

## Microbial biogeography?

Until quite recently microbial biogeography has existed more as a 'statistically improbable phrase' than a field of study. For example, biogeography is accorded but two pages in the otherwise exhaustive text on microbial diversity by Ogunseitan (2005). Likewise microbes can be completely missing from current discussions of biogeography (e.g. Lomolino & Heaney, 2004). A conceptual prejudice was that there is no microbial biogeography as microorganisms are easily dispersed: the famous 'all microbes are everywhere, the environment selects'. This may seem curious to non-microbiologists. Most would agree that dispersal ability may dilute the impact of vicariance events but in and of itself does not obliterate all distributional patterns in time and space; witness those of birds and butterflies.

The attitude of microbial ecologists was also quite likely a self-defence mechanism, a reaction to an inability to begin to grapple with the subject because of problems which existed in simply counting organisms in natural samples of soil or water and the limited number of morphological characters that distinguish species and genera (Fig. 1). However, tools have changed and so have the perceptions of microbial ecologists.

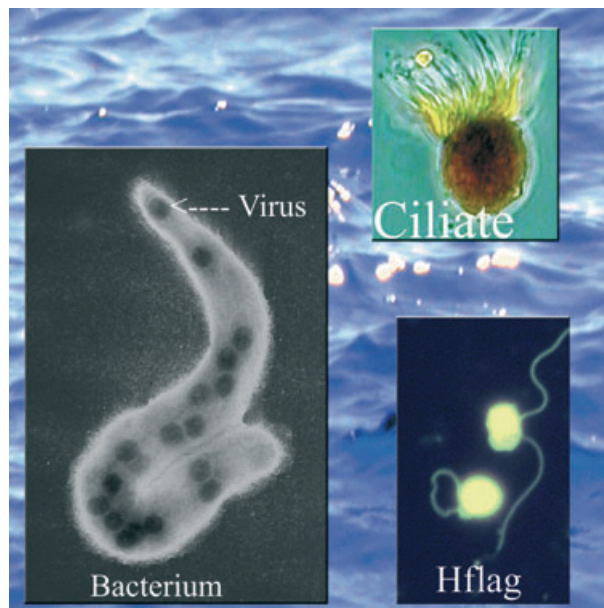
Discussions of whether all species are everywhere or not have given way to the realization that indeed many, if not most, protist species appear to be very widely distributed. However, these 'species', distinguished via morphology, probably do not correspond with interbreeding populations. Cryptic species, forms genetically distinct but morphologically similar, appear to be common. Intriguingly, genetically distinct populations occur among more or less continuously distributed species, such as the dinoflagellate 'species complex' of *Alexandrium tamarense*, some of which are toxic. The toxicity of the dinoflagellate population appears to be a quite variable character, unpredictable from phylogeny (Uwe *et al.*, 2003). Thus, for protists, it appears that all 'morpho-types' may be everywhere but not all genotypes. The

mechanisms maintaining genetic isolation among protists are obscure.

The sequencing of DNA from natural samples is showing not only new groups but also unexpectedly high species richness. For example, Countway *et al.* (2005) obtained surprising results by using sophisticated molecular techniques to analyse samples from a very simple experiment with seawater. A single seawater sample was distributed into a set of 4-L bottles. DNA was collected from two bottles at the start of the experiment, then from three bottles after 24 h and again after 72 h from the last three bottles. The DNA in the seawater obtained from time zero, after 24 h and after 72 h was cloned and sequenced, thus allowing estimation of species abundance. Sampling with time allowed the experimenters to exploit the fact that placing microbial populations in bottles alters the composition of

the population. Thus, species in low, difficult to detect concentrations often become more abundant with time in 'bottled water'. Species composition did change with time and a total of 165 species or phylotypes of protists were found. Statistical estimators of sampling error suggested that about 300 protist species were present in the original 32 L of seawater.

As for prokaryotes, molecular tools allow us to distinguish bacteria from one another on a genetic basis, rather than relying on their abilities to use a particular substrate or show a particular colony type – characteristics requiring cultivation of the organisms. Thus, using sequence data, an entire new kingdom of life, the archaeobacteria, was discovered. The first application of molecular approaches, sequencing sections of ribosomal RNA, also reinforced the idea that all bacteria were everywhere. The strain SAR



**Figure 1** Examples of heterotrophic aquatic microbes from marine plankton. Ciliates and heterotrophic flagellates (Hflag) are protists which feed on bacteria and small algae. Most bacteria break down and absorb organic matter. The bacterium shown is infected with viral particles. Most viruses reproduce by infecting free-living prokaryotes. The actual sizes of these organisms are 20  $\mu\text{m}$  for the ciliate, 5  $\mu\text{m}$  for the heterotrophic flagellates, 2  $\mu\text{m}$  for the bacterium and 50 nm for the viral particles in the bacterium.

11, originally found in the Sargasso Sea, appeared in nearly every marine sample subsequently examined. The ubiquitous distribution of SAR 11 in the world's oceans has even entered popular culture. In a recent novel SAR 11 is cast as the remnant of when the earth was a single organism (Moore, 2004). However, it is worth noting that SAR 11 is not a species in any sense of the word but rather a 'ribo-type', a grouping crude enough to lump together, for example, all primates.

Interestingly enough, physical isolation and vicariance events may be of some importance since dispersal ability is probably not high for all bacteria (Papke & Ward, 2005). Perhaps more importantly, though, molecular tools now allow bacterial communities to be analysed like other communities, establishing, for instance, distributional patterns on small and medium spatial scales.

Sampling different spatial scales as an orthodox ecologist would, but using a molecular technique to fingerprint bacterial communities, Noguez *et al.* (2005) examined the soil of a tropical forest. Based on the bacterial DNA found in 32 samples of 1 g, they estimated a total species richness of about 200. Rather than 'all species everywhere' they discovered that species structures differed with spatial scale, much like those found among groups of multicellular organisms. In fact, the authors likened the distribution of bacteria in a 64 m<sup>2</sup> area of soil to that of vertebrates at a continental scale.

Microbiologists have begun testing the predictions of island biogeography in natural systems. For example, the relationship between ecosystem size and the number of distinct bacterial 'ribo-types' was examined by Reche *et al.* (2005) in lakes differing in isolation and size. Lake remoteness alone had little effect on the composition of the bacterial community. In contrast, lake size was related positively to the number of bacterial 'ribo-types' found. Such a positive relationship between lake area and species richness is known for a large number of easily dispersed lake taxa ranging from insects to crustacean zooplankton.

A fascinating field beginning to be exploited is that of endosymbionts. For example, sponges are known to harbour distinct communities of bacteria. A species of sponge found in Australian coastal waters contains different communities of bacteria depending on whether or not the sponge

occurs in temperate or tropical waters (Taylor *et al.*, 2005). It is not known if distinct endosymbiotic communities correspond with genetic differences between temperate and tropical sponge populations.

While bacteria, in part, conform to patterns known from multicellular organisms, another group of microbes, viruses, appear to be truly ubiquitous but locally diverse (Breitbart & Rohwer, 2005). There are perhaps 5000 distinct types of viruses in 200 L of seawater but as very similar types are found in different environments, viruses appear to move between systems as distinct as seawater and soil. Thus local diversity is quite high but almost the same as global diversity.

While microbial biogeography now exists it appears that different groups of microbes may show very different biogeographies. Among protists, species defined via morphology are most often very widely distributed but are probably composed of genetically distinct populations. With regard to bacteria, despite the fact that our level of taxonomic resolution is very low, a variety of distributions have been documented ranging from quite wide to limited to distinct environments. Viruses, on the other hand, differ from both bacteria and protists. Among viruses local diversity is very high but so is dispersal so that local and global diversity may be equivalent. As a final note, it should be emphasized that these generalities are tentative, drawn from recent studies, and honestly, it would be surprising if they withstand the test of time – and therein lies the interest!

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