

## Highlight

# Microbial biogeography: the end of the ubiquitous dispersal hypothesis?

Christopher J. van der Gast\*

NERC Centre for Ecology & Hydrology, Wallingford  
OX10 8BB, UK.

Ken Timmis is a difficult scientist to refuse when he asks you a favour. In his capacity as senior editor of the *Environmental Microbiology* journal, he asked me to write a research highlight on the paper by Ryšánek and colleagues (2014), which I had originally reviewed and made one of those very rare (for me) recommendations to 'accept as is'. In the paper, the authors examined the continental-scale spatial distributions of a single lineage of terrestrial protists within the genus *Klebsormidium*; using *rbcL* sequences to screen the isolated strains, which they asserted would provide better resolution than an internal transcribed spacer (ITS) targeted approach (Ryšánek *et al.*, 2014). Interestingly, from a natural history perspective, they identified novel genotypes from the 190 *Klebsormidium* colonies isolated from their samples. In addition, and particularly fascinating to me, the authors presented strong evidence for both cosmopolitanism and endemism in terms of the biogeographical distribution across the *Klebsormidium* genotypes. Below, I set out a brief potted history on the rise of microbial biogeography in order to provide context on how this work, in my view, significantly contributes to our growing knowledge on this important fundamental subject.

It is now widely accepted that to better understand the ecology of microorganisms (inclusive of archaea, bacteria, fungi, and protists) and their roles in ecosystem functioning could be achieved if traditional ecological theories can be applied to microorganisms (Carbonero *et al.*, 2014). The great promise is that this would help us better understand and predict changes in the natural environment, would allow improved manipulation of agricultural and engineered systems, and would give improved protection of human health. It would be fair to state that the

adoption and adaptation of ecological theory in microbial ecology began to really gain momentum from the middle of the last decade (Prosser *et al.*, 2007). A particular emphasis is placed on 'adaptation', as it would be naïve to ever lose sight of/or ignore the fact that the biology of animals and plants, of which traditional ecology is almost exclusively based upon, are different from that of microorganisms. Moreover, even the biology of different microorganisms can be staggeringly different, and assuming equivalence based on microscopic body size is similarly naïve. On this critical point, Carbonero and colleagues (2014) stated that due to differences in scale and physiologies between macroorganisms and microorganisms [and indeed between types of microorganisms (my addendum)], there will be principles of ecology that are difficult to reconcile between traditional and microbial ecology. Therefore, this represents a substantial challenge to the worthwhile cause of developing an inclusive ecology.

From a fundamental perspective, the growing acceptance and incorporation of traditional ecological principles and theory into microbial ecological research over the last 10 years has started to move us away from what Prosser and colleagues (2007) opined was the accumulation of situation-bound statements that are of limited predictive ability, offering few insights. Indeed, this was exemplified at the time by an anonymous referee's quote published in this journal, '*There is no apparent study concept other than "we went out to the campus pond one day and took 2 samples for sequencing"*', and found they were different [my addendum] (Anon, 2006). The interest in translating principles and theories from traditional ecology to microbial ecology has largely centred on the question of microbial biogeography. As a basic definition, '*biogeography is the study of the distribution of biodiversity over space and time. It aims to reveal where organisms live, at what abundance, and why?*' (Hughes Martiny *et al.*, 2006). An initial grounding on the subject of microbial biogeography can be gained from the review and analysis papers by Jennifer Martiny and colleagues (Hughes Martiny *et al.*, 2006; Hanson *et al.*, 2012).

\*For correspondence. E-mail [cjvdg@ceh.ac.uk](mailto:cjvdg@ceh.ac.uk); Tel. (+44) 0 1491 692647; Fax (+44) 0 1491 692424 .

Over the last 10 years, there have been an ever-growing number of studies published on the biogeography of microorganisms. Some recent personal highlights, inclusive of the Ryšánek and colleagues (2014) paper, include the first multiscale national-level studies investigating patterns and processes underpinning soil bacterial and fungal distributions (Griffiths *et al.*, 2011; Hazard *et al.*, 2013; Ranjard *et al.*, 2013); a convincing assessment of both bacterial taxa–area relationships and distance–decay relationships (Zinger *et al.*, 2014); following my own work on temporal scaling of bacterial diversity (e.g. van der Gast *et al.*, 2008; Oliver *et al.*, 2012), Shade and colleagues (2013) provided an important meta-analysis of taxa–time relationships of archaeal and bacterial communities (it is important to note that temporal distributions of microbial diversity have been much less studied than spatial distributions and certainly require more attention); and finally, the study by Carbonero and colleagues (2014) challenges the traditional ecological concept of specialist and generalist species by demonstrating that metabolic flexibility can be a major predictor of spatial distribution in microbial communities – which, as the authors state, if this is a common feature of microorganisms in general, will represent a distinct microbial ecological principle and a challenge to developing an inclusive ecology.

The subject of whether microorganisms are globally dispersed or could be biogeographically restricted has been the subject of high-profile debate (e.g. Bell *et al.*, 2005; Whitfield, 2005), with the old tenet of microbiology ‘*Everything is everywhere, but, the environment selects*’ used as a focus for that debate (Baas Becking, 1934). That debate has unquestionably acted as a key driver for the subsequent research effort. From observations of protist morphospecies, Finlay and colleagues (e.g. Finlay and Clarke, 1999; Finlay, 2002) proposed what could be termed a general ubiquitous dispersal hypothesis for microorganisms (Bass *et al.*, 2007). Their data implied that although there was high local diversity, globally, the studied protist morphospecies were ubiquitous. Further, this could be explained by the small body size of protists and that ubiquity was due to global dispersal by, for example, wind and water currents. Extrapolating this ubiquitous dispersal hypothesis to bacteria, they reasoned that bacteria have much smaller body sizes than protists, have many orders of magnitude more abundant and are therefore more likely to be globally dispersed; and from a morphospecies perspective that would certainly be the case for bacteria, being mainly comprised of rod and cocci morphologies. Therefore, microbial cosmopolitanism was thought to be primarily driven by random dispersal generated by large population sizes of organisms with body sizes below 1 mm (Finlay and Fenchel, 2004). However, Bass and colleagues (2007) stated that a large part of the

perception of greater cosmopolitanism in microorganisms was attributable to the taxonomic artefact of lumping large numbers of genetically very different organisms into single crude morphospecies.

The study by Ryšánek and colleagues (2014) and the work by others (e.g. Bass *et al.*, 2007; Bates *et al.*, 2013) using molecular approaches to examine the distributions of different protistan groups from across the eukaryote tree strongly support what Foissner (1999; 2006) proposed as a moderate endemism model of microbial biogeography, which puts forward that although some protists may have cosmopolitan distributions, others have restricted distributions. Combined, this should allow us to finally and irrevocably reject a generalized ubiquitous dispersal hypothesis for microorganisms. It should also allow us to move on from using the Baas Becking tenet as a ‘crutch’ when investigating the biogeographical distributions of microorganisms as it is more probably the case that ‘*[s]ome things are everywhere and some things are not. Sometimes the environment selects and sometimes it doesn’t*’ (van der Gast, 2013).

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