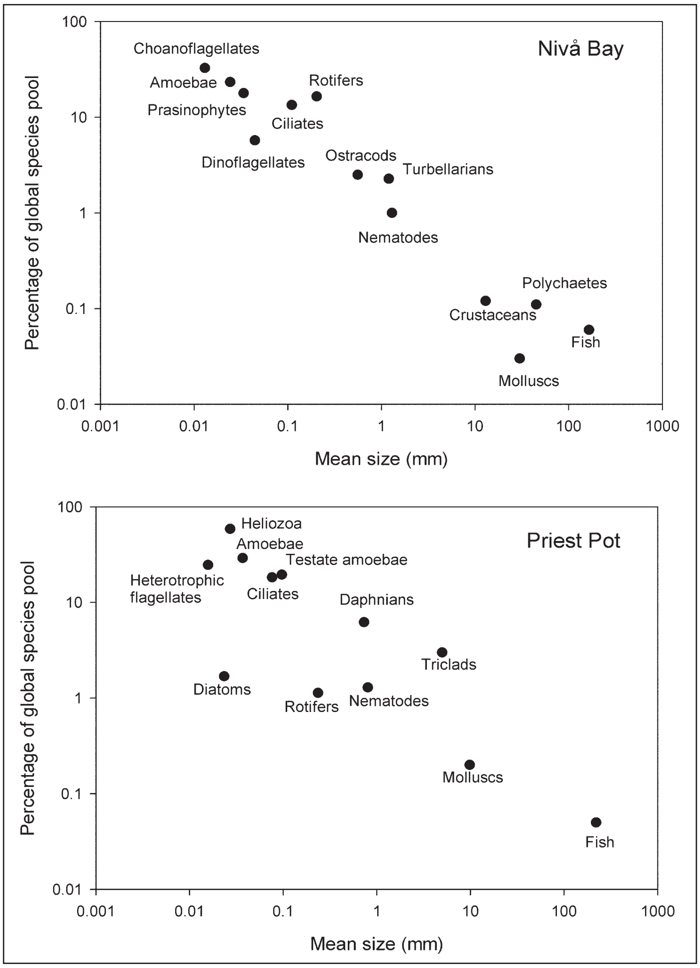

Figure 5. Percentage of global species pools for different taxonomic groups in relation to mean body length. Above: Results for the marine site (Nivå Bay) as a percentage of the global number of marine species. Below: Results for the freshwater site (Priest Pot) as a percentage of the global number of freshwater species.

Some corollaries

The global body-size distribution of aquatic organisms (figure 4) is very different from the distribution in the pond and in the marine shallow-water habitats that we studied (figure 2). Compilations of the global inventory of species are uncertain. On the one hand, many species may remain undescribed; on the other, many taxonomic groups are burdened by synonyms (species that have been given two or more names), thus inflating the number of nominal species. Also, different taxonomic experts differ in their estimates of the global number of species for particular taxa. Nonetheless, it is evident that among the roughly 180,000 species of heterotrophic aquatic organisms named so far, the majority measure more than 1 cm, and less than 10 percent are protozoa. Probably only some 10,000 to 15,000 living protists (including phototrophic forms) have so far been discovered and named.

As a consequence, for any given area, the species present will represent an increasing fraction of the global species pool with decreasing body size (figure 5). Again, this compilation probably underestimates this relation because, given sufficient time and effort, there is no doubt that an additional number of small organisms (and especially protists) can be found at the two sites we studied, whereas our survey of macroscopic organisms is probably almost complete. Also, the particular sites we chose—a eutrophic pond and a sandy, shallow-water area with fluctuating salinities and temperatures—represent a limited subset of the local biota. Had we extended the marine sampling site to adjacent deeper offshore waters with a stable high salinity or, in the freshwater case, included a neighboring oligotrophic lake, we undoubtedly would have recovered an even larger fraction of the global pool of small organisms.

It is an empirical observation that for any group of similar (related) species, the species–area curve can—within a certain area range—be described as a power function:

$$S \propto A^z.$$

For large organisms (e.g., insects and vascular plants), the parameter z typically has values of approximately 0.3, corresponding to a doubling of the number of species S when increasing the surveyed area A by a factor of 10. When the area is sufficiently large to cover more biogeographic zones, the value of z will increase. That the species–area curve is a power function has in part been rationalized by assumptions underlying the "neutral communities models" (Bell 2001). The expectation from the present results is that the slope of the species–area curve decreases with decreasing size of organisms.

Figure 6 shows the species–area curves for some selected marine groups. The areas include Nivå Bay (2 ha), Kiel Bight (4.6×10^5 ha), European waters (from the North Pole along the east coast of Greenland and the Mid-Atlantic Ridge to 26° north, including the Mediterranean, Baltic, Black, and Barents Seas; altogether about 2.7×10^9 ha) and the world oceans (3.6×10^{10} ha), representing the global inventory of species. The value of z diminishes with the decreasing size range of organisms belonging to different taxonomic groups. For the smallest group (heterotrophic flagellates, excluding dinoflagellates), the relationship is almost totally flat (about 50 percent of all named species have been recorded in Nivå Bay). For the macrofaunal groups, the curves tend to be upward concave, reflecting the cumulative addition of new habitat types and climatic zones and—when going from the North Atlantic to the world's oceans—the inclusion of new faunal provinces with endemic faunas.

One of the most striking patterns of macroecology is the latitudinal diversity gradient (Rosenzweig 1995), the increase in species numbers when moving from higher to lower latitudes. Hillebrand and Azovsky (2001) showed that the effect of the latitudinal diversity gradient decreases with decreasing body size and almost vanishes for protists. Although the causes of the latitudinal diversity gradient are still debated, its absence for the smallest organisms is another prediction that follows from the idea that for microbes "everything is everywhere."

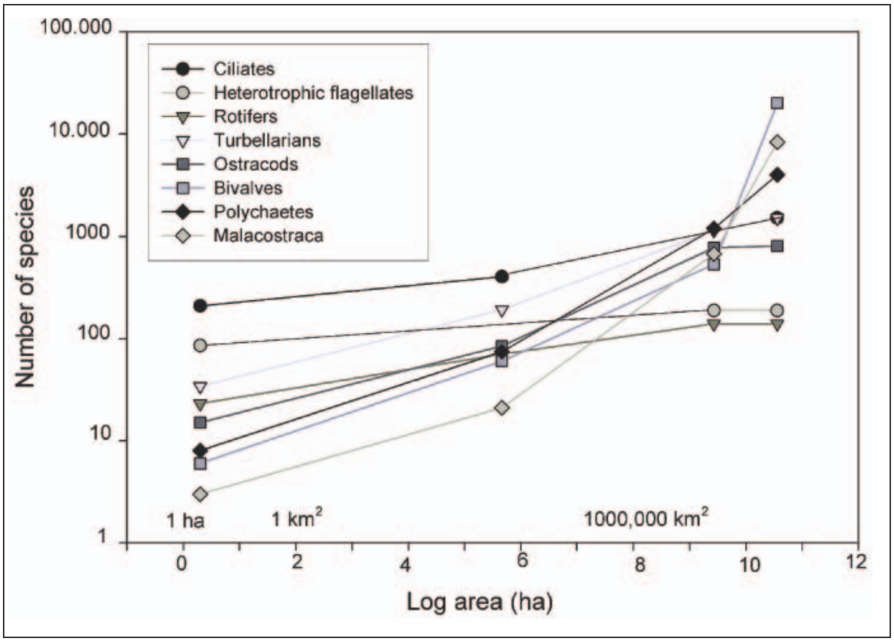

Figure 6. Species–area curves based on the biota from cumulatively larger areas: Nivå Bay, Kiel Bight (Baltic coast, Germany; Gerlach 2000), North-East Atlantic Ocean (including the Barents, Baltic, Mediterranean, and Black Seas; Costello et al. 2001), and the world oceans.

Perspectives for community ecology

A simple implication of our findings is that those who are interested in microbes need not travel to exotic places to find interesting creatures to study: Most microorganisms can be found at the local seashore or lake—or, for that matter, in a garden pond. The results also may illuminate mechanisms that determine local and global biodiversity and community structure. Recent understanding of community structure and diversity emphasizes dispersal and extinction as statistical phenomena rather than as results of special species interactions (Lawton 1999). The "unified neutral theory of biodiversity and biogeography" (Bell 2001, Hubbell 2001) is a formalized version of these ideas. Strictly speaking, the neutral models apply only to guilds of species limited by a single resource, and they imply that all species are ecologically identical. These models further assume constant probabilities of per capita reproduction, dying, and migration to a neighboring site. Nevertheless, they provide predictions of patterns of diversity, relative species abundance, and species–area curves that resemble the findings for real biotic communities.

The requirement of ecological identity of species (in which intensities of intra- and interspecific competition are identical and predatory interactions are absent) is rarely met in the real world. A group such as ciliates includes a great variety of functional forms with respect to the nature of food particles and microhabitat preferences, and most species in a given community probably interact weakly, if at all. But perhaps real communities may be considered as the sum of many subcommunities that can be described by a neutral model. The neutral models predict that the probability of dispersal is proportional to absolute population size and that the probability of local species extinction decreases sharply with increasing population size. This again means that there is a positive correlation between absolute population size and distribution range, and between population size and the frequency of local occurrence.

Comparing larger and smaller organisms is basically the same as comparing organisms with smaller and with larger absolute population sizes. Microorganisms represent the extreme case, in which population sizes are so huge that "everything is everywhere." The local distribution of species richness for different size groups, with increasing species diversity for smaller species (figure 2), may simply reflect such a basic mechanism rather than more subtle and complex ecological interactions described in terms of food webs and interspecific competition.To some extent, this effect is now being tested experimentally for larger organisms. Anthropogenic introductions of invasive species—whether deliberate or accidental—have resulted in greater local and regional species richness, because competitive extinction of the original residents has in most cases not taken place or, if it is taking place, is doing so very slowly (Davis 2003). Such large-scale introductions of exotic species around the world, the equivalent of an increased dispersal of larger organisms, could eventually mean that while local biodiversity expands, global biodiversity declines.

Acknowledgments

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