

15

Microbes as a test of biogeographic principles

DAVID G. JENKINS¹, KIM A. MEDLEY² AND
RIMA B. FRANKLIN³

¹ *Department of Biology, University of Central Florida, Orlando, USA*

² *Department of Biology, University of Central Florida, Orlando, USA*

³ *Department of Biology, Virginia Commonwealth University, Richmond, USA*

15.1 Introduction

In the hierarchy of scientific knowledge, a principle, rule or law describes consistent observations and precedes hypothesis and theory. Given consistent observations, other information or insight may suggest mechanisms, and a hypothesis can be formed. For example, the first principle of biogeography, Buffon's law, states that disjunct regions have distinct species assemblages despite similar environments. Buffon proposed a mechanism to explain biogeographic patterns: that species 'improve' or 'degenerate' according to their environment. Given generality and often incorporating multiple facets, a theory may emerge that explains the patterns well (e.g. evolutionary theory).

As in ecology, biogeographic principles may include speculations that 'have often been elevated to laws merely by the passing of time' (Loehle, 1987). Tests of

Biogeography of Microscopic Organisms: Is Everything Small Everywhere?, ed. Diego Fontaneto. Published by Cambridge University Press. © The Systematics Association 2011.

biogeographic laws/principles/rules are thus valuable for biogeography in general and for understanding the tested system.

In that context, the statement for microbes that 'Everything is everywhere, but the environment selects' (Finlay, 2002; de Wit and Bouvier, 2006; hereafter abbreviated as EiE) is valuable to test the generality of biogeography's principles and their hypothesised mechanisms. Generality is tested best by extremes, and microbes (defined here as $< \sim 1\text{--}2\text{ mm}$; Finlay, 2002) certainly represent the lower margin of body size for most biogeographic evidence because most biogeography research has been conducted with macrobes (defined here as larger than $1\text{--}2\text{ mm}$; Finlay, 2002). According the EiE, microbes have no biogeographic pattern due to their enormous population sizes and high probability of ubiquitous dispersal (Finlay, 2002). If so, then biogeographic principles derived from macrobes are not general, and subsequent hypotheses and theory must be also be constrained. In addition, the EiE claim tests biogeographic principles because EiE argues that macrobes have biogeographies (Finlay, 2002). The EiE claim is thus double-edged because it also expects definitive patterns (laws, principles or rules) for macrobes.

In this chapter we evaluate the evidence for biogeographic principles of macrobes and the extension of those principles to microbes. We do not claim to have found all literature on this rather broad topic, though we conducted a thorough literature search. Specifically, we evaluate the evidence that:

- (1) Abundance, body size and distribution are inter-related for both macrobes and microbes.
- (2) Niche affects spatial distribution for both macrobes and microbes;
- (3) Microbes and small macrobes have phylogeographies (i.e. geographic pattern in phylogenetic structure).

Topics 1 and 2 address mechanisms (e.g. high abundance causes a large range), while topic 3 is about biogeographic patterns that may result from multiple mechanisms. These topics are important to biogeography (Lomolino et al., 2006) and have not been explored for microbial biogeography, while other related topics have been explored. For example, Green and Bohannan (2006) focused on questions of spatial scale (greater community dissimilarity with greater distance, taxa-area relationships, and the ratio of local:global taxa richness). Martiny et al. (2006) considered non-random spatial distributions of microbes and general approaches to examine contemporary and/or historical processes acting on microbial community structure. Others have considered speciation and extinction rates (e.g. Horner-Devine and Lage, 2004; Ramette and Tiedje, 2007) but concluded that too few data exist, especially for extinction rates.

15.2 Abundance, body size and distribution

Abundance is important to ecological, biogeographic and macroecological concepts. Here we focus on three abundance relationships: abundant–centre, abundance–range and size–abundance.

15.2.1 Abundant–centre

According to the abundant–centre principle, a species reaches its greatest local abundance near its range centre, related to increasingly detrimental conditions toward its range edge (Andrewartha and Birch, 1954; Whittaker, 1956; Westman, 1980; Hengeveld and Haeck, 1982; Brown, 1984; Brown et al., 1995; Thomas and Kunin, 1999; Gaston, 2003). This relationship has been influential in ecology and biogeography (Sagarin et al., 2006) and assumes that a species' range is determined by environmental conditions, that the species' range has an edge, and that the range is roughly equilibrational. These assumptions are most likely true for native species inhabiting a relatively stable landscape, but may not be expected for native species during climate change, for an invasive species still expanding its non-native range, or in the case of invasional ratcheting, in which an invasive species adapts to a new range and then is re-introduced to its native region and expands that native range (Medley, 2009).

Evidence for the abundant–centre relationship was reviewed by Sagarin and Gaines (2002). They found only 39% of studies support the relationship and concluded that 'more exploration of species' abundance distributions is necessary', including more sampling near range edges. The abundant–centre principle is better characterised as an assumption than as a principle for macrobes (Sagarin and Gaines, 2002; Sagarin et al., 2006).

The EiE claim for cosmopolitan distributions and 'astronomical' abundances of microbes (Finlay, 2002) translates to an expectation that microbes do not decline in abundance from range centre to range edge (no range edge exists for cosmopolitan species). Most biogeographic information has been collected for macrobes, so it should be no surprise that less is known about the distribution of abundance across microbial species ranges. The best example we could find for microbes was that of Krasnov et al. (2008), in which fleas and mites on Palearctic small mammals tended to correspond to the expected abundant–centre pattern for macrobes. However, parasitic organisms have been excluded from the EiE claim (Finlay, 2002; Finlay and Fenchel, 2004) because patterns should mirror host patterns, plus Krasnov et al. (2008) demonstrated that the patterns are likely affected by other factors. We conclude that the abundant–centre 'principle' can hardly be considered definitive for macrobes, and is far less understood for microbes.

15.2.2 Abundance–range and size–abundance

The abundance–range principle holds that species with greater local abundance have greater distributional ranges, and has been considered a generality among diverse macrobes (e.g. Andrewartha and Birch, 1954; Gaston et al., 1997; Blackburn et al., 1997; Hubbell, 2001; Harte et al., 2001). The EiE claim is a corollary of this principle because microbial species can attain ‘astronomical’ local abundance and thus are argued to have very large (i.e. cosmopolitan) distributions (Finlay, 2002). As described above for the abundant–centre principle, the EiE claim essentially states that the abundance–range principle is saturated for microbes. Likewise, a negative relationship between body size and local abundance is regarded as well-supported for macrobes (Damuth, 1987; Brown et al., 1995) and is consistent with EiE (Finlay, 2002). This principle has the advantage that is intuitive, in that many microbes can be visualised as fitting into the space occupied by one macrobe.

Given that abundance appears to be positively related to range area and that body size is logically and negatively related to abundance, then body size should be negatively related to range area (smaller organisms should have larger ranges; Fig 15.1). In addition, this relationship should apply to macrobes and microbes. However, this does not seem to be the case. Most (80%) of macrobial studies reviewed by Gaston (1996) observed a positive relationship between body size and range, rather than a negative relationship as predicted by the combination of the abundance–range and size–abundance principles. We know of no comparable data to evaluate the size–range relationship among microbes, but a random pattern may be expected (Martiny et al., 2006; Jenkins et al., 2007).

What may reconcile the contrast between individual well-founded principles and observations of their combination? A negative size–range relationship requires only simple diffusive (random) dispersal because no factors are needed to explain the pattern other than a density-dependent probability of dispersal from a local population into the surrounding landscape. This relationship should be most appropriate for passive dispersers, including free-living microbes that are the focus of the EiE claim (Finlay, 2002). On the other hand, actively dispersing organisms (typically macrobes) have a positive size–range relationship (Gaston, 1996). As evidence to support this difference between passive and active dispersers, maximal observed dispersal distance is a random function of body size for passive dispersers, while dispersal distance increases with body size for active dispersers (Jenkins et al., 2007). Maximal observed dispersal distance is relevant to range area but should be more proximal to dispersal-based differences among organisms because many other

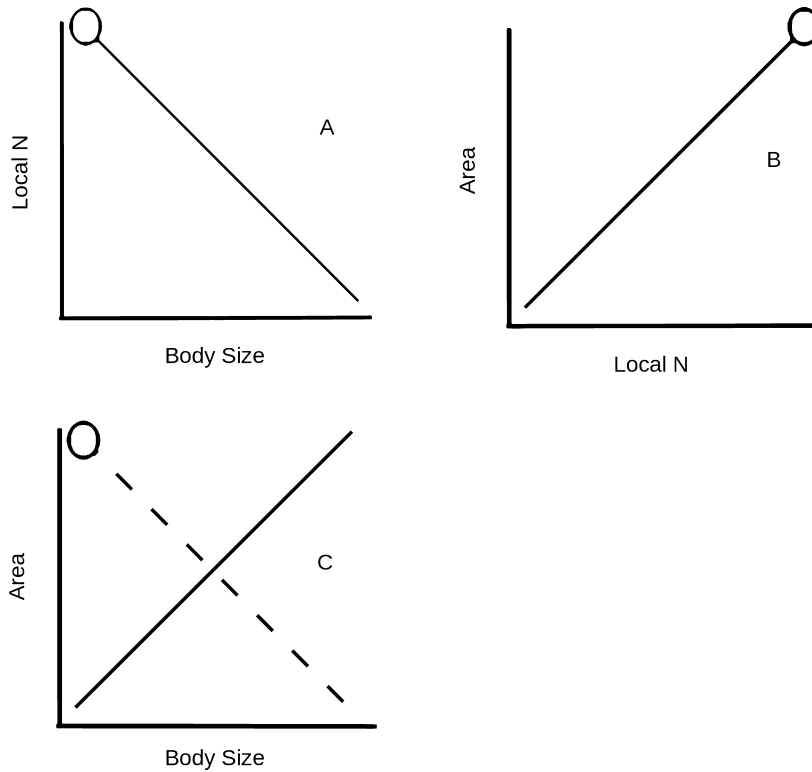


Fig 15.1 Interrelationships between abundance, body size and range. Microbial organisms are indicated with the open circle on each plot. (A) Logic and evidence support the negative relationship between body size and local abundance (Damuth, 1987; Brown et al., 1995). (B) The positive relationship between local abundance and range size is also well documented for macrobes (Gaston et al., 1997). (C) Given A and B, then smaller organisms that have larger local abundance should also have larger range sizes, whereas larger organisms with less abundance should have smaller range sizes (dashed line). In fact, the opposite (solid line) is well documented for macrobes (Gaston, 1996).

factors (e.g. landscape heterogeneity, climate, biological interactions) also may affect range area.

Our brief evaluation of abundance, body size and distribution for microbes and macrobes suggests that dispersal mode (passive vs. active) actually causes observed patterns, rather than simple body size per EiE. Overall, the microbial and microbial evidence for abundance, body size and distribution do not support the EiE claim because the principles for macrobes are not definitive and because the evidence for microbes is grossly inadequate at this time.

15.3 Niche and distribution

The ecological niche has been conceptually related to organismal distributions for nearly a century (Grinnell, 1917) and niche-based distribution models continue to be important for predicting biogeographic distributions (Wiley et al., 2003; Reed et al., 2008; Kearney and Porter, 2009; Medley, 2009). Much has been written about the niche concept (see reviews by Pulliam, 2002; Chase and Leibold, 2003; Soberón and Nakamura, 2009; Colwell and Rangel, 2009). The niche is classically related to distribution in terms of the fundamental niche, defined as the multidimensional space within which a species can attain positive population growth. When the fundamental niche is projected onto geographic space, species occupy that subset of the fundamental niche that is actually available at a given space and time (potential niche, Jackson and Overpeck, 2000; Soberón and Nakamura, 2009). Finally, additional constraints by biotic interactions yield the realised niche (Hutchinson, 1957; Pulliam, 2002; Colwell and Rangel, 2009; Soberón and Nakamura, 2009). These niche concepts do not incorporate other processes (e.g. source-sink dynamics, dispersal limitation) that appear to also affect distributions (Fig 15.2; after Pulliam, 2002). The EiE claim ('... but the environment selects'; Fig 15.2A) is consistent with the Grinnellian niche concept, or the Hutchinsonian niche concept if biotic interactions further limit distributions (Fig 15.2B). However, alternative mechanisms of source-sink dynamics (Fig 15.2C) or dispersal limitation (Fig 15.2D) are inconsistent with EiE because microbial species are presumed to be uniformly abundant and cosmopolitan (Finlay, 2002).

What evidence exists that the niche affects microbial distributions? We surveyed the literature for studies examining either niche or distribution for organisms with propagules < 1–2 mm. While many studies report ecological differences between species, we focused our search on those studies of quantitative niche characteristics that cause spatial segregation between species or result in apparent distributional boundaries at some scale. All studies we found consistently reported niche differences or local adaptation at intra- or inter-specific levels, consistent with the fundamental niche in all cases and potentially related to the realised niche in a few cases (Table 15.1). Given that niche constraints on local persistence/occurrence have been observed for microbes, it is reasonable to expect that niche affects distribution of multiple microbial species, consistent with the 'environment selects' portion of the EiE claim (and with much of evolutionary ecology). Tests for source-sink dynamics or dispersal limitation as alternative explanations of microbial niche-distribution relationships will require that the fundamental niche for a species is already

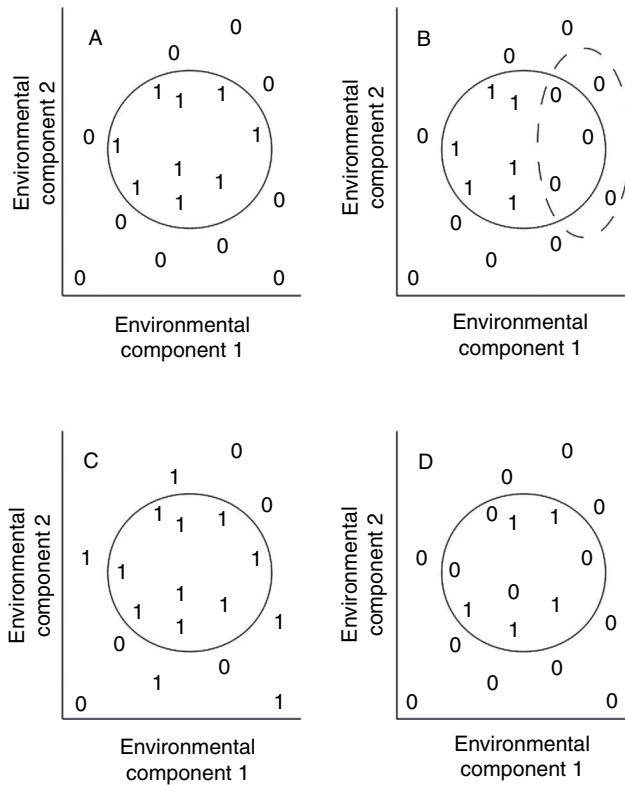


Fig 15.2 Niche-distribution relationships, based on Pulliam (2002). Zeros represent absence, and ones represent presence in niche space (e.g. two ordination axes). (A) The fundamental (Grinnellian) niche (or potential niche, Jackson and Overpeck, 2000; Soberón and Nakamura, 2009) is related to abiotic interactions. (B) The realised niche (*sensu* Hutchinson) is due to the combined influence of abiotic and biotic interactions, where the dashed line represents niche space of a second species. (C) Source–sink dynamics represent one alternative to (A) and (B), where sink populations outside the fundamental (or realised) niche exist due to immigration from source populations. (D) Dispersal limitation is a second alternative, where some combinations of environmental components have not been colonised, even within the fundamental niche space.

well characterised and that multiple sites within and beyond that niche space are thoroughly sampled for microbes and environmental conditions (Fig 15.2). Such data do not yet exist, but may soon be approached for marine microbes in the form of the International Census of Marine Microbes (ICoMM; <http://icomm.mbl.edu/microbis/>).

Table 15.1 Example evidence of niche differences resulting in spatial discontinuity for microbial species or genera with body sizes < -1-2 mm. Niche differences have been demonstrated for diverse microbes at multiple scales and using both experimental and observational evidence.

Taxon	Habitat ¹	Approach ²	Niche-related traits measured	Spatial scale (km)	Conclusions	Source
<i>Euchaeta norvegica</i> , <i>Calanus finmarchicus</i> , <i>Pleuromamma robusta</i> , <i>Metridia lucens</i> (copepods)	M	O	Abundance	North Atlantic Ocean	Species partition niches in horizontal and vertical space	Williams (1988)
<i>Balanion planctonicum</i> , <i>Urotricha farcta</i> , <i>U. furcata</i> (ciliates)	F	E	Temperature and food (growth rate)	700	Niche differentiation within and between competing species and genera	Weisse et al. (2001)
<i>Cephalodella hoodi</i> , <i>Elosa worallii</i> (rotifers)	F	E	Temperature, food, and predation	0.008 (vertical samples)	Vertical niche separation related to temperature and food	Weithoff (2004)
<i>Actinobacteria</i> (bacteria)	F	E	Temperature	13000	Local thermal adaptation; identical 16S sequences but some genetic variation at other loci	Hahn and Pöckl (2005)
<i>Spumella</i> sp. (chrysophyte flagellate)	F and T	E	Temperature (growth rate)	17000	Local thermal adaptation among strains	Boenigk et al. (2007)

<i>Sellaphora pupula</i> , <i>S. bacillum</i> , <i>S. laevissima</i> (diatoms)	F	O	Trophic status of local habitat	600	<i>Sellaphora</i> demes (putative species) differ in environmental tolerances	Pouličková et al. (2008)
<i>Micromonas pusilla</i> (chlorophyte flagellate)	M	O	Genetic differentiation	12500	Niche partitioning evident for this widely distributed morphospecies	Foulon et al. (2008)
<i>Daphnia magna</i> (cladoceran)	F	E and O	Ca ⁺⁺ , pH requirements	600	Experimental niche accurately predicted 56 of 58 occurrences in Europe	Hooper et al. (2008)
diatoms, rotifers, crustacean zooplankton, aquatic insects	F	O	multiple physical- chemical and biotic variables	3000	Local habitat variables and regional location determine community structure.	Kernan et al. (2009)

¹ Habitats: F: Freshwater, M: Marine, T: Terrestrial.

² Study Approach: E: Experimental, O: Observational.

15.4 Microbial phylogeographies

Phylogeography is pattern analysis that indicates evolutionary processes in space and time, and thus enables phylogenetic and geographic history to be evaluated as a potential mechanism of microbial biogeography. In contrast to the large body of knowledge on macrobe biogeography (e.g. Lomolino et al., 2006), EiE argues that the high dispersal rates and frequent dispersal events of microbes swamp any spatial structure that may otherwise arise through vicariance, historical dispersal and local adaptation. Given the repeated reshuffle of microbial populations predicted by EiE, phylogeographic patterns concordant with geological processes of plate tectonics, glaciations, geographic barriers, etc. should not apply because phylogeography should be swamped by contemporary dispersal.

According to the EiE claim, microbes do not have biogeographies while macrobes do. Finlay (2002) presented the 1 mm cutoff between microbes and macrobes as two mirror-image, logistic curves (Fig 15.3A); the proportion of species that are ubiquitous purportedly decreases abruptly at ~1 mm (dashed line, Fig 15.3A), while the proportion of species that have biogeographies increases abruptly at ~1 mm (solid line, Fig 15.3B). Because these two curves are mirror images, we can focus here on the curve for species with biogeographies, with the understanding that evidence for one curve necessarily provides evidence for the other. In addition, Finlay (2002) stated that ubiquity–biogeography transition should be in the 1–10 mm size range.

We tested Finlay's clear and specific prediction (Fig 15.3A) for the presence of a logistic function in the proportion of species with biogeographies and a transition in the 1–10 mm size range. Phylogeography studies focus on closely related lineages and provide specific tests of the EiE claim that microbes do not have biogeographies. We collected 51 phylogeographic studies published in the peer-reviewed literature (1998–2009) of organisms for which the dispersive life stage is < 10 mm. All studies applied molecular phylogeographic approaches at regional to global spatial scales and included Archaea, Bacteria, Protista, fungi, bryophytes, Rotifera, Annelida, Mollusca, Copepoda and Cladocera.

We evaluated the evidence by recording whether or not the authors concluded that the subject species had phylogeographies (1 = yes, 0 = no). We then computed a logistic regression of those binary conclusions as a function of body size to estimate the probability of a biogeography for a given body size. If Finlay's prediction is correct, a significant logistic function with a transition ~1–10 mm should be observed. The alternative null model (i.e. biogeography is not a function of body size) is a linear fit that has no significant slope but a significant intercept.

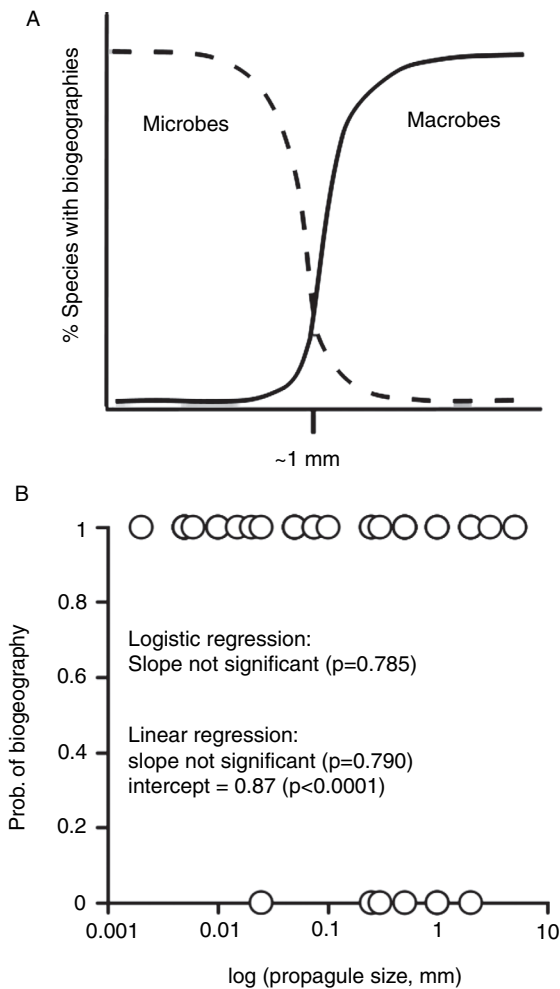


Fig 15.3 Size-based expectations and empirical results from the 'Everything is everywhere' claim (EiE; Finlay, 2002). (A) Microbes and macrobes present mirror-image trends in the predicted proportion of species that have biogeographies (from Finlay, 2002). We tested evidence for the macrobe curve (solid line) in empirical phylogeographies. (B) Empirical patterns, where circles represent conclusions by phylogeography study authors for the study organism's propagule size (0: no biogeography observed; 1: biogeography observed; N = 51).

Forty-four of the 51 papers concluded that studied organisms had biogeographies, while only seven of 51 found no evidence for biogeographic structure (Fig 15.3B). A logistic regression did not significantly fit the data ($p = 0.785$), nor did a linear regression have a significant slope ($p = 0.790$), though the linear regression did have a significant intercept ($\beta_0 = 0.87$, $p < 0.0001$). Thus, evidence we found

indicates that microbes ($< \sim 1$ mm) are just as likely to exhibit biogeographies as macrobes, and that there is no support for the logistic, mirror-imaged distinction between ubiquitous microbes vs. macrobes with biogeographies.

Phylogeographies may arise by multiple mechanisms, but the fact that they are repeatedly observed for microbes is strong evidence that the same biogeographic mechanisms (e.g. vicariance, dispersal, speciation, adaptation, extinction) that affect macrobes also affect microbes. A more interesting challenge is to learn why some microbial species are widespread while others are not. To begin to address this challenge we will need to move beyond simple size-based distinctions and take account of life-history traits more likely to be related to dispersal (e.g. active or passive mode, dormancy, adaptations for phoretic transport) *and* success upon arrival (abiotic tolerance limits, nutrient requirements, trophic interactions, etc.).

In summary, we conclude that:

- Too few data exist to evaluate relationships between abundance, body size and distribution for microbes, and remain unclear (in part) for macrobes. Thus, the EiE claim is not supported for these basic components of biogeography. However, the EiE claim has been useful for biogeographic principles because it led to consideration of relationships for macrobes and microbes and revealed potential new research directions.
- Evidence exists for fundamental niche constraints in microbes, plus some evidence for realised niche constraints. Niche-distribution relationships that are consistent with the EiE claim await more extensive and intensive sampling to fully characterise the role of niche in affecting microbial distributions. As for macrobes, we expect niche-distribution relationships will be found to constrain some microbes to distributions that are less than cosmopolitan.
- Most (86%) of phylogeographic analyses do not support the EiE claim that microbes have no biogeography. Contrary to the EiE prediction that the proportion of species with biogeographies declines logistically ~ 1 – 10 mm in body size, no such trend was observed among empirical data sets.
- The EiE claim has helped turn biogeographic research attention to small organisms, especially in its recent revival during the era of molecular systematics. We expect that the stark contrasts in the EiE claim will be replaced over time with more sophisticated understanding of patterns and processes that more fully reflect Nature's complexity. The clear and simple EiE claim will likely give way to a more nuanced but representative understanding of microbial biogeography that is based on more salient metrics than body size alone.

References

- Andrewartha, H.G., Birch, L.C. (1954). *The Distribution and Abundance of Animals*. Chicago, IL: University of Chicago Press.
- Blackburn, T.M., Gaston, K.J., Quinn, R.M., Arnold, H., Gregory, R.D. (1997). Of mice and wrens: the relation between abundance and geographic range size in British mammals and birds. *Philosophical Transactions of the Royal Society of London B* **352**, 419–427.
- Boenigk, J., Jost, S., Stoeck, T., Garstecki, T. (2007). Differential thermal adaptation of clonal strains of a protist morphospecies originating from different climatic zones. *Environmental Microbiology* **9**, 593–602.
- Brown, J. H. (1984). On the relationship between abundance and distribution of species. *American Naturalist* **124**, 255–279.
- Brown, J.H., Mehlman, D.W., Stevens, G.C. (1995). Spatial variation in abundance. *Ecology* **76**, 2028–2043.
- Chase, J.M., Leibold, M.A. (2003). *Ecological Niches: Linking Classical and Contemporary Approaches*. Chicago, IL: University of Chicago Press.
- Colwell, R. K., Rangel, T.F. (2009). Hutchinson's duality: The once and future niche. *Proceedings of the National Academy of Sciences USA* **106**, 19651–19658.
- Damuth, J. (1987). Interspecific allometry of population density in mammals and other animals: the independence of body mass and population energy use. *Biological Journal of the Linnean Society* **31**, 193–246.
- de Wit, R., Bouvier, T. (2006). 'Everything is everywhere, but the environment selects'; what did Baas Becking and Beijerinck really say? *Environmental Microbiology* **8**, 755–758.
- Finlay, B.J. (2002). Global dispersal of free-living microbial eukaryote species. *Science* **296**, 1061–1063.
- Finlay, B.J., Fenchel, T. (2004). Cosmopolitan metapopulations of free-living microbial eukaryotes. *Protist* **155**, 237–244.
- Foulon, E., Not, F., Jalabert, F., Cariou, T. et al. (2008). Ecological niche partitioning in the picoplanktonic green alga *Micromonas pusilla*: evidence from environmental surveys using phylogenetic probes. *Environmental Microbiology* **10**, 2433–2443.
- Gaston, K.J. (1996). Species–range-size distributions: patterns, mechanisms and implications. *Trends in Ecology and Evolution* **11**, 197–201.
- Gaston, K.J. (2003). *The Structure and Dynamics of Geographic Ranges*. New York, NY: Oxford University Press.
- Gaston, K.J., Blackburn, T.M., Lawton, J.H. (1997). Interspecific abundance–range size relationships: an appraisal of mechanisms. *Journal of Animal Ecology* **66**, 579–601.
- Green, J., Bohannan, B.J.M. (2006). Spatial scaling in microbial biodiversity. *Trends in Ecology and Evolution* **21**, 501–507.
- Grinnell, J. (1917). The niche-relationships of the California Thrasher. *The Auk* **34**, 427–433.
- Hahn, M.W., Pöckl, M. (2005). Ecotypes of planktonic actinobacteria with identical 16s rRNA genes adapted

- to thermal niches in temperate, subtropical, and tropical freshwater habitats. *Applied and Environmental Microbiology* **71**, 766–773.
- Harte, J., Blackburn, T., Ostling, A. (2001). Self-similarity and the relationship between abundance and range size. *American Naturalist* **157**, 374–386.
- Hengeveld, R., Haeck, J. (1982). The distribution of abundance. I. Measurements. *Journal of Biogeography* **9**, 303–316.
- Hooper, H.L., Connon, R., Callaghan, A., Fryer, G. et al. (2008). The ecological niche of *Daphnia magna* characterized using population growth rate. *Ecology* **89**, 1015–1022.
- Horner-Devine, M.C., Lage, M., Hughes, J.B., Bohannan, B.J. (2004). A taxa–area relationship for bacteria. *Nature* **432**, 750–753.
- Hubbell, S.P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton, NJ: Princeton University Press.
- Hutchinson, G.E. (1957). Concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology* **22**, 415–427.
- Jackson, S.T., Overpeck, J.T. (2000). Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology* **26 (Suppl)**, 194–220.
- Jenkins, D.G., Brescacin, C.R., Duxbury, C.V. et al. (2007). Does size matter for dispersal distance? *Global Ecology and Biogeography* **16**, 415–425.
- Kearney, M., Porter, W. (2009). Mechanistic niche modelling: combining physiological and spatial data to predict species ranges. *Ecology Letters* **12**, 334–350.
- Kernan, M., Ventura, M., Bitušik, P., Brancelj, A. et al. (2009). Regionalisation of remote European mountain lake ecosystems according to their biota: environmental versus geographical patterns. *Freshwater Biology* **54**, 2470–2493.
- Krasnov, B.R., Shenbrot, G.I., Khokhlova, I.S., Vinarski, M. et al. (2008). Geographical patterns of abundance: testing expectations of the ‘abundance optimum’ model in two taxa of ectoparasitic arthropods. *Journal of Biogeography* **35**, 2187–2194.
- Loehle, C. (1987). Hypothesis testing in ecology: psychological aspects and the importance of theory maturation. *Quarterly Review of Biology* **62**, 397–409.
- Lomolino, M.V., Riddle, B.R., Brown, J.H. (2006). *Biogeography*, 3rd Edition. Sunderland, MA: Sinauer Associates.
- Martiny, J.B.H., Bohannan, B., Brown, J. et al. (2006) Microbial biogeography: putting microorganisms on the map. *Nature Reviews Microbiology* **4**, 102–112.
- Medley, K.A. (2009). Niche shifts during the global invasion of the Asian tiger mosquito, *Aedes albopictus* Skuse (Culicidae), revealed by reciprocal distribution models. *Global Ecology and Biogeography* **19**, 122–133.
- Pouličková, A., Špačková, J., Kelly, M.G., Duchoslav, M., Mann, D.G. (2008). Ecological variation within *Sellaphora* species complexes (Bacillariophyceae): specialists or generalists? *Hydrobiologia* **614**, 373–386.
- Pulliam, H.R. (2002). On the relationship between niche and distribution. *Ecology Letters* **3**, 349–361.
- Ramette, A., Tiedje, J.M. (2007). Biogeography: an emerging cornerstone for understanding prokaryotic diversity, ecology, and evolution. *Microbial Ecology* **53**, 197–207.

- Reed, K.D., Meece, J.K., Archer, J.R., Peterson, A.T. (2008). Ecologic niche modeling of *Blastomyces dermatitidis* in Wisconsin. *PLoS ONE* **3**, 1–7.
- Sagarin, R.D., Gaines, S.D. (2002). The 'abundant centre' distribution: to what extent is it a biogeographical rule? *Ecology Letters* **5**, 137–147.
- Sagarin, R. D, Gaines, S.D., Gaylord, B. (2006). Moving beyond assumptions to understand abundance distributions across the ranges of species. *Trends in Ecology and Evolution* **21**, 526–530.
- Soberón, J., Nakamura, M. (2009). Niches and distributional areas: concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences USA* **106**, 19644–10650.
- Thomas, C.D., Kunin, W.E. (1999). The spatial structure of populations. *Journal of Animal Ecology* **68**, 647–657.
- Weisse, T., Karstens, N., Meyer, V.C.L. et al. (2001). Niche separation in common protome freshwater ciliates: the effect of food and temperature. *Aquatic Microbial Ecology* **26**, 167–179.
- Weithoff, G. (2004). Vertical niche separation of two consumers (Rotatoria) in an extreme habitat. *Oecologia* **139**, 594–603.
- Westman, W.E. (1980). Gaussian analysis: identifying environmental factors influencing bell-shaped species distributions. *Ecology* **61**, 733–739.
- Whittaker, R.H. (1956). Vegetation of the Great Smoky Mountains. *Ecological Monographs* **26**, 2–80.
- Wiley, E.O., McNyset, K.M., Peterson, A.T., Robins, C.R., Stewart, A.M. (2003). Niche modeling and geographic range predictions in the marine environment using a machine-learning algorithm. *Oceanography* **16**, 120–127.
- Williams, R. (1988). Spatial heterogeneity and niche differentiation in oceanic zooplankton. *Hydrobiologia* **167–168**, 151–159.