

Article (refereed) - postprint

van der Gast, Christopher J. 2015. **Microbial biogeography: the end of the ubiquitous dispersal hypothesis?** *Environmental Microbiology*, 17 (3). 544-546. [10.1111/1462-2920.12635](https://doi.org/10.1111/1462-2920.12635)

© 2014 Society for Applied Microbiology and John Wiley & Sons Ltd

This version available <http://nora.nerc.ac.uk/509283/>

NERC has developed NORA to enable users to access research outputs wholly or partially funded by NERC. Copyright and other rights for material on this site are retained by the rights owners. Users should read the terms and conditions of use of this material at <http://nora.nerc.ac.uk/policies.html#access>

This document is the author's final manuscript version of the journal article, incorporating any revisions agreed during the peer review process. There may be differences between this and the publisher's version. You are advised to consult the publisher's version if you wish to cite from this article.

The definitive version is available at <http://onlinelibrary.wiley.com/>

Contact CEH NORA team at
noraceh@ceh.ac.uk

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

2 Christopher J. van der Gast

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

4 *For correspondence: Email cjvdg@ceh.ac.uk; Tel. +44(0)1491 692647*

5

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

93 **References**

- 94 Anon (2006) Referees' quotes - 2006. *Environ Microbiol* **8**: 2233-2234.
- 95 Baas Becking, L.G.M. (1934) *Geobiologie of inleiding tot de milieukunde*. The Hague, The
96 Netherlands (In Dutch): W.P. van Stockum & Zoon.
- 97 Bass, D., Richards, R.A., Matthai, L., Marsh, V., and Cavalier-Smith, T. (2007) DNA evidence for
98 global dispersal and probable endemism of protozoa. *BMC Evol Biol* **7**: doi:10.1186/1471-2148-1187-
99 1162.
- 100 Bates, S.T., Clemente, J.C., Flores, G.E., Walters, W.A., Wegener Parfrey, L., Knight, R., and Fierer,
101 N. (2013) Global biogeography of highly diverse protistan communities in soil. *ISME J* **7**: 652-659.
- 102 Bell, T., Newman, J.A., Thompson, I.P., Lilley, A.K., and van der Gast, C.J. (2005) Bacteria and island
103 biogeography. *Science* **309**: 1998-1999.
- 104 Carbonero, F., Oakley, B.B., and Purdy, K.J. (2014) Metabolic flexibility as a major predictor of spatial
105 distribution in microbial communities. *PLoS One* **9**: e85105.
- 106 Finlay, B.J. (2002) Global dispersal of free-living microbial eukaryote species. *Science* **296**: 1061-
107 1063.
- 108 Finlay, B.J., and Clarke, K.J. (1999) Ubiquitous dispersal of microbial species. *Nature* **400**: 828.
- 109 Finlay, B.J., and Fenchel, T. (2004) Cosmopolitan metapopulations of free-living microbial eukaryotes.
110 *Protist* **155**: 237-244.
- 111 Foissner, W. (1999) Protist diversity: Estimates of the near-imponderable. *Protist* **150**: 363-368.
- 112 Foissner, W. (2006) Biogeography and dispersal of micro-organisms: A review emphasizing protists.
113 *Acta Protozool* **45**: 111-136.
- 114 Griffiths, R.I., Thomson, B.C., James, P., Bell, T., Bailey, M., and Whiteley, A.S. (2011) The bacterial
115 biogeography of British soils. *Environ Microbiol* **13**: 1642-1654.
- 116 Hanson, C.A., Fuhrman, J.A., Horner-Devine, M.C., and Martiny, J.B.H. (2012) Beyond biogeographic
117 patterns: processes shaping the microbial landscape. *Nature Rev Microbiol* **10**: 497-506.
- 118 Hazard, C., Gosling, P., van der Gast, C.J., Mitchell, D.T., Doohan, F.M., and Bending, G.D. (2013)
119 The role of local environment and geographical distance in determining community composition of
120 arbuscular mycorrhizal fungi at the landscape scale. *ISME J* **7**: 498-508.
- 121 Hughes Martiny, J.B., Bohannan, B.J.M., Brown, J.H., Colwell, R.K., Fuhrman, J.A., Green, J.L. *et al.*
122 (2006) Microbial biogeography: putting microorganisms on the map. *Nat Rev Micro* **4**: 102-112.
- 123 Oliver, A., Lilley, A.K., and van der Gast, C.J. (2012) Species-time relationships for bacteria. In
124 Microbial Ecological Theory: Current Perspectives. Hirsch, P.R., and Ogilvie, L.A. (eds). Norwich, UK:
125 Horizon Scientific Press, pp. 71-86.

- 126 Prosser, J.I., Bohannon, B.J.M., Curtis, T.P., Ellis, R.J., Firestone, M.K., Freckleton, R.P. *et al.* (2007)
127 The role of ecological theory in microbial ecology. *Nature Rev Microbiol* **5**: 384-392.
- 128 Ranjard, L., Dequiedt, S., Chemidlin Prévost-Bouré, N., Thioulouse, J., Saby, N.P.A., Lelievre, M. *et*
129 *al.* (2013) Turnover of soil bacterial diversity driven by wide-scale environmental heterogeneity. *Nat*
130 *Commun* **4**: 1434.
- 131 Ryšánek, D., Hrčková, K., and Škaloud, P. (2014) Global ubiquity and local endemism of free-living
132 terrestrial protists: Phylogeographic assessment of the streptophyte alga *Klebsormidium*. *Environ*
133 *Microbiol* doi: 10.1111/1462-2920.12501.
- 134 Shade, A., Gregory Caporaso, J., Handelsman, J., Knight, R., and Fierer, N. (2013) A meta-analysis
135 of changes in bacterial and archaeal communities with time. *ISME J* **7**: 1493-1506.
- 136 van der Gast, C.J. (2013) Microbial biogeography and what Baas Becking should have said.
137 *Microbiology Today* **40**: 108-111.
- 138 van der Gast, C.J., Ager, D., and Lilley, A.K. (2008) Temporal scaling of bacterial taxa is influenced by
139 both stochastic and deterministic ecological factors. *Environ Microbiol* **10**: 1411-1418.
- 140 Whitfield, J. (2005) Biogeography: Is everything everywhere? *Science* **310**: 960-961.
- 141 Zinger, L., Boetius, A., and Ramette, A. (2014) Bacterial taxa–area and distance–decay relationships
142 in marine environments. *Mol Ecol* **23**: 954-964.
- 143