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1 **Microbial biogeography: the end of the ubiquitous dispersal hypothesis?**

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6 Ken Timmis is a difficult scientist to refuse when he asks you a favour. In his capacity as  
7 senior editor of the Environmental Microbiology journal, he asked me to write a research highlight on  
8 the paper by Ryšánek and colleagues (2014), which I had originally reviewed and made one of those  
9 very rare (for me) recommendations to 'accept as is'. In the paper, the authors examined the  
10 continental-scale spatial distributions of a single lineage of terrestrial protists within the genus  
11 *Klebsormidium*; using rbcL sequences to screen the isolated strains, which they asserted would  
12 provide better resolution than an internal transcribed spacer (ITS) targeted approach (Ryšánek et al.,  
13 2014). Interestingly, from a natural history perspective, they identified novel genotypes from the 190  
14 *Klebsormidium* colonies isolated from their samples. In addition, and particularly fascinating to me, the  
15 authors presented strong evidence for both cosmopolitanism and endemism in terms of the  
16 biogeographical distribution across the *Klebsormidium* genotypes. Below, I set out a brief potted  
17 history on the rise of microbial biogeography in order to provide context on how this work, in my view,  
18 significantly contributes to our growing knowledge on this important fundamental subject.

19 It is now widely accepted that to better understand the ecology of microorganisms (inclusive  
20 of archaea, bacteria, fungi, and protists) and their roles in ecosystem functioning could be achieved if  
21 traditional ecological theories can be applied to microorganisms (Carbonero et al., 2014). The great  
22 promise is that this would help us better understand and predict changes in the natural environment,  
23 would allow improved manipulation of agricultural and engineered systems, and would give improved  
24 protection of human health. It would be fair to state that the adoption and adaptation of ecological  
25 theory in microbial ecology began to really gain momentum from the middle of the last decade  
26 (Prosser et al., 2007). A particular emphasis is placed on 'adaptation', as it would be naïve to ever  
27 lose sight of/ or ignore the fact that the biology of animals and plants, of which traditional ecology is  
28 almost exclusively based upon, are different from that of microorganisms. Moreover, even the biology  
29 of different microorganisms can be staggeringly different, and assuming equivalence based on  
30 microscopic body size is similarly naïve. On this critical point, Carbonero and colleagues (2014)

31 stated that due to differences in scale and physiologies between macroorganisms and  
32 microorganisms [and indeed between types of microorganisms (my addendum)], there will be  
33 principles of ecology that are difficult to reconcile between traditional and microbial ecology.  
34 Therefore, this represents a substantial challenge to the worthwhile cause of developing an inclusive  
35 ecology.

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

49 Over the last 10 years, there have been an ever-growing number of studies published on the  
50 biogeography of microorganisms. Some recent personal highlights, inclusive of the Ryšánek and  
51 colleagues (2014) paper, include the first multiscale national-level studies investigating patterns and  
52 processes underpinning soil bacterial and fungal distributions (Griffiths et al., 2011; Hazard et al.,  
53 2013; Ranjard et al., 2013); a convincing assessment of both bacterial taxa–area relationships and  
54 distance–decay relationships (Zinger et al., 2014); following my own work on temporal scaling of  
55 bacterial diversity (e.g. van der Gast et al., 2008; Oliver et al., 2012), Shade and colleagues (2013)  
56 provided an important meta-analysis of taxa–time relationships of archaeal and bacterial communities  
57 (it is important to note that temporal distributions of microbial diversity have been much less studied  
58 than spatial distributions and certainly require more attention); and finally, the study by Carbonero and  
59 colleagues (2014) challenges the traditional ecological concept of specialist and generalist species by  
60 demonstrating that metabolic flexibility can be a major predictor of spatial distribution in microbial

61 communities – which, as the authors state, if this is a common feature of microorganisms in general,  
62 will represent a distinct microbial ecological principle and a challenge to developing an inclusive  
63 ecology.

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

82         The study by Ryšánek and colleagues (2014) and the work by others (e.g. Bass et al., 2007;  
83 Bates et al., 2013) using molecular approaches to examine the distributions of different protistan  
84 groups from across the eukaryote tree strongly support what Foissner (1999; 2006) proposed as a  
85 moderate endemicity model of microbial biogeography, which puts forward that although some  
86 protists may have cosmopolitan distributions, others have restricted distributions. Combined, this  
87 should allow us to finally and irrevocably reject a generalized ubiquitous dispersal hypothesis for  
88 microorganisms. It should also allow us to move on from using the Baas Becking tenet as a ‘crutch’  
89 when investigating the biogeographical distributions of microorganisms as it is more probably the

90 case that '[s]ome things are everywhere and some things are not. Sometimes the environment selects  
91 and sometimes it doesn't' (van der Gast, 2013).

92

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